

Evidence of a rapid and adaptive response of hemipteran mouthparts to a physical barrier

Pablo E. Allen¹  | Quentin Cui^{1,2} | Christine W. Miller¹

¹Entomology and Nematology Department, University of Florida, Gainesville, FL, USA

²Southern California Edison, Los Angeles, CA, USA

Correspondence

Pablo E. Allen, Entomology and Nematology Department, University of Florida, Gainesville, FL, USA.

Email: pabloallen@ufl.edu

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Abstract

Animals have encountered novel foods at points throughout history, due to factors such as range expansions and niche shifts driven by competition. One of the first challenges presented by novel foods is how to eat them. Mouthpart morphology is thus critical during the process of host shifts. Developmental plasticity in mouthparts is one potential mechanism that may allow animals to tolerate new foods and eventually to thrive upon them. Here, we investigated the extent to which insect mouthparts from two geographically distant populations can converge in morphology when feeding on common resources. We conducted a common garden/reciprocal transplant experiment using two populations of the cactus bug, *Narnia femorata*, that differ in mouthpart length. This insect uses straw-like mouthparts (hereafter 'beak') to get through the cactus fruit wall to reach the pulp inside. Our experimental results revealed clear developmental plasticity in beak length. Insects from both populations grew longer beaks when they fed on the cactus fruit with the thicker walls, and they grew shorter beaks when they fed on the cactus fruit with the thinner walls. Thus, insects from distant populations exhibited immediate developmental responses to a new food, and in the predicted directions. These results suggest that some fauna may be able to respond more rapidly than predicted when they encounter novel plants.

KEYWORDS

allometry, developmental plasticity, local adaptations, phenotypic plasticity, rostrum length, sexual dimorphism

1 | INTRODUCTION

Species interactions are dynamic. Throughout history, animals have encountered novel foods when ranges expand, and niches shift. Today, human activities move thousands of organisms to new environments, especially plants and insects (Seebens et al., 2017; van Kleunen et al., 2015). When herbivores are exposed to novel plants (Bezemer et al., 2014; Burghardt & Tallamy, 2015; Graves & Shapiro, 2003; Parker et al., 2006), they may initially avoid them because they present new challenges. Indeed, individuals using

novel plants may have reduced survivorship, growth and fecundity relative to those feeding on native hosts (Forister et al., 2009; Fukano et al., 2016; García-Robledo & Horvitz, 2012). Plasticity in the shape and size of mouthparts is one potential mechanism that allows herbivores to have access to new food items and eventually to thrive upon them (Carroll et al., 2005; Hughes & Vogler, 2004). The initial stages of these interactions are essential to understand, because they provide evidence on how organisms can overcome challenges that lead to the colonization of new niches. Thus, host shifts can have cascading impacts on biodiversity, as these shifts

increase trophic interactions and can lead to speciation (Forbes et al., 2017).

The ability to use a new food begins with the ability to physically ingest it. The capacity to change mouthpart morphology exists in nature (Gil et al., 2008; Mainwaring et al., 2010, 2012; Pfennig, 1992; Relyea & Auld, 2005; Stoler & Relyea, 2013; Thompson, 1992, 1999; Watanabe & Young, 2006) and can be effective in allowing alternate foods to be consumed. However, in most documented cases of mouthpart plasticity, the focal populations have had a long-term history with different foods. Thus, it is largely unknown the extent to which mouthparts can respond immediately and plastically to novel food challenges (*but see* Bernays, 1986; Wund et al., 2012; Anderson et al., 2014). Our goal in this study was to test the extent to which mouthparts can developmentally respond to novel and varied food challenges within one generation. We focused on geographically separate populations of an insect that feed on different species of prickly pear cacti. Via a reciprocal common garden experiment, we found that both populations responded rapidly to the new host,

growing mouthparts either longer or shorter in response to the challenge presented.

