Seasonal effects on offspring reproductive traits through maternal oviposition behavior

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Offspring phenotypes are often influenced by natal habitats, and these locations are commonly determined by mothers. The location where mothers leave their offspring may have different implications for offspring at different times of the year due to seasonal changes in the quality of resources available. Such dynamic effects of maternal behaviors for offspring are only beginning to be explored. I examined the changing effects of oviposition sites for adult offspring mating behaviors and fecundity in the heliconia bug, *Leptoscelis tricolor* (Hemiptera: Coreidae). Female heliconia bugs lay eggs on multiple heliconia plant species, and offspring grow and develop on the plant where they hatch. I found that the host plant species where offspring are raised influenced mating probability, expression of copulatory courtship behaviors, and fecundity. Moreover, the effects of the different plant species on daughter reproductive traits shifted and even reversed over time, and the changes parallel seasonal changes in plant resources. These results demonstrate that seasonal changes can affect the implications of maternal behaviors for offspring phenotypes. *Key words:* copulatory courtship, Coreidae, fecundity, habitat selection, maternal effects, oviposition, phenology. [*Behav Ecol 19:1297–1304 (2008)*]

A cross taxa, individual offspring phenotypes are often influenced by their natal habitat, a location commonly determined by mothers (Mayhew 1997; Mousseau and Fox 1998a, 1998b; Kolbe and Janzen 2002; Lloyd and Martin 2004; Marshall and Uller 2007). In herbivorous insects, offspring commonly experience discretely different natal habitats due to the use of multiple host plant species for oviposition by mothers (Sutherland 1969; Jaenike 1978; Thompson 1988; Mayhew 1997; Mousseau and Fox 1998b; Awmack and Leather 2002). Most studies of the effects of different host plant species on the phenotypes of insect offspring have examined such effects at only one point in time. However, the "relative" effects of different host plant species on offspring may vary over the course of the season, with one plant species providing better resources at one time and another plant species providing better resources at a later time. These changes may be caused directly or indirectly by the distinct timing of growth, maturation, and senescence of tissues (i.e., phenology) of each plant species. Because of such changes in host plants, the usage of different host species by ovipositing mothers may have different effects on offspring depending on the time of year. Dynamic effects of maternal behaviors on offspring may be ubiquitous in natural populations; however, they have received relatively little attention (for exceptions, see Rossiter 1998; Marshall and Uller 2007).

Maternal behaviors may affect offspring at various stages of their life histories (Kerr et al. 2007); however, relatively few studies have examined effects on adult offspring reproductive traits such as mating behaviors and fecundity. These traits are often directly related to reproductive success; thus, maternal effects on their expression may be important for offspring fitness. Maternal effects are not often simply positive or negative for offspring but can instead result in offspring adopting alternate life-history strategies (Mousseau and Fox 1998a; Massot et al. 2002). In many insects, offspring reared on host plants of declining quality develop into dispersal-ready adults with delayed reproduction (Zera and Denno 1997).

Here, I investigated the effects of maternal host plant use for offspring phenotypes in the heliconia bug, *Leptoscelis tricolor.* I also examined whether the month of year during which offspring development occurred affected the consequences of the maternal behavior for offspring phenotypes. The traits measured in this study were adult offspring mating behaviors and fecundity. The particular ecology of this species allowed me focus on the consequences of maternal host plant choice for offspring without manipulating the behaviors of mothers. I explain below.

Ovipositing female heliconia bugs move frequently among heliconia plants and may lay eggs on multiple heliconia species during their lifetimes (Miller 2007). The location of oviposition determines the host plant species that offspring will experience during growth and development due to the limited mobility of the wingless juveniles (Miller CW, personal observation). Thus, researchers can associate offspring with their natal host plant species (and, thus, the host plant use of their mothers) simply by detecting juveniles before they have molted into flight-capable adults. This aspect of their biology greatly facilitated extensive field sampling of large numbers of offspring.

I collected offspring on 2 different species of wild heliconia plants in Panama. Virgin adult sons and daughters were paired in all possible combinations of natal host plant species. I recorded mating attempts by males, female responses to these mating attempts, copulation duration, copulatory courtship behaviors, and female fecundity. To assess the influence of seasonality on offspring phenotypes, I repeated my study monthly for 4 cohorts of insects. Altogether, this work allowed me to simultaneously evaluate the effects of host plant species and month of adult emergence on adult offspring phenotypes. I also estimated the phenology of heliconia plants in the population over this time period to compare changes in the host plants with differences in the behaviors of each cohort of insects.

