Dynamic effects of oviposition site on offspring sexually-selected traits and scaling relationships

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Abstract   The expression of sexually-selected traits such as bright plumage, exaggerated antlers, and elongated eyestalks can be highly influenced by environmental factors, including the behaviors of mothers. Many recent studies have described the ways that maternal behavior can influence the expression of sexually-selected traits in offspring, however, few studies have investigated if and how such maternal effects might change, over time, in natural populations. Here, we examine the influence of maternal oviposition site on the expression of offspring sexually-selected traits in four successive cohorts of the heliconia bug, *Leptoscelis tricolor* (Hemiptera: Coreidae). Female heliconia bugs lay eggs on multiple host plant species, and offspring remain on these plants for the entirety of growth and development. We found that natal plant species had significant effects on the expression of male sexually-selected traits and the degree of sexual dimorphism. Moreover, these effects changed over time for later cohorts, concurrent with changes in host plant resources. Our results suggest that maternal effects can be a significant and dynamic influence on the sexually-selected traits of offspring. Such environmental effects on sexually-selected traits could have broad implications for the processes and outcomes of sexual selection.

Introduction

Sexually-selected traits such as elaborate plumage, horns, and spurs are characterized by extensive intra-population phenotypic variation, with measurable effects on reproductive success. Prior to the previous decade, many researchers assumed that this variation was due

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to genetic differences among individuals (Andersson 1994). However, recent empirical work has demonstrated that phenotypic variation in sexually-selected traits can be largely due to environmental factors (e.g., Griffith et al. 1999; Moczek and Emlen 1999; Qvarnström 1999; David et al. 2000; Griffith and Sheldon 2001; Jensen et al. 2006). The environmental sensitivity of sexually-selected traits may have far-reaching implications, including affecting the reliability of sexual signals as indicators of genetic quality (e.g., Qvarnström 2001; Greenfield and Rodriguez 2004), the direction and speed of the response to selection (e.g., Lande and Kirkpatrick 1990; Charmantier and Garant 2005), and the maintenance of genetic variation in sexually-selected traits (e.g., Kokko and Heubel 2008).

Insects are well suited to address the role of natural environmental variation in sexual selection. Juvenile insects commonly experience different rearing environments due to the oviposition behaviors of their mothers, with effects on development, life history, and adult morphology (Sutherland 1969; Jaenike 1978; Thompson 1988; Mayhew 1997; Mousseau and Fox 1998; Awmack and Leather 2002). Such maternal effects on offspring characteristics may potentially be modified by the dynamic nature of most natural environments. For instance, in many herbivorous insects, mothers lay eggs on multiple host plant species. The distinct, seasonal timing of growth, maturation, and senescence of plant tissues (hereafter, phenology) of each plant species may result in one plant species providing better resources for offspring at one time and another plant species providing better resources at a later time. Changes in host plants may mean that the usage of different host plant species by ovipositing mothers can have different effects on offspring at different times of year. Such dynamic maternal effects are only beginning to be examined, and may have far-reaching consequences for sexual interactions and evolutionary change (Rossiter 1998; Marshall and Uller 2007; Miller 2008).

We investigated potential effects of oviposition location and seasonality on the expression of sexually-selected traits in the heliconia bugs, *Leptoscelis tricolor* Westwood (Hemiptera: Coreidae). Heliconia bugs feed, compete, mate, and oviposit on heliconia plants (Zinzerberales: Heliconiae). Ovipositing females move among heliconia plants and may lay eggs on multiple species during their lifetimes (Miller 2007). The location where females oviposit determines the plant species where offspring will complete growth and development, due to the restricted mobility of the wingless juveniles. Thus, researchers are able to associate offspring with their natal host plant species (and the host plant use of their mothers) simply by finding juveniles before they become flight-capable adults. This characteristic of heliconia bugs allows field collection of large numbers of offspring.

A previous study of heliconia bugs found low heritabilities of body size and weapon size (Miller 2007), demonstrating the importance of environmental variation for morphology in this species. This previous experiment was conducted over a relatively short period of time and manipulated the locations where females laid their eggs. Thus, we aimed here to examine broad patterns of trait expression naturally occurring in this population. We predicted that the different phenology of each heliconia host plant species (Fig. 1) would translate into seasonal differences in the morphology of insects emerging from the plants over our study period.