Narnia femorata Stål (Hemiptera: Coreidae), the leaf-footed cactus bug, feeds using its straw-like mouthparts (hereafter 'beak') on the core (i.e. pulp and seeds) of cactus fruit (Allen & Miller, 2017). Throughout its distribution in the United States, *N. femorata* feeds on different prickly pear cacti with fruit walls that vary in depth. Field measurements have revealed that mouthpart length correlates with fruit wall depth (Figure 1a,b and Figure S1–2). Some populations of these insects feed where multiple species of prickly pear are available and fruit wall thickness varies extensively. In such populations, mouthpart length shows greater variation than in populations where the insects feed on just a single fruit (unpublished data). We provided juvenile insects from two populations ripe cactus fruit from their local host plant and fruit from a novel host plant—the other population's host (Figure 1a,b and Figure S1). Our experimental design was thus a classic common garden/reciprocal transplant design (Kawecki & Eber, 2004; Svensson et al., 2018; Via, 1984). Wild-caught individuals from the two populations exhibit a 10%–13% (depending on

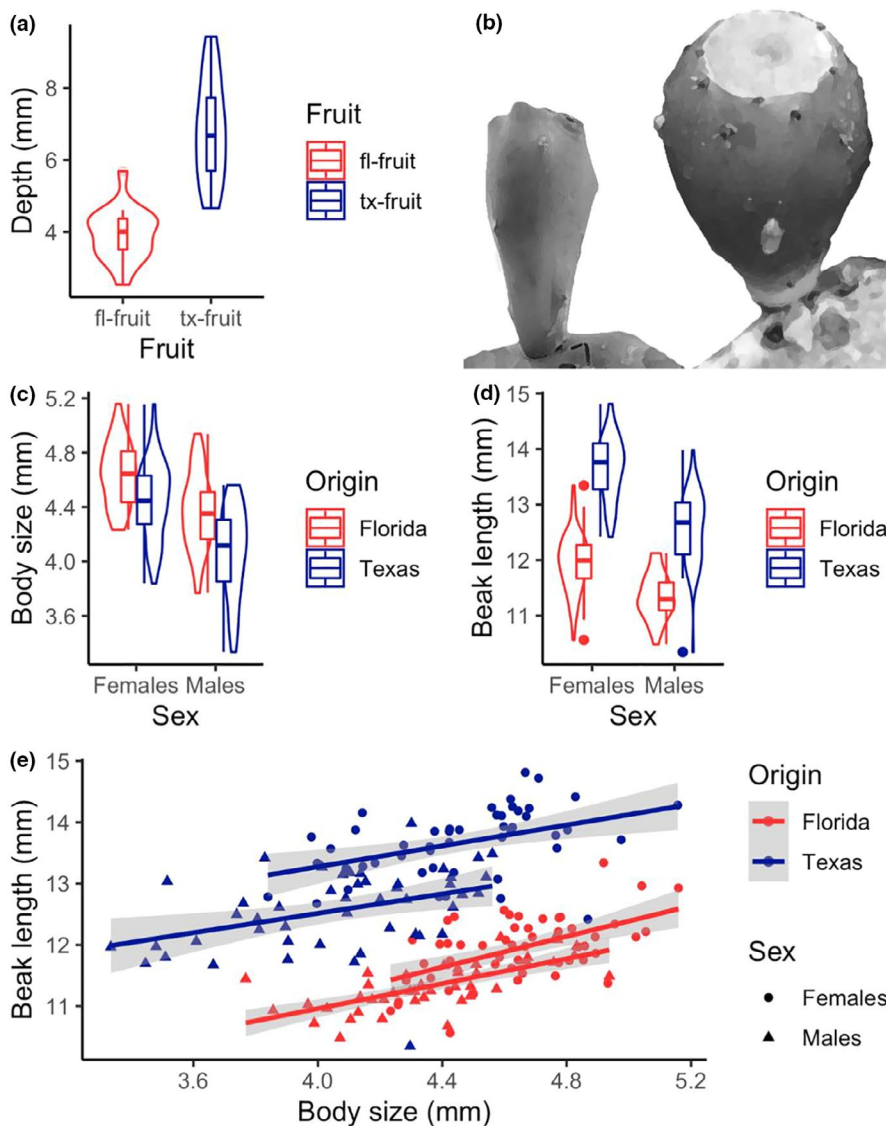


FIGURE 1 In the wild *Narnia femorata* body size is larger in the north-central Florida population (GLM [$df = 1,185$], origin: $F = 39.1$, $p < .0001$, sex: $F = 66.7$, $p < .0001$), but beak length is longer in the Texas population (ANCOVA [$df = 1,184$], origin: $F = 582.9$, $p < .0001$, sex: $F = 42.3$, $p < .0001$, sex-by-site interaction: $F = 7.36$, $p = .007$; covariate - body size: $F = 19.9$, $p < .0001$). The longer beak in this Texas population is likely due to this population feeding from fruits with pulp and seed enclosed deeper inside than in the Florida fruits. (a) Box plots and violin plots of depth of fruit to pulp (Florida fruit $n = 18$; Texas fruit $n = 15$). (b) Florida fruit (*Opuntia mesacantha*, left) and Texas fruit (*O. engelmannii* var. *lindheimeri*, right) next to each other for size comparison. (c) Box plots and violin plots of body size (pronotum width) and (d) beak length for wild-caught individuals from both populations (origin) and sexes. (e) Scaling relationship between body size and beak length for both populations and sexes from wild-caught individuals

the sex) difference in mean beak length (Figure 1c–e). Beak length is longer in insects native to Texas where the core of the large cactus fruits (*Opuntia engelmannii* var. *lindheimeri*) is surrounded by a thicker fruit wall (Figure 1a,b and Figure S1a). In contrast, beak length is shorter in insects from Florida where the core of the smaller cactus fruits (*O. mesacantha*) is surrounded by a thinner wall (Figure 1a,b). At our laboratory in Florida, we raised insects from both populations on their native host and the novel host. We predicted insects, regardless of the population origin, would