MATERIALS AND METHODS

Study species

Heliconia bugs, *L. tricolor* (Hemiptera: Coreidae), feed, mate, and oviposit on the inflorescences of many heliconia species existing in different assemblages in Costa Rica and Panama. Adult and juvenile insects feed on the phloem, nectar, and fruits of these inflorescences. Males and females become reproductively mature after approximately 1 week as an adult. Both adult males and females commonly fly among inflorescences and rarely stay on an inflorescence for more than a few days (Miller CW, unpublished data). I previously found that 92% of adult, ovipositing females in one population had changed host plants when resighted and 35% changed host plant species (Miller 2007). Because this mark–resight study was limited to a small area (ca., 1 km^2) and a short period of time (1 month), these numbers are likely an underestimate of the true movement of mature female insects.

Mating occurs on or near inflorescences and may last for several hours. Males often perform stereotyped copulatory courtship behaviors during mating (sensu Eberhard 1994) including shaking and stroking the abdomen of females with their hind legs. After mating, females begin laying fertile eggs. Females lay eggs individually (clutch size = 1) on or very near to heliconia inflorescences of various phenological stages, from inflorescences that are just beginning to bloom to those that have ripe fruits and no flowers. They may lay 200 or more eggs and live as reproductive adults 80 days or more. Total development time from egg to adult is approximately 40 days (Miller 2007). Juvenile heliconia bugs develop on the same host plant species where they hatch.

Survivorship of offspring from egg to adult can be as low as 11% on *Heliconia platystachys* and 30% on *Heliconia mariae*, as measured in October 2004 (Miller 2007). Thus, differential survivorship of juveniles raised on these 2 species of plants might result in selection for particular offspring characteristics and have some influence on adult characteristics. The possibility exists that the effects measured in this study might be a result of both natal environmental influences and differential survivorship of particular types of offspring. However, it is difficult to conceive how differential survivorship of nymphs alone could translate into the strong patterns in adult phenotypes within host plant species and across host plant species, as shown below.

Study procedures

Insect collection

I located fifth-instar nymphs on the inflorescences of *H. platystachys* and *H. mariae*, growing naturally near Gamboa, Panama, from June to September 2005. Each nymph and its host inflorescences were enclosed within a mesh bag. If additional nymphs were present on an inflorescence, I moved them to another plant and did not include them in the experiment. When the bagged nymphs emerged as adults (up to 7 days later), the mesh bags prevented them from escaping.

I returned to the bags after 2 weeks to collect the virgin adults. The first cohort of new adults was collected on 23 July 2005, the second on 20 August 2005, the third on 17 September 2005, and the fourth on 21 October 2005. All insects in a cohort were collected within 6 h of one another. I immediately placed collected insects individually in mesh-covered cups with moistened paper towels. They were sorted according to sex and natal host plant species and then assigned randomly to 4 pairing groups of all possible sex and natal host plant combinations. Sixty-two insects were used in each of the first 3 cohorts, divided nearly equally among the pairing groups. Fewer insects (*n* = 36) were available for the fourth (October)

cohort; thus, I eliminated groups 2 and 3 in this cohort to maintain a high sample size in groups 1 and 4. The total sample size for this study was 222 insects (111 pairs).

On returning to the laboratory, I placed male insects into the cups of their predetermined mates, taking approximately 7 min to complete all pairings. Insects were kept at ambient outdoor temperatures. I observed pairs under both diffuse natural and artificial light. Previous observations indicated that light conditions do not influence copulatory and oviposition behaviors in *L. tricolor* (Miller CW, personal observation).

Copulatory behavior

After all pairs of bugs were placed together, I immediately began recording the behavior of the insects, observing each pair every 5 min for 4 h. I recorded if males were attempting to copulate with females, the response of females to mating attempts, and if pairs were copulating, I recorded whether copulatory courtship behaviors were being performed.