To test our prediction, we measured sexually-selected traits and metric traits of individual insects from four cohorts of new adult offspring emerging from two of the most common heliconia plant species near Gamboa, Panama. We also determined scaling relationships (allometries) between morphological traits and body size. Such scaling relationships can contain important information regarding the responsiveness of trait growth to body size and individual condition during development (Emlen and Allen 2003; Shingleton et al. 2007). Theory predicts that secondary-sexual traits should be more
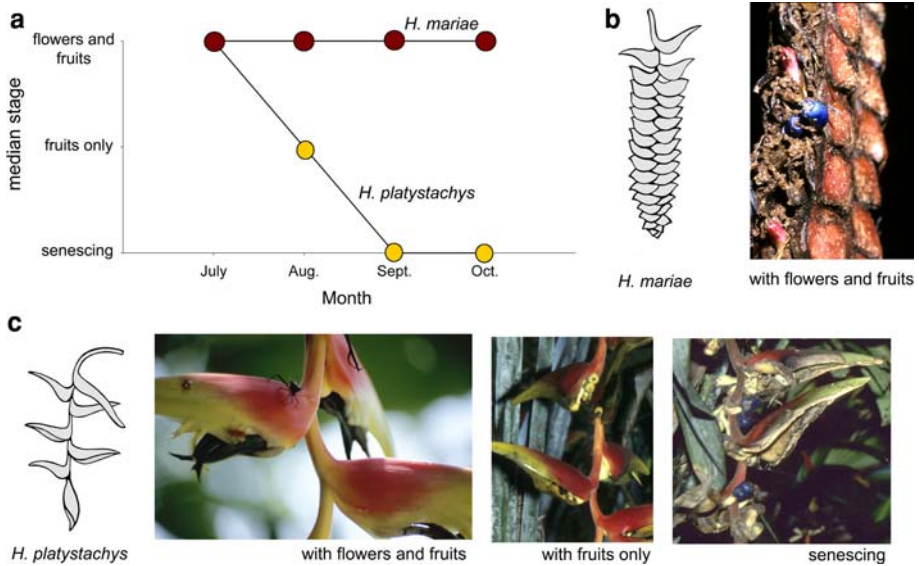
Fig. 1 The phenology of two common host plant species, *Heliconia platystachys* and *H. mariae* in 2005, the year the current study was conducted (other years show similar patterns). The median stage of *H. platystachys* inflorescences in the population declined over time, (**a**) and (**c**), while the median stage of *H. mariae* remained constant during this time period, (**a**) and (**b**). Drawings by David Tuss, photographs by Christine W. Miller. Modified from Miller (2008)

responsive to individual condition than metric traits (Cotton et al. 2004b), demonstrated by a shift in the allometric intercept between trait size and body size (Bonduriansky and Rowe 2005).

Methods

Research species

Male heliconia bugs, *Leptoscelis tricolor* Westwood (Hemiptera: Coreidae) often establish territories on the inflorescences of heliconia plants and will chase away or fight with intruding males. When two males encounter one another, one male commonly begins twitching his front legs up and down (Fig. 2a). If the other male responds in turn, then both males pivot away from each other and grapple with their hind legs (Fig. 2b). One or a series of intense squeezing bouts follow, with each male's hind legs wrapped around the abdomen of his opponent. The interaction terminates when one male disentangles from the other and leaves the area.

Females fly from plant to plant, and are often courted by males when they arrive on inflorescences. The front legs of males figure prominently in this courtship. When one sex approaches the other, males often begin to twitch their front legs up and down, as they do before male–male competitions. The male then begins to tap a female's abdomen with his front legs. A female may respond by leaving the area, by swinging her abdomen away from the male and hitting him with her front legs, or by allowing the male to copulate. Females will commonly adopt one of the first two behaviors when initially contacted by a male and
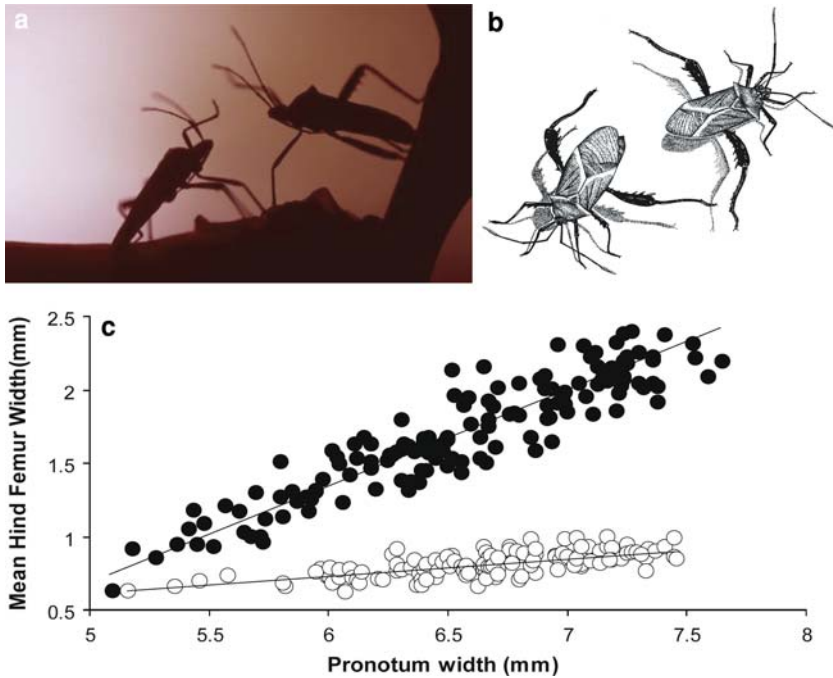
Fig. 2 **a** Two male heliconia bugs initiating a competition and displaying their front legs. **b** Males involved in an escalated competition. **c** The scaling relationship between body size (measured as pronotum width) and hind femur width in this population. Males (*solid circles*) have larger legs than females (*hallow circles*), and their legs scale more steeply with body size. Photograph by Christine W. Miller, drawing by David Tuss

then, after he has courted her further, allow copulation. Thus, it appears that male forelegs function in visual displays both to rival males and to females.