grow longer beaks when raised on the Texas fruit. We expected the opposite for insects raised on the Florida fruit. Thus, we predicted an immediate convergence in beak development when the disparate populations were raised on the same host, a result enabled by phenotypic plasticity. We further tested for sex differences in mouthpart plasticity, as well as development time and survivorship effects of the original versus novel host.

2 | MATERIALS AND METHODS

2.1 | Study species

Narnia femorata is found in the US Southwest, Florida, Mexico and Guatemala. This cactus-feeding bug has known association with at least four genera and 13 species of cacti through its extensive range (Vessels et al., 2013). Adult females lay eggs on the cactus spines and nymphs can develop completely on a single cactus fruit. In this hemimetabolous insect species, juvenile individuals go through five stages (instars) before moulting into their adult form. *Narnia femorata* feeds on the pulp and seeds within the core of cactus fruit. Longer beaks should be most effective in reaching the food when the walls surrounding the core are thicker (Figure 1a and Figure S1a–S2b). Heteropteran insects have no additional moults after reaching adulthood; thus, the beaks (mouthparts) of new adults will not grow further after the adult form is achieved.

2.1.1 | Adult field data

We collected between 90 and 110 adult *N. femorata* from two populations separated by more than 1,500 km; each population appeared to feed only from a single host plant species (Figure S1b,c). Our Texas sample was collected in late August 2016 from the Brackenridge Field Laboratory at the University of Texas, Austin (bfl.utexas.edu; 30°17'03.4"N, 97°46'41.5"W). These Texas specimens were used as the parental stock for the experimental bugs. We also collected fruits from their local host plant, *Opuntia engelmannii* var. *lindheimeri* (Texas fruit, tx-fruit), at the same time for the experiment. Fifteen Texas fruits were assessed on site, where fruit radius (=fruit size) and core depth (=thickness of fruit wall) were measured with hand-held dial calipers after cutting the fruits in half longitudinally (Figure S1a).

The adult field data (Figure 1c–e) from the Florida population were collected from the Ordway-Swisher Biological Station (29°41'44"N, 81°59'35.5"W) in north-central Florida in early September 2014;

the parental stock Florida individuals were collected from the same site exactly two years later. Measurements of field-collected adults from this same site and month, from multiple years (including this one), suggest that there are no significant differences in body size in this population across years (Cirino & Miller, 2017). At this Florida site, we collected and then measured 18 *O. mesacantha* (Florida fruit, fl-fruit) for fruit measurements in a similar manner to the fruit measurements conducted in Texas.