Fecundity

After adults were paired, the bugs were left in cups with ample water but without food for 2 days. Heliconia bugs can live without feeding for at least 7 days (Miller CW, unpublished data). After 2 days, I counted any eggs laid in the cups. Fecundity was measured as the number of fertile eggs produced, and all females were included in the analyses, even if they did not mate during the 4-h observation period. I took this approach for 2 reasons 1) because some females may have mated outside of the observation period and 2) including females that did not mate or lay eggs permitted an overall picture of female reproductive status in the population. I also ran a separate analysis including only females that were observed mating.

After the 2-day fecundity experiment, all pairs in the first 3 cohorts were placed in mesh bags, 1 pair per bag, on naturally growing *Heliconia latispatha* inflorescences. *Heliconia latispatha* is a common host plant for heliconia bugs in the area and was equally new to all focal individuals, making it an appropriate host for this next stage of the experiment. I selected only *H. latispatha* inflorescences with both flowers and fruits available so that insects would experience hosts of equal phenological stages. Pairs on *H. latispatha* were checked weekly and all eggs were counted and removed. Five males in the first (July) cohort died within 2 weeks of pairing, leaving 5 females without mates. I assigned these females a new mate who was raised on the same natal host plant in the same cohort as their previous mate, and I subsequently treated these pairs as all others for measures of long-term female fecundity. Egg numbers for these pairs were within one standard deviation of the average for the cohort.

Pairs in the first 3 cohorts were monitored for fecundity for a minimum of 23 days and a maximum of 80 days (Figure 3). All observations of the first 3 cohorts were terminated on 10 October 2005, and all insects were released. The final cohort was collected late in the field season (21 October 2005), and insects were released after the mating behavior and 2-day fecundity experiments. Due to slightly different care protocols, egg counts after the first 2 days were not statistically compared across cohorts.

Host plant phenology

Heliconia platystachys and *H. mariae* differ markedly in their phenology (Croat 1978). *Heliconia platystachys* plants only produce inflorescences once per year, generally during the months of May and June. Over the next few months, these inflorescences progress through distinct phenological stages, until, by November, few viable inflorescences remain. *H. mariae* plants, in contrast, produce inflorescences in a staggered fashion year-round (Stiles 1975). Thus, the different

phenological schedules of these 2 host plant species result in striking changes in the relative resources available.

I estimated the changing resources available for each cohort of insects by walking transect lines through patches of *H. platystachys* and *H. mariae*, counting, and scoring inflorescences based on the presence and condition of flowers or fruits. The transect line for *H. platystachys* was based on an arbitrarily chosen 160-m line through one large monotypic stand of the plant. The transect line for *H. mariae* was a 2000-m section of Pipeline Road in Soberania National Park with intermittent patches of *H. mariae* plants. The phenology of plants on both of these transects appeared to be representative of plants in the entire study area. I walked these transect lines each month concurrent with searches for fifth-instar nymphs in the same areas.

Statistical analyses

I used analysis of variance (ANOVA) to examine the effects of host plant species and month of adult emergence on continuous reproductive traits such as female fecundity. Logistic regression was used to examine the effects of these explanatory variables on binary response variables such as whether or not insects mated. These models included female natal host plant species, male natal host plant species, month of emergence, and all 2-way interactions as explanatory variables. Type IV sums of squares were used to conservatively accommodate the 2 missing cells in the October cohort. I log transformed continuous dependent variables when necessary to meet statistical assumptions of normality. All statistical analyses were performed with SPSS 15.0.

RESULTS

Host plant phenology in the study area

The median stage of *H. platystachys* inflorescences along transect lines changed over the study period, whereas the median stage of *H. mariae* inflorescences remained consistent (Figure 1). Such phenological changes in *H. platystachys* parallel variation across cohorts in the probability of mating by females and also in female fecundity (see below).

Mating behavior

Ninety-five of 112 (85%) females were observed receiving mating attempts from males on one or more occasions during the first 4 h after pairs were formed. Neither natal host plant species of males or females nor their month of emergence (their cohort) had a significant effect on which females received mating attempts and which ones did not (Table 1).