Both adult females and males rarely stay on any inflorescence for more than a few days. In a mark-resight study conducted concurrent to the study here, I found that 92% of ovipositing females in one population changed host plants, and 35% changed host plant species (Miller 2007). Because this particular study was limited to 1 month observation period and a small area (~ 1 km^2), the numbers likely underestimate the true movement of mature female insects as they are laying eggs. Host switching by females provides opportunity for female host preference behavior to influence the natal environments of their offspring. Females lay eggs singly on or very near to heliconia inflorescences, and may continue laying eggs for up to 80 days or longer. Eggs hatch after approximately 10 days, and nymphs molt into adults about a month later.

During their juvenile stages, nymphs remain on the host plant species where they hatched. Only in rare circumstances when different heliconia species grow in close enough proximity to touch one another might a heliconia bug nymph venture onto the inflorescence of another host plant species (C. W. Miller, personal observation). This situation is unusual, because heliconia plants propagate vegetatively by rhizomes and many species naturally grow in monospecific, often monoclonal, stands (Stiles 1975). Stands of different species are commonly separated by habitat requirements (Stiles 1975) over distances too great for a walking nymph to survive. All insects sampled in this study were collected from naturally separated stands of *H. platystachys* and *H. mariae*.

Detection and measurements of new adults in the field

During the rainy season of 2005, naturally-growing heliconia inflorescences near Gamboa, Panama were searched for fifth-stage *Leptoscelis tricolor* nymphs. Fine mesh bags were slipped over each inflorescence where a nymph was found. Occasionally additional nymphs were present on an inflorescence. These nymphs were removed and not included in the study. The mesh bags over the inflorescences prevented the insects from leaving the inflorescence when they later emerged as flight-capable adults. The first cohort of insects was detected between June 22 and July 1, hereafter "July" cohort because they emerged as adults in July; the second cohort between July 27 and July 30, hereafter "August" cohort, the third between August 24 and September 3, hereafter "September" cohort, and the final cohort between September 23 and October 1, hereafter "October" cohort. We monitored insects until they had emerged as adults and had fully sclerotized cuticles (up to 2 weeks after detection).

Based on behavioral interactions among insects, we considered male hindlegs to be weapons and forelegs to be signals used in the assessment interactions between rival males and in courtship of females (C. W. Miller, unpublished data). Pronotum width and head length were not obviously connected with a sexual selection function. Studies incorporating multi-trait comparisons are important for establishing the relative degree of environmental sensitivity of sexually-selected traits (Cotton et al. 2004b).

We measured live insects with Mitutoyo digital calipers with a maximal precision of 0.01 mm. Hind femur width was determined by measuring both hind legs at the third distal spine and taking the mean of these measurements. Our hind femur width measurement includes both the width of the femur itself and the length of the spine. This is the widest part of the hind femur, and this area frequently comes into contact with the abdomens of rival males during male–male competitions (C. W. Miller, personal observation). Pronotum width was used as a metric of body size because it is a common proxy for body size in insects and easy to measure accurately due to its relatively large size. We estimated front femur length by measuring the left front femur from the thorax at the base of the leg to the top of the proximal tip of the tibia. Head length was measured dorsally from the point of connection with the thorax.

Statistical analyses

We tested for effects of host plant species, sex, cohort (month of emergence) and all possible interactions explaining among-individual variation in insect morphological traits with analyses of variance.

We examined the effects of these factors on the allometric scaling relationships between trait size and body size using analysis of covariance with pronotum width as the covariate. To this end, we first performed a separate ANCOVA for hind femur width, front leg length, and head length to test for effects of the explanatory variables on the slope of the scaling relationship between these traits and body size, indicated by a significant interaction with pronotum width. If slopes did not differ according to pronotum width, we next examined effects of explanatory variables on the intercept of the scaling relationships (i.e., trait size when controlling for body size). We repeated all analyses using both raw and log-transformed data, and all gave qualitatively equivalent results. Thus, we only present the analyses using the raw data.

Results

Host plant effects on absolute trait sizes and sexual dimorphism

Insects that developed on *H. platystachys* were larger than insects from *H. mariae* for all body size characteristics measured (Table 1; Figs. 3, 4). The host plant effect varied over time, however. The differences in trait size resulting from alternative host plant species were dramatic early in the season but declined over time so that most body size characteristics did not differ for insects from the two host plant species by the October cohort (Fig. 4).

Sexual dimorphism was found in hind femur width, front femur length, and head length (Table 1; Fig. 4). The magnitude of sexual dimorphism for hind femur width was affected significantly by natal host plant species. The degree of sexual dimorphism in hind femur width was greater for *H. platystachys* offspring than for *H. mariae* offspring (Fig. 4).