2.1.2 | Rearing and experimental design

Colonies of Texas and Florida *N. femorata* were established simultaneously at the University of Florida in a greenhouse (temperature ranged between 24 and 30°C, from September to November) using the adults collected from the field. Insects were haphazardly paired with individuals of their own population and kept in plastic deli containers with a local cactus pad and topsoil (for further details see Allen et al., 2018, Allen & Miller, 2020). These parental pairs were fed the same host cacti fruit with which they co-occur in the wild. Females laid eggs for three weeks or until they reached 60 eggs. First-generation (G_1) laboratory nymphs from each population were split across the two fruit treatments (tx-fruit and fl-fruit) starting at the 2nd instar (1st instar juveniles do not feed) in a common garden/reciprocal transplant design. The local Florida host plant, *Opuntia mesacantha* (fl-fruit), was collected as needed from another nearby location in north-central Florida, Camp Blanding, Starke, FL (29°57'06.8" N, 81°58'47.6" W).

Parental pairs founded 10 Florida families and 18 Texas families. Nymphs (juveniles) were raised in sibling groups of 10. We provided half of the nymphs from each location with Florida fruits starting at the 2nd instar, while the other half received Texas fruits. Nymphs were assigned to each fruit haphazardly, while assigning an equal number of nymphs to each treatment and splitting families equally into each fruit treatment. In total 200 Florida nymphs were raised in Florida fruit and 200 in Texas fruit, two cups per family on each treatment, while 180 Texas nymphs were raised in Florida fruit and 180 in Texas fruit, one cup per family on each treatment.

New adults were separated from the remaining nymphs in each container and kept as singles or same-sex pairs until they were fully sclerotized with the final adult body dimensions. At that time, they were frozen for subsequent measurement. Ten Florida families and 15 Texas families produced adults of both sexes on both treatments; only these were used for the morphological analyses.

2.2 | Morphological measurements

We froze the mature adults and then photographed them using a digital camera (Canon EOS 50D) attached to a dissecting microscope (Leica M165 C). We used ImageJ (Schneider et al., 2012) to obtain linear measurements of beak length, front femur length and pronotum width. Front femur length was used as comparative metric trait.

We used pronotum width as our measurement of body size (Allen et al., 2018; Allen & Miller, 2017, 2020; Miller et al., 2016).

2.3 | Statistical analysis

All analyses were conducted with R (R Core Team, 2017). We examined survivorship differences across site of origin, host (both fixed factors) and their interaction using a binary logistic regression. Each individual nymph was assigned either a '0' if it died before reaching adulthood or a '1' if it survived. We did not separate our survivorship analysis by sex, as it is not feasible to determine the sex of the nymphs.

We tested for population origin, host plant (diet) and sex effects, and their interactions on growth rate (developmental time) and all morphological traits individually using generalized linear mixed models (GLMMs). All three independent variables were treated as fixed factors, and family was included as a random factor and nested within origin. In the case of the Texas population, each cup per treatment represented each family; for the Florida population, two cups in each treatment represented each family. All the models included family to account for genetic and shared-environment contribution to overall trait variation.

We next tested for sex, population origin, diet and their interaction effects on the investment in beak relative to body size. For this purpose, we performed a GLMM with body size as a covariate, again,

including family as a random factor and nested within origin. This test allows detecting differences in elevations [*intercept*] of linear regressions accounting for body size. First, we tested for slope [*b*] interactions between main factors (Analysis of covariance—slope homogeneity test), using the \log_{10} - \log_{10} Ordinary Least Squares (OLS) regression method to compare slopes (Voje et al., 2014; Warton et al., 2006). We found no significant main factor interactions (see Table S1); thus, we proceeded with the GLMM.

3 | RESULTS

3.1 | Life history

In total, we obtained 509 adult *Narnia femorata* out of the initial 760 nymphs. We found no effect of population origin (Logistic regression; Wald $\chi^2 = 1.04$, $df = 1$, $p = .300$) on survivorship from 2nd instar to adulthood (Figure 2a). There was a nonsignificant trend towards lower survivorship when raised on the fruit from Texas (Wald $\chi^2 = 1.615$, $df = 1$, $p = .110$), with no significant interaction between population origin and their diet (Wald $\chi^2 = 0.17$, $df = 1$, $p = .865$).