In contrast, the probability of a female responding to these mating attempts by copulating with the male was significantly influenced by the natal host plant species on which she was raised (Table 1). However, this effect of natal host plant species was not consistent across cohorts (Table 1). Females from
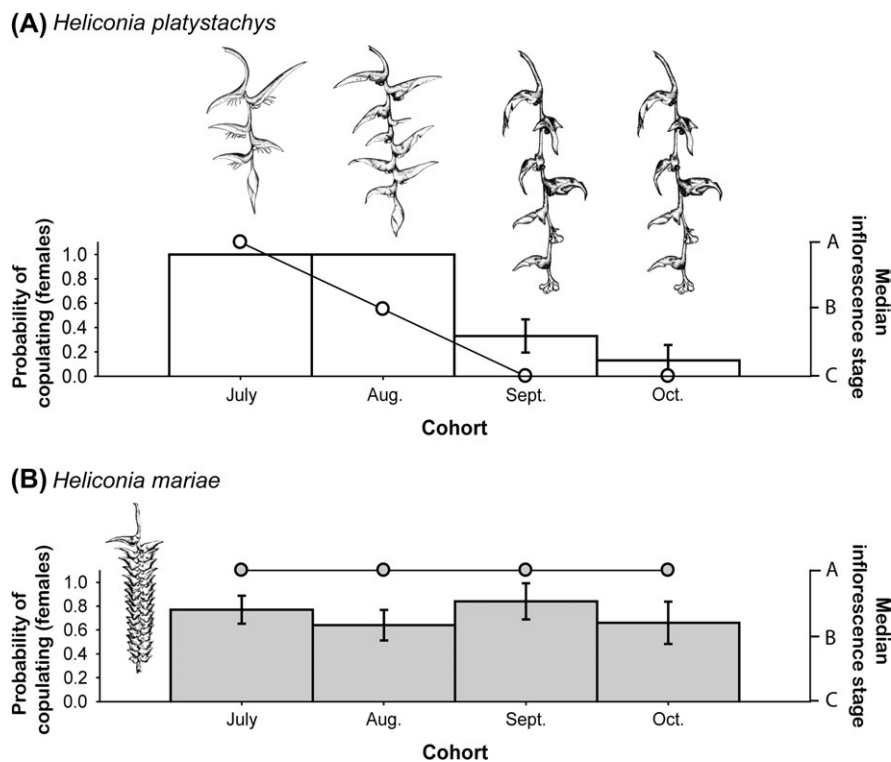

Figure 1
The probability of females copulating (bars) with courting males as related to the median inflorescence stage of heliconia host plants available in the population over time (circles). In (A), *Heliconia platystachys* inflorescences exhibited a seasonal pattern of maturation and senescence (open circles) from Stage A (both flowers and fruits available), to Stage B (only fruits available), and Stage C (inflorescence senescing). By September and October, most inflorescences were deteriorating and falling off the plants. Females raised on these inflorescences tracked this seasonal pattern (open bars): all females emerging from *H. platystachys* in the July and August cohorts copulated during our observation period, whereas females in the September and October cohorts had a lower probability of copulating. (B) In contrast, *Heliconia mariae* inflorescences exhibited no such pattern of seasonal senescence (solid circles), and suitable inflorescences of this host species were available throughout the season. Females raised on *H. mariae* maintained a similar probability of mating across cohorts (closed bars). Drawings of heliconia illustrate representative inflorescences in each category (heliconia illustrations by David Tuss).

Table 1

Logistic regressions and ANOVA for mating behaviors

Source	Mating attempts on females		Probability of mating		Copulation duration		Copulatory courtship start time[a]		Copulatory courtship rate[a]	
	df	χ^2	df	χ^2	df	F ratio	df	F ratio	df	F ratio
Female natal species	1	<0.01	1	7.00**	1	1.85	1	0.49	1	4.58*
Male natal species	1	1.34	1	0.02	1	0.21	1	2.61	1	4.21*
Month of adult emergence	1	1.49	1	0.02	3	1.69	1	1.19	1	1.91
Female natal × month	1	0.68	1	7.91**	2	0.88	1	0.10	1	1.90
Male natal × month	1	1.50	1	<0.01	2	2.02	1	0.40	1	0.07

Error degrees of freedom (df) = 102 (mating attempts), 85 (probability of mating), 56 (duration), 38 (copulatory courtship start), 46 (copulatory courtship rate).

[a] Copulatory courtship analyses include data from only July and August cohorts (see text).

*$P < 0.05$, **$P < 0.02$.