Table 1 Results of analysis of variance for body size traits

Source	df	Hind femur width F	Front femur length F	Pronotum width F	Head length F
Sex	1	757.81***	8.90**	2.01	0.56
Plant species	1	37.66***	32.23***	35.36***	10.94***
Cohort	3	4.56**	5.61**	4.86**	10.68***
Sex × plant	1	17.38***	3.29	0.69	4.73*
Sex × cohort	3	1.50	0.79	0.54	0.18
Plant × cohort	3	4.02**	3.46**	5.18**	1.26
Sex × plant × cohort	3	2.61	0.38	0.38	2.43

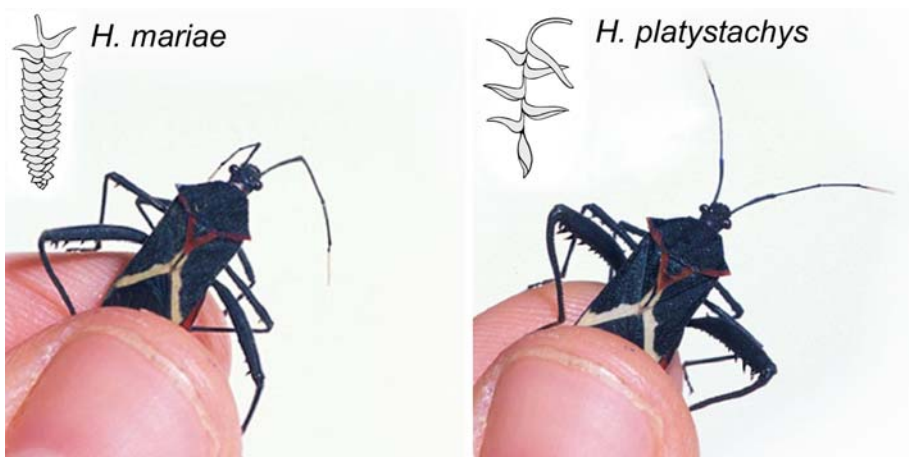Error $df = 247$–250; * $P < 0.05$, ** $P < 0.02$, *** $P < 0.001$

Fig. 3 Body size differences in male heliconia bugs from the July cohort. The male on the left emerged from *H. mariae*, and the male on the right emerged on *H. platystachys*. Note the visible differences in hind femur width
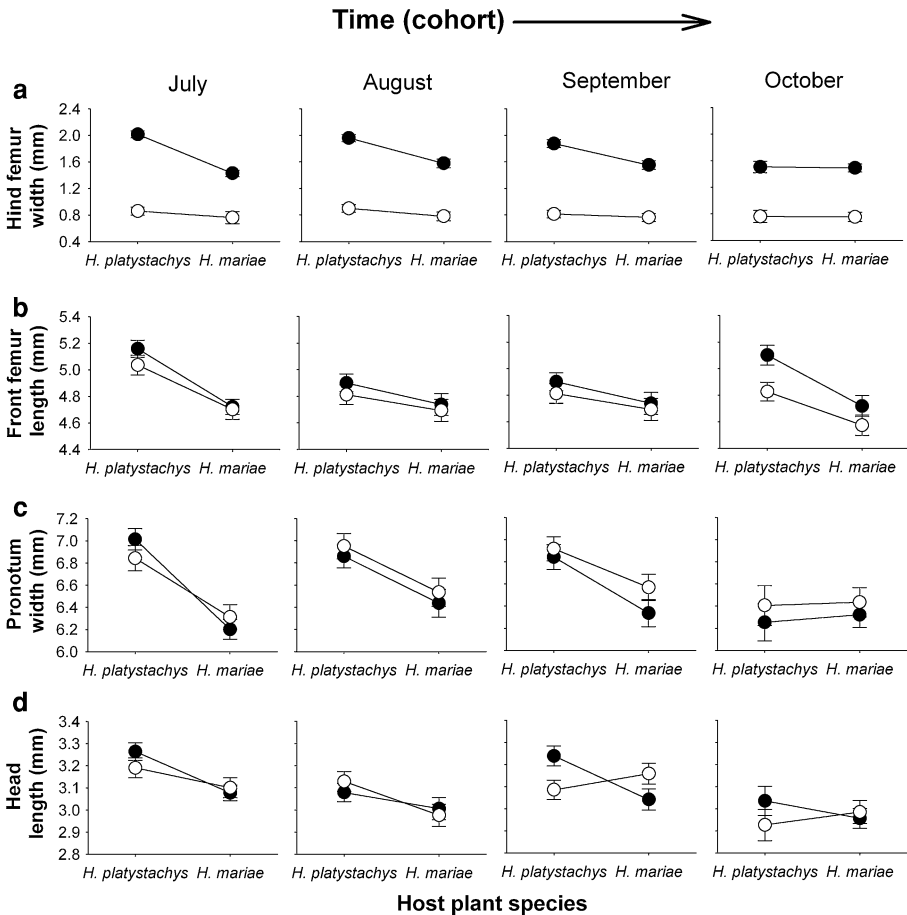
Fig. 4 Least-squares estimates (±SE) for morphological traits (**a–d**) for males (*solid circles*) and females (*hollow circles*) for each of the separate cohorts of insects

Interestingly, natal host plant species influenced the magnitude *and direction* of sexual dimorphism in head length (Table 1; Fig. 4d). Males that developed on *H. platystachys* had longer heads than females, whereas males from *H. mariae* had shorter heads than females. This pattern was especially pronounced in the September cohort. In contrast to the patterns presented by hind femur width and head length, front femur length did not vary in the degree of sexual dimorphism either between plant species or across cohorts (Fig. 4b).