Overall, we found no differences in development rates between the sexes (GLMM, sex: $F_{1,492} = 1.060$, $p = .305$; Figure 2b). However, developmental time was slower for both males and females that developed on Texas fruit when compared to those that were raised on Florida fruit (GLMM, host: $F_{1,492} = 161.4$, $p < .0001$). Furthermore,

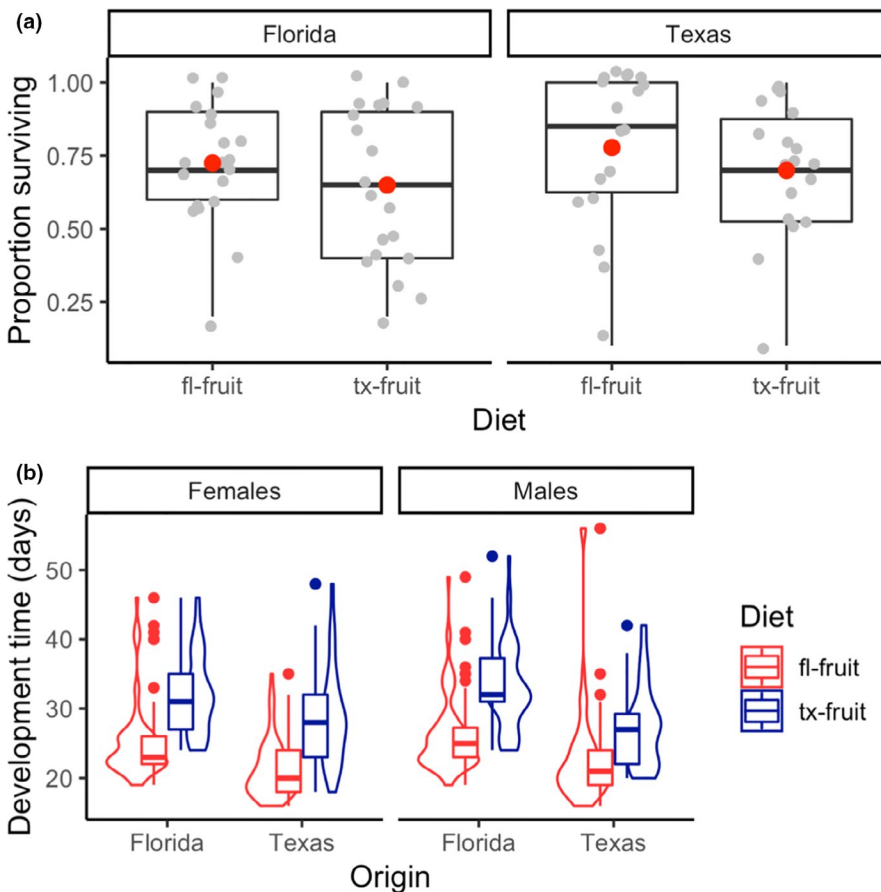


FIGURE 2 (a) Box plots and raw data (proportion per cup—grey dots) of survivorship to adulthood of *Narnia femorata* bugs from Florida and Texas populations on *Opuntia mesacantha* (Florida host, fl-fruit) and *O. engelmannii* var. *lindheimeri* (Texas host, tx-fruit). Red dots represent treatment means. Survivorship did not differ significantly across populations (origin) or diet treatments. (b) Violin plots and box plots of days to adulthood from start of 2nd instar of *N. femorata* on both hosts, separated by sex and population origin. Texas nymphs developed faster than Florida nymphs (GLMM, $p = .001$), and nymphs developed faster when they were raised in Florida fruit ($p < .0001$). There were no overall differences between the sexes ($p = .30$), and no significant factor interactions

Florida insects took longer to develop on both diets than Texas insects (GLMM, origin: $F_{1,23} = 15.3$, $p = .001$), with no origin-by-diet interaction ($F_{1,492} = 0.090$, $p = .764$).

3.2 | Morphology

Both males and females reared on the Texas fruit became smaller adults than those reared on the Florida fruit (Table 1, Figure 3a). Front femur length (Figure 3b) exhibited a similar pattern of expression as body size, larger when insects developed on Florida fruit (Table 1, Figure 3b). However, unlike body size, front femurs were longer on individuals that originated from the Texas population when compared to those from Florida.