H. platystachys emerging in later cohorts were less likely to mate in response to male attempts than females from earlier cohorts (Figure 1). Also, the plant species producing females with the highest probability of mating switched over this time period. In earlier cohorts, females from *H. platystachys* have a higher probability of mating during the first 4 h, whereas in later cohorts, females from *H. mariae* have a higher probability of mating (Figure 1). In fact, only one of the 8 females from *H. platystachys* in October cohort mated during the 4-h observation period. These 4 h of observations did not capture all matings, as evidenced by the 10% of females across cohorts that did not mate during the observation period, yet produced fertile eggs within the first 2 days that insects were paired. Interestingly, neither male or female host plant species nor their month of emergence affected the duration of copulation over the observation period once the copulation began (Table 1).

Because of the strong effect of host plant species and month of emergence on female mating behavior, few copulations occurred and could be monitored for insects from *H. platystachys* in the later cohorts. I therefore analyzed copulatory courtship behaviors for only the July and August cohorts. Males in the July and August cohorts emerging from *H. platystachys* performed copulatory courtship behaviors at a faster rate than males from *H. mariae* (Table 1, Figure 2A). Furthermore, males performed a faster rate of copulatory courtship when they were paired with "females" from *H. platystachys* (Table 1, Figure 2B). I examined whether the rate of copulatory court-

ship behavior influenced female egg production and found no direct correlation (Spearman rank correlation: $r = -0.029$, $P = 0.875$).

Fecundity

Overall, females from *H. platystachys* laid more eggs than did females from *H. mariae* during the first 2 days after insects were paired (ANOVA: $F_{1,99} = 15.542$, $P < 0.001$). However, the effect of natal host plant species on initial egg production changed dramatically across cohorts (ANOVA: $F_{2,99} = 6.606$, $P = 0.002$; Figure 3B) in tandem with the seasonal changes in *H. platystachys* inflorescences. Females from *H. platystachys* that emerged as adults in July laid on average over 7 times more eggs than females from *H. mariae* (means ± standard errors [SEs] for females from *H. platystachys*: 11.40 ± 1.18 eggs vs. 1.57 ± 1.36 eggs for females from *H. mariae*; Figure 3B). However, by the October cohort, females from *H. mariae* laid significantly more eggs than did females from *H. platystachys* (mean ± SE for females from *H. mariae*: 4.10 ± 1.14, whereas none of the 8 females from *H. platystachys* produced any eggs; Figure 3B).

The fecundity differences of July and August females from *H. platystachys* and *H. mariae* did not simply reflect the higher probability of mating for females from *H. platystachys*. In a separate analysis, I examined the 2-day egg production for only those females observed mating during the 4-h observation period. Of females observed mating, those from *H. platystachys*
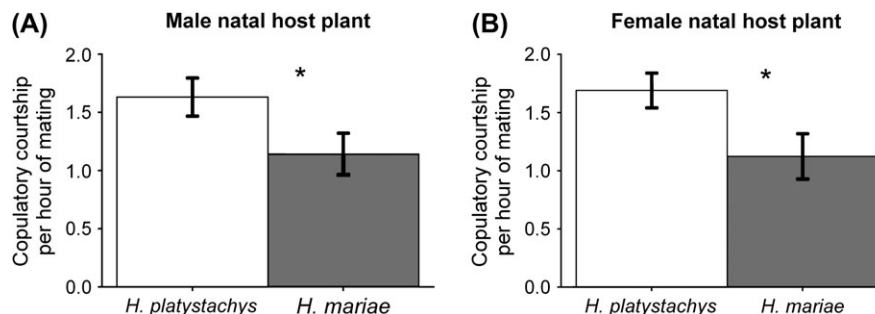