Host plant effects on trait scaling (allometry)

The slope of the scaling relationship between hind femur width and body size (pronotum width) differed by sex (Table 2; Fig. 2). Therefore, we tested for allometric intercept differences of hind femur width separately for males and females. Natal host plant species had significant effects on the intercept of hind legs for both males and females, though the effects on males were more pronounced (Table 3; Figs. 5, 6). Separate analyses by cohort revealed that males from the July and August cohorts had a greater allometric intercept

Table 2 Results of analysis of covariance for effects on scaling slope with body size, measured as pronotum width, as a covariate

Source	df	Hind femur width F	Front femur length F	Head length F
Body size (pw)	1	373.16***	120.77***	41.16***
Sex	1	86.04***	0.04	0.02
Plant species	1	0.07	0.30	0.61
Cohort	3	1.15	0.38	1.23
Body size × sex	1	178.87***	0.28	0.01
Body size × plant	1	0.01	0.10	0.70
Body size × cohort	3	0.90	0.39	0.87
Sex × plant	1	0.73	0.06	0.01
Sex × cohort	3	0.49	0.91	1.91
Plant × cohort	3	3.21*	1.69	0.93
Sex × plant × cohort	3	1.01	1.36	2.23
Body size × plant × cohort	3	2.88*	1.61	0.91
Body size × plant × sex	1	1.04	0.02	0.03
Body size × cohort × sex	3	0.51	0.81	1.84

Error df = 231–241; * $P < 0.05$, ** $P < 0.02$, *** $P < 0.001$

(wider legs for a given body size) if they were raised on *H. platystachys* (ANCOVA: July, $F_{1,49} = 10.41$, $P = 0.002$; August: $F_{1,42} = 5.43$, $P = 0.026$; Fig. 5a, b). In the September and October cohorts, males raised on the two species of plants did not differ in the allometric intercept of hind femur size (ANCOVA: September, $F_{1,30} = 0.37$, $P > 0.10$; October: $F_{1,22} = 0.74$, $P > 0.10$; Fig. 5c, d). Surprisingly, female natal host plant species was also important for the intercept of the scaling relationship between body and leg sizes. Females emerging from *H. platystachys* in August had wider hind legs at the mean body size than females from *H. mariae* (ANCOVA: $F_{1,28} = 28.37$, $P < 0.001$; Fig. 6b). In no other cohort did natal host plant species have a detectable effect on the allometric intercept of leg size of females (ANCOVA: July $F_{1,32} = 0.53$, $P > 0.10$; September, $F_{1,32} = 0.01$, $P > 0.10$; October: $F_{1,17} = 0.23$, $P > 0.10$; Fig. 6a, c, d).

The slopes of the allometric scaling relationships of both head length and front leg length were not significantly affected by plant species, sex, or cohort (Table 2). Therefore, we proceeded to look for effects of the explanatory variables on allometric intercept. We

Table 3 Results of analysis of covariance for the allometric intercept of hind femur width with body size (pronotum width)

Source	Males		Females	
	df	F	df	F
Body size (pw)	1	497.48***	1	83.52***
Plant species	1	11.30***	1	5.93*
Cohort	3	0.93	3	8.67***
Plant × cohort	3	1.06	3	2.39

The analyses were performed separately for males and females

Error df: Males = 135; Females = 112; * $P < 0.05$, ** $P < 0.02$, *** $P < 0.001$
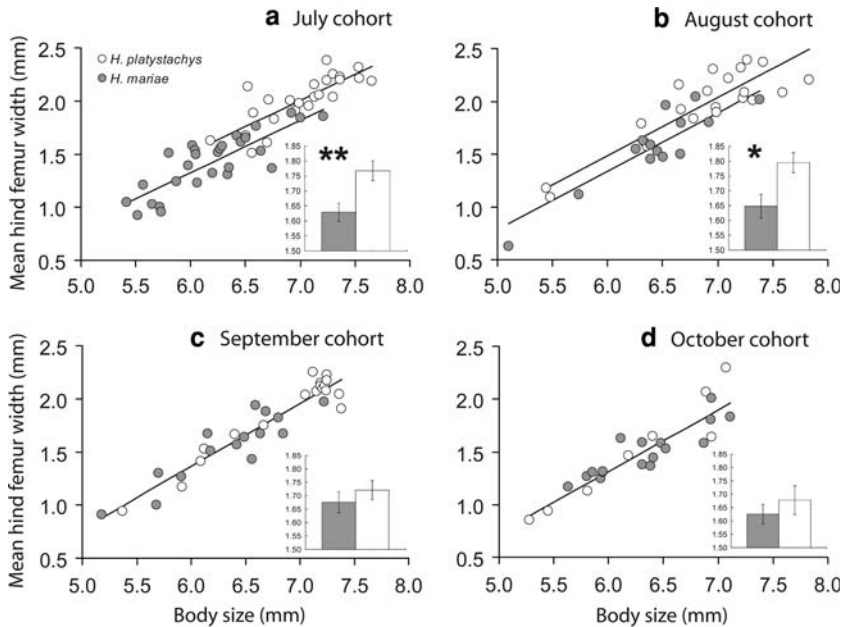
Fig. 5 Scaling relationships between body size (pronotum width) and mean hind femur width for males over the four cohorts. *Insets* show least-squares estimates (±SE) for hind femur width at the mean body size. *Asterisks* denote significant differences in allometric intercepts when each cohort was analyzed separately (* $P < 0.05$, ** $P < 0.01$)

found that the intercept of front leg length was significantly influenced by host plant species (Table 4). At the mean body size, those insects raised on *H. platystachys* had longer front femurs (Table 5). The investment in front femurs was more pronounced for males. The intercept of head length was not significantly affected by host plant species (Tables 4, 6).

Discussion

We found that both natal host plant and cohort had complex effects on morphological traits in both male and female heliconia bugs, influencing absolute body size, the slopes of the scaling relationships between trait sizes and body size, and the allometric intercepts of sexual and nonsexual traits with body size. Importantly, the expression of sexually-selected traits and morphology of offspring was affected by host plant species and this effect changed for sequential cohorts, concurrent with apparent changes in the quality of plant resources. Because the natal host plants of offspring are determined by the oviposition behaviors of mothers, these seasonal changes in offspring phenotypes can be considered dynamic maternal effects.

Host plant species, cohort effects, and overall offspring size

Females that laid eggs on *Heliconia platystachys* produced offspring that were larger in all measured traits than offspring from *H. mariae* (Figs. 3, 4; Table 1). However, these
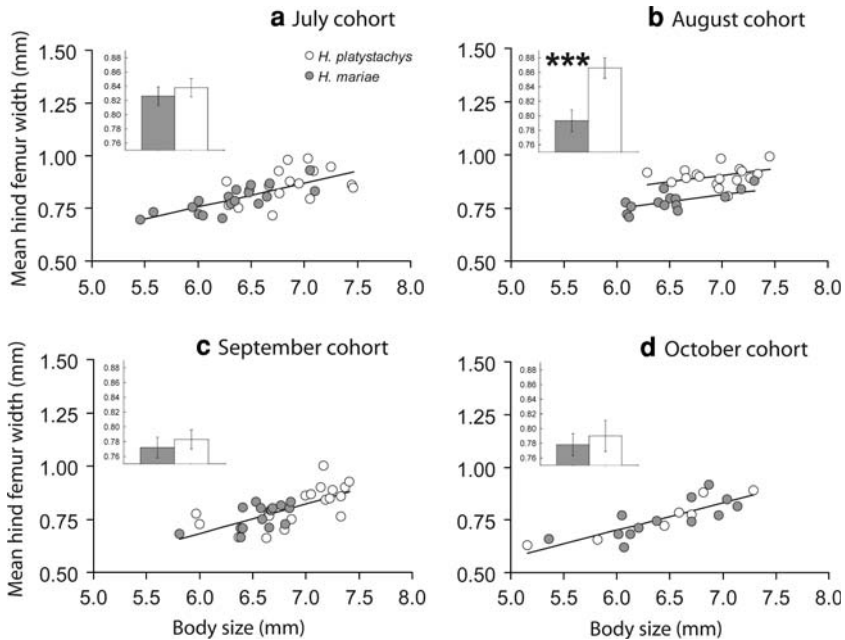
Fig. 6 Scaling relationships between body size (pronotum width) and mean hind femur width for females over the four cohorts. *Insets* show least-squares estimates (±SE) for hind femur width at the mean body size. *Asterisks* denote significant differences (*** $P < 0.001$) in allometric intercepts when each cohort was analyzed separately

Table 4 Results of analysis of covariance for allometric intercept of head length and front femur length in males and females	Source	*df*	Front femur length *F*	Head length *F*
	Body size (pw)	1	153.85***	57.06***
	Sex	1	24.24***	2.33
	Plant species	1	5.94**	0.63
	Cohort	3	6.34***	10.09***
	Sex × plant	1	2.69	4.00*
	Sex × cohort	3	2.63	0.29
	Plant × cohort	3	1.69	0.25
Error $df = 246$; * $P < 0.05$, ** $P < 0.02$, *** $P < 0.001$	Sex × plant × cohort	3	1.14	2.79*

morphological effects were not consistent over time (Fig. 4; Table 1). Early in the season, offspring from *H. platystachys* were substantially larger than offspring from *H. mariae*. This size difference steadily reduced, until, by the October cohort, offspring from the two host plant species were practically morphologically indistinguishable.