Figure 2
Means (±SEs) of copulatory courtship behaviors observed per hour of mating. In (A), males from *Heliconia platystachys* performed a significantly higher rate of copulatory courtship behaviors than males from *Heliconia mariae*. In (B), males performed a higher rate of copulatory courtship behaviors when paired with females from *H. platystachys* than when paired with females from *H. mariae*. *$P < 0.05$.
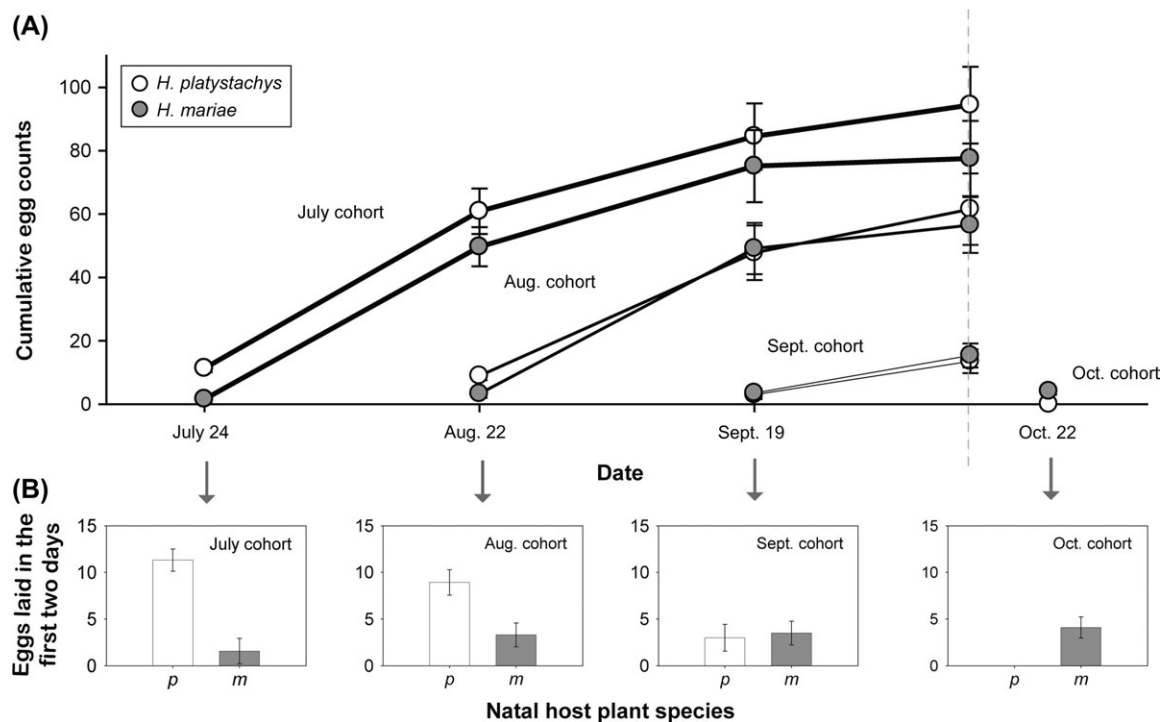
Figure 3
Means (±SEs) of the numbers of eggs produced by females in all 4 cohorts. In (B), females from *Heliconia platystachys* in July and August laid significantly more eggs during the first 2 days after being paired. This pattern reverses, and by October, females emerging from *Heliconia mariae* laid more eggs initially. Initial differences in egg production of females emerging in the same cohort (B) did not translate into long-term effects on fecundity (A). The dotted line indicates when (10 October) insects from the first 3 cohorts were released.

produced significantly more eggs than females from *H. mariae* (means ± SEs for July and August females from *H. platystachys*: 10.28 ± 1.13 eggs vs. 3.71 ± 1.45 eggs for females from *H. mariae*; ANOVA: $F_{1,45} = 12.811$, $P = 0.001$). This particular analysis only included data from the first 2 cohorts. The low mating rate of females from *H. platystachys* in the final 2 cohorts prohibited analysis of whether the egg production of females observed mating was dynamic across cohorts.

The large initial fecundity differences between *H. platystachys* and *H. mariae* females in the July and August cohorts dissipated over time as female insects were all confined on the same species of plant. By day 30 of egg laying, differences between females from *H. platystachys* and *H. mariae* were no longer statistically significant (ANOVA: $F_{1,57} = 0.435$, $P = 0.512$; Figure 3A; analysis includes all females, those observed mating, and those that did not mate during the brief observation period), and total female fecundities were not different when cumulated over periods longer than 30 days ($P > 0.4$).

DISCUSSION

In this study, I found significant effects of host plant species on multiple reproductive traits in both sons and daughters. In particular, host plant species influenced offspring copulatory courtship behaviors and had dynamic effects over time on daughter mating probability and fecundity. These effects of host plant species on offspring can be described as maternal effects (Mousseau and Fox 1998a) because the host plant species where these insects grow and develop is determined by ovipositing mothers. The recognition of the role mothers play in determining offspring environments, and thus influencing offspring phenotypes, is an important part of identifying predictable sources of variation in offspring traits (Mousseau and Fox 1998a; Miller and Moore 2007).

Copulatory courtship

Although courtship prior to mating has long intrigued researchers, the broad recognition of courtship behaviors during mating as a common and important phenomena has occurred only recently (Eberhard 1991, 1994, 1996). Copulatory courtship often involves tapping, shaking, and stroking behaviors performed while copulating, and these behaviors may have sizeable implications for male fitness (Otronen 1990; Watson and Lighton 1994; Edvardsson and Arnqvist 2000; Schäfer and Uhl 2002; Tallamy et al. 2002, 2003). For example, female cucumber beetles preferentially use the sperm of males who perform a high rate of copulatory courtship. The rate of copulatory courtship in cucumber beetles is condition dependent and heritable (Tallamy et al. 2003). Whereas copulatory courtship may have a heritable component in many species, my study is one of the first to explicitly demonstrate that it can also be significantly influenced by environmental factors. When female heliconia bugs laid eggs on *H. platystachys* early in the season, their sons performed copulatory courtship at a higher rate (Table 2, Figure 2A). Such effects of mothers on the reproductive traits of sons may be common and affect the process and outcomes of sexual selection (Qvarnström and Price 2001; Miller and Moore 2007).

My study design allowed me to examine not only whether maternal oviposition behavior altered the copulatory behaviors of sons but also whether it altered the copulatory behaviors of males mating with their daughters. Indeed, I found that males

performed a higher rate of copulatory courtship when paired with daughters from *H. platystachys* (Figure 2B). Across taxa, males are expected to invest more heavily in a copulation when females are likely to have greater reproductive output (Bonduriansky 2001). Indeed, females from *H. platystachys* in these cohorts did have significantly greater initial fecundity than did females from *H. mariae* (Figure 3; see also below). Males may have been able to perceive the reproductive potential of females, possibly through cues such as the size of the female abdomen, and in response, they may have modulated their copulatory courtship behavior. Alternatively, male copulatory courtship rate may have been the cause of female fecundity differences. This scenario is unlikely because the rate of copulatory courtship received and the number of eggs produced by females were not directly correlated.

Due to the strong effect of month of emergence on daughter mating probability (see below), few matings occurred in the September or October cohorts. Thus, I only assessed copulatory courtship behaviors for the July and August cohorts. I did not find dynamic maternal effects of host plant species choice on copulatory courtship behaviors over this reduced period (Table 1).

Daughter reproductive traits

The host plant chosen by mothers influenced daughter mating probability and initial egg production. Daughters emerging in July and August from *H. platystachys* had a higher probability of being receptive to male mating attempts than daughters emerging from *H. mariae*. However, this maternal effect reversed over time. Later cohorts of daughters from *H. platystachys* were much less likely to copulate during the 4-h observation period than were those from *H. mariae* (Table 1, Figure 1). These patterns mirror the patterns observed in the number of eggs produced within 2 days after pairing (Figure 3). Daughters emerging as adults in July from *H. platystachys* laid over 7 times more eggs on average over these first 2 days than daughters from *H. mariae*. These patterns gradually shifted until, in the October cohort, daughters from *H. mariae* laid more eggs than daughters from *H. platystachys*.

Initial differences in egg production did not translate into long-term, cumulative fecundity differences for daughters from *H. platystachys* and *H. mariae* in this study (Figure 3). Could high initial egg production have advantages for female fitness? Unlike the insects in this study, wild insects not protected by mesh bags are likely to experience high rates of predation from birds, lizards, spiders, and ants (Miller CW, personal observation). Thus, producing large quantities of offspring quickly could have fitness advantages. Females that delay reproduction or produce fewer eggs initially may die before "catching up" to females with high initial fecundity.

Given the potential fitness costs of delaying reproduction, why did the daughters that matured in later months on *H. platystachys* invest so little in copulation and egg laying? Certainly, variation in host plant quality might be responsible for the differences among females. Daughters in the later cohorts developed on older inflorescences which may have provided lower quality food, preventing daughters from acquiring sufficient resources for high initial egg production (see also Miller 2007). Indeed, as plant tissues age, correlated changes in the levels of carbon, nitrogen, and defensive metabolites are known to influence the fecundity of insect herbivores (Awmack and Leather 2002).