Size differences in these insects may have consequences for reproductive success for both males and females. Larger males may have an advantage in male–male competitions and mating with females, as is seen in related species of coreids (Mitchell 1980; Fujisaki 1981; Miyatake 1993; Nageon de Lestang 2010) and in many other organisms (Andersson 1994). The host plant species a mother insect uses for oviposition may also affect the

Table 5 Least-squares means ± SE on the allometric intercept of front femur length

Cohort	Males		Females	
	H. platystachys	*H. mariae*	*H. platystachys*	*H. mariae*
July	4.99 ± 0.05	4.88 ± 0.05	4.94 ± 0.06	4.81 ± 0.06
August	4.80 ± 0.05	4.81 ± 0.07	4.67 ± 0.06	4.72 ± 0.07
September	5.01 ± 0.06	4.82 ± 0.06	4.70 ± 0.06	4.59 ± 0.06
October	4.98 ± 0.09	4.74 ± 0.06	4.64 ± 0.09	4.71 ± 0.07

Table 6 Least-squares means ± SE for the allometric intercept of head length

Cohort	Males		Females	
	H. platystachys	*H. mariae*	*H. platystachys*	*H. mariae*
July	3.19 ± 0.04	3.15 ± 0.03	3.15 ± 0.04	3.15 ± 0.04
August	3.04 ± 0.04	3.04 ± 0.05	3.07 ± 0.04	2.99 ± 0.05
September	3.20 ± 0.04	3.09 ± 0.04	3.03 ± 0.04	3.17 ± 0.04
October	3.10 ± 0.06	3.01 ± 0.04	2.96 ± 0.06	3.02 ± 0.05

reproductive success of her female offspring, because the size of female invertebrates is often strongly correlated with fecundity (Roff 1992). Indeed, females from *H. platystachys* during this time period had higher egg production early in adulthood than did females from *H. mariae* (Miller 2008).

Variation in the degree of sexual dimorphism according to the environment

Male heliconia bugs have wider hind femurs and longer front femurs than females (Figs. 2, 4; Table 1). In addition, male hind femur width scales more steeply with body size than female hind femur width (Fig. 2; Table 2). Males and females of many species differ in the slope of the scaling relationships between secondary-sexual traits and body size (e.g., Hughes 1996; Emlen and Nijhout 2000; Green 2000; Kelly 2005). Differences in slope result in changing levels of sexual dimorphism according to the size of individuals. Large animals with such a scaling relationship are highly sexually dimorphic, while small animals are not. This pattern of sexual dimorphism can be described as incomplete when small animals approach sexual monomorphism (Bonduriansky 2007).

Here, we have found that the degree of sexual dimorphism in a natural population of animals is influenced by the natal environment. Heliconia bugs emerging from *H. platystachys* early in the season have more sexually dimorphic hind femurs than those insects emerging from *H. mariae* (Fig. 4; Table 1). Thus, mothers that laid their eggs on *H. platystachys* during this time period produced offspring with greater sexual dimorphism than those that laid eggs on *H. mariae*. This variation in sexual dimorphism appears to be only partially due to the overall size differences of insects emerging from the two plant species. Males that emerged from *H. platystachys* early in the season were not only larger (Fig. 4; Table 1), but they also expressed disproportionately larger hind legs for their body size (Fig. 5; Table 3).

Environmental effects on the degree of sexual dimorphism in sexually-selected traits may be common. Animals as diverse as ungulates and flies vary in sexual dimorphism

according to environmental conditions (David et al. 1994; Post et al. 1999; Karan et al. 2000; Weladji et al. 2005; Bonduriansky 2007). However, intra-population variation in the degree of sexual dimorphism has often been assumed to be non-existent and has been ignored in many studies (discussed in Teder and Tammaru 2005). Explicitly addressing this phenomenon may improve understanding of the sex-specific selection regimes faced by animals as well as the consequences of environmental change for sexual selection.

Sexual dimorphism and condition-dependent sexual selection

The observed changes in sexual dimorphism across host plant species may reflect the heightened condition dependence of male hind femurs in this species. Theory suggests that sexual dimorphism and condition dependence should be tightly linked (Bonduriansky 2007). Directional sexual selection for a male trait should result in a greater displacement from the viability-selected phenotype expressed by females, leading to more pronounced sexual dimorphism. The extent of trait displacement from the viability optimum should, therefore, reflect the extent of the viability costs of trait expression incurred by males. Males in good condition will be able to better withstand these viability costs, and thus should express the sexually-selected trait to the fullest extent. Males in poor condition should express the trait to a reduced extent. Such heightened condition-dependent expression is widely predicted for sexually-selected traits (Kodric-Brown and Brown 1984; Nur and Hasson 1984; Andersson 1986; Rowe and Houle 1996; Cotton et al. 2004b).

Other patterns of trait expression across environments provide further evidence of male condition-dependent expression of hind femurs in this species. Male heliconia bugs from *H. platystachys* early in the season exhibited a greater allometric intercept in hind femur size. In other words, for a given body size, males from *H. platystachys* expressed wider hind legs than males from *H. mariae* (Fig. 5). Such allometric shifts in the expression of traits are thought to indicate heightened condition dependence, especially when compared to traits not involved in sexual selection (Cotton et al. 2004b; Bonduriansky and Rowe 2005). Head length, a trait with no known use in sexual selection, did not exhibit a scaling shift with environmental differences. Unexpectedly, females from *H. platystachys* did have a shift in the allometric intercept of hind femurs in the August cohort (Fig. 6; Table 3). However, this shift was smaller in extent than the response in males, and was limited to only one cohort of females.

Responses of other traits to environmental variation

We examined another sexually-selected trait used in male–male competitions and in courtship: the length of front femurs. We found that front femur length was also sexually dimorphic, however, it responded differently to environmental variation than did hind femur width. Like hind femur width, the front femur length of both males and females was affected by host plant species and cohort (Table 1; Fig. 4). In addition, males had longer front femurs than females, and they scaled differently with body size. However, unlike hind femurs, the *slope* of the scaling relationship did not differ between males and females, but the *intercept* did differ (Tables 2, 4, 5). Thus, this trait exhibited complete sexual dimorphism in both absolute size and allometric intercept for this population over this time period. Complete sexual dimorphism is seen in some sexually-selected traits such as eye stalks in the stalk-eyed fly, *Cyrtodiopsis dalmanni* (Cotton et al. 2004a) and the horns of the dung beetle *Onthophagus pentacanthus* (Emlen et al. 2005).

Not only did natal host plant species affect the morphology of offspring, but it also affected behavior (Miller 2008). Host plant species influenced the probability of mating, female fecundity, and performance of copulatory courtship behaviors by males. Some offspring behaviors were also significantly modified by seasonal changes, as we found here. These studies, along with the low heritabilities of morphological traits in this species (Miller 2007), emphasize the importance of maternal phenotypes and environmental context in determining offspring phenotypes.

Plant phenology and seasonal effects for insect offspring

What was responsible for the dynamic effects of oviposition location on heliconia bug morphology? Each species of heliconia has a unique phenology, flowering and fruiting at different times of the year and for different lengths of time (Stiles 1975; Croat 1978). Two common host plants of this study population, *Heliconia platystachys* and *H. mariae*, differ markedly in their timing of flowering and fruiting (Croat 1978; Miller 2008; Fig. 1). *H. platystachys* plants produce inflorescences only once per year, generally during May and June. These inflorescences progress through distinct phenological stages, until, by November, only dead inflorescences remain. In contrast, *H. mariae* plants produce inflorescences year-round (Stiles 1975). Thus, throughout our study period, most *H. mariae* inflorescences had both flowers and fruits available (Fig. 1). These changes in host plants correspond to changes in the morphology (here) and behavior (Miller 2008) of heliconia bug offspring. As *H. platystachys* inflorescences degrade in apparent quality, the size of new adult heliconia bugs emerging from these plants and the relative allocation to hind femur growth decreases (Figs. 4, 5). *H. mariae* provides much more consistent resources over this time period, and the morphologies of insects emerging from this plant are also more consistent (Fig. 4).

Why would mothers ever choose an inferior host plant for offspring?

When maternal phenotypes influence the phenotypes of offspring, natural selection may improve the ability of mothers to choose the best resources available for offspring at any one time. However, theory predicts that mothers will often have conflicting fitness demands, and should often enhance their own fitness even at a cost to individual offspring (Godfray 1995; Nylin and Janz 1996; Mayhew 1997; Scheirs et al. 2000; Mayhew 2001). Such conflicting fitness demands may explain why females continue to use *H. mariae* early in the season even when ample *H. platystachys* inflorescences are available. During our study period, we found that over 70% of *H. platystachys* inflorescences were not occupied by heliconia bugs (C. W. Miller, unpublished data). Patches of these two plant species only occasionally grow in close proximity, and considerable travel may be required to reach *H. platystachys* as it becomes available as a resource. The expenditure of time and energy and the risk of predation by birds and spiders may reduce the proportion of females investing in this journey. Such fitness trade-offs may help maintain genetic variation in maternal phenotypes and thus sustain the considerable phenotypic variation in offspring morphological trait expression.

The meaning behind complex patterns of trait expression

This study reveals a rich natural setting where the location in which mothers lay eggs, combined with host plant phenology, result in dynamic patterns of offspring trait

expression over time. Because the patterns examined here are those naturally occurring in a wild population of insects, they are relevant to a breadth of natural phenomena.

Studies have increasingly suggested that sexually-sexual traits, like the ones measured here, are highly sensitive to environmental factors, including the phenotypes of mothers (e.g., Emlen 1997; Griffith et al. 1999; Moczek and Emlen 1999; Qvarnström and Price 2001). Therefore, the expression of ornaments (used to attract mates) or weapons (used in intrasexual contexts) may more accurately reflect maternal behaviors and other environmental factors than direct genetic factors (Miller and Moore 2007).

Environmental variation in male morphology may influence the processes and outcomes of sexual selection by influencing success in male–male competitions and male attractiveness to females. In addition, this variation may negatively affect the reliability of male ornaments as signals of "good genes," or may select for females that can simultaneously assess the phenotypic quality of males as well as the males' natal environment (Greenfield and Rodriguez 2004). It is becoming increasingly clear that sexual selection does not often operate in a simple, straightforward manner. More empirical and theoretical work is greatly needed to better understand the processes of sexual selection under a natural range of environmental conditions.

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