The seasonal decline in daughter reproductive status may have been caused by a seasonal decline in resource quality, but it may also reflect a change in daughter reproductive strategies. Although these explanations are not mutually exclusive, the changing phenology of *H. platystachys* suggests that females

emerging in September and October might do best to adopt a migratory phenotype. Females emerging from *H. mariae*, on the other hand, encounter a much more consistent resource over this time period (Figure 1). I elaborate on these patterns below.

Within a single *H. mariae* patch, inflorescences are commonly available year-round, with plants producing them in a staggered fashion (see also Stiles 1975). Each month that I walked transects, the majority of inflorescences on this transect line were producing both flowers and fruits (Figure 1). When inflorescences eventually senesce, other, younger, inflorescences are often available within a few meters. Thus, females emerging in different cohorts will always have viable inflorescences nearby for oviposition. Based on these ecological observations, daughters raised on this host plant species should be predicted to be relatively constant in reproductive status across cohorts and they are (Figure 1).

In contrast, a patch of *H. platystachys* provides only ephemeral resources to heliconia bugs. Inflorescences bloom in the months of May and June. Over the next few months, they go through distinct phenological stages (Figure 1). By October, most plants in the population have dropped their brown, rotten inflorescences, and all resources for these insects effectively disappear from the area until the next year. Thus, females emerging in September and October are surrounded by older, dying inflorescences (Figure 1). Laying eggs on dying inflorescences may result in high offspring mortality (Miller CW, personal observation), small offspring of poor condition (Miller CW, in preparation), or offspring with reduced reproductive potential (Figures 1 and 3). Therefore, females developing later in the season should presumably allocate resources differently, away from current reproduction and instead to traits that will facilitate dispersal to viable heliconia inflorescences, which can, in some situations, be kilometers away. Reproduction is delayed in the migratory forms of many female insects (reviewed in Zera and Denno 1997).

Further studies are needed to examine whether these differences truly represent migratory versus nonmigratory phenotypes. If they do, a myriad of research questions arise, including: What are the specific environmental factors that result in the different phenotypes? Can these differences help explain how isolated patches of heliconia species are colonized when inflorescences are first produced each year? And, what are the fitness consequences of adopting migratory versus nonmigratory phenotypes under different environmental conditions?

The perspective of the ovipositing mother

In this study, *H. platystachys* appeared to be the best quality host plant for offspring early in the season and *H. mariae* appeared to be superior later in the season. However, I found heliconia bug offspring developing on both *H. platystachys* and *H. mariae* throughout the season. Why would ovipositing mothers lay eggs on apparently inferior host plants? Why not shift to the best available host plant species for offspring at any given time?

These questions may be part of the larger puzzle of why females do not always choose the best environment for individual offspring. In fact, females should not always do what is best for individual offspring. Females should maximize their own fitness even if it comes at a cost to individual offspring quality (Godfray 1995; Scheirs et al. 2000; Mayhew 2001; Webb et al. 2002). Female heliconia bugs may limit their search for optimal habitat for offspring due to limitations in their own energy reserves, to minimize adult predation risk, and because the best plant for female feeding may be different than the best plant for offspring.

CONCLUSIONS

I examined effects of natal host plant species and phenology in the heliconia bug, *L. tricolor*. The host plant species where mothers laid eggs influenced the reproductive traits of offspring, and the effects on daughter mating probability and fecundity changed over time. These dynamic effects may be due to seasonal changes in the host plant species. As the resources of *H. platystachys* naturally mature and senesce, the phenotypes of offspring emerging from this plant species also change. *Heliconia mariae* is a much more consistent resource, and the phenotypes of offspring emerging from this plant species are relatively consistent over time.

This study and others are beginning to suggest that maternal effects may be commonly, even universally, dynamic (e.g., Kaplan 1992; Einum and Fleming 1999; McAdam and Boutin 2003; Plaistow et al. 2006). The dynamics in maternal effects may be predictable, and even adaptive, when they are related to seasonal changes in natural environments (Moran 1992; Mousseau and Fox 1998a). Because maternal effects likely have broad ecological and evolutionary implications (Falconer 1965; Kirkpatrick and Lande 1989; Lande and Kirkpatrick 1990; Bernardo 1993; Ginzburg 1998; Inchausti and Ginzburg 1998; Beckerman et al. 2002; Benton et al. 2005; Smith et al. 2006), more work is desperately needed to explore their consequences in ever-changing natural environments.

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