Beak length was the only trait that was larger, in both absolute terms (Table 1, Figure 3c) and relative to body size (Table 2; Figure 3d and Figure S3) for adults raised on the Texas fruit; thus, for any given body size, beaks grew longer when insects developed on Texas fruit. Beak length was also proportionately longer for insects of Texas origin and females (Table 2). No main factor interactions were statistically significant except for sex-by-diet ($F_{1,471} = 4.75$, $p = .030$), as the impact of diet on beak length was of greater magnitude in females than males (Figure 3d and Figure S3).

4 | DISCUSSION

Regardless of population origin, *Narnia femorata* grew longer beaks when they completed development on the larger Texas fruit with thicker walls, and shorter beaks when they completed development on the small Florida fruit with thinner walls (Figure 3c–d). Thus, we found notable convergence in mouthpart morphology based on the fruit experienced during development. The responses were not due to simple changes in body size. For example, insects raised on Texas fruit grew longer mouthparts even as they emerged smaller in all other measured characteristics. The patterns suggest that mouthparts may be grown to maximize feeding efficiency.

Our findings suggest that individuals can grow mouthparts suited for specific foods not routinely encountered. *Narnia femorata*

has been documented feeding on at least 13 species of cacti across its extensive range (Vessels et al., 2013). Encountering diverse cacti with thicker and thinner fruit walls may not have been uncommon in the evolutionary history of these populations, though their exposure to different cactus species appears limited based on extensive field observations (unpublished data). It is also possible that the ability to respond to novel foods is rooted in a more routine factor, such as cactus phenology. We have observed that wild populations of *N. femorata* feeding just on a single cactus species show fluctuations in mouthpart length that are consistent with the seasonal ripening of cactus fruit. Early-season unripe cactus fruit has a much thicker fruit wall than ripe cactus fruit, and beak length tracks this change in food accessibility (Cirino & Miller, 2017). The phenotypic plasticity of mouthparts documented in this study is suggestive of developmental selection plasticity. This form of plasticity is thought to be especially expensive because an organism has to repeatedly sample its environment during development (Snell-Rood et al., 2018). Thus, this type of plasticity that is unlikely to be maintained unless it is routinely needed. We need additional studies to examine how organismal responses to environmental challenges are affected by the geographic mosaic of biodiverse interactions and simple seasonal changes in food structure.

Should longer mouthparts always be better? Here, we saw that insects from the Texas population grew shorter beaks when raised on Florida fruit with pulp and seeds closer to the surface. These results suggest a developmental, physiological or another cost of the longer beaks. We have observed that insects startled during feeding require time to pull out and pack away their feeding machinery. Selection via predation pressure may act to reduce beak length when extra length is not needed. Further, we have witnessed insects getting mouthparts stuck while feeding, which perhaps is more likely with longer mouthparts. Finally, the cost of building and maintaining effective mouthparts may be greater with longer length. It is interesting in this study that our populations revealed not just increases, but also decreases in mouthpart length in response to feeding challenges.

The responses of *Narnia femorata* to novel cactus fruit is somewhat reminiscent of the response of soapberry bugs (Hemiptera: Rhopalidae) to introduced plants, but with some striking differences.

TABLE 1 Three separate generalized linear mixed models (GLMMs) evaluating the effects of sex, population origin and diet (host plant) on the three morphological traits: body size (pronotum width), beak length and front femur length on *Narnia femorata* adults from Texas and Florida (Figure 2). Family was included in all models as a random effect nested within origin but are otherwise not reported. Probabilities under 0.05 are highlighted in bold

Factor	Body size		Beak length		Front femur length	
	F	p	F	p	F	p
Origin ($df=1,23$)	1.574	.222	59.0	<.0001	30.6	<.0001
Sex	88.8	<.0001	274.6	<.0001	3.5	.063
Diet	141.4	<.0001	11.9	.0006	64.9	<.0001
O*Sx	3.37	.067	0.87	.350	0.94	.330
O*D	0.150	.700	0.00	.970	0.09	.760
Sx*D	0.310	.580	0.69	.410	1.75	.190
O*Sx*D	1.272	.260	0.03	.870	0.885	.350
$df = 1, 472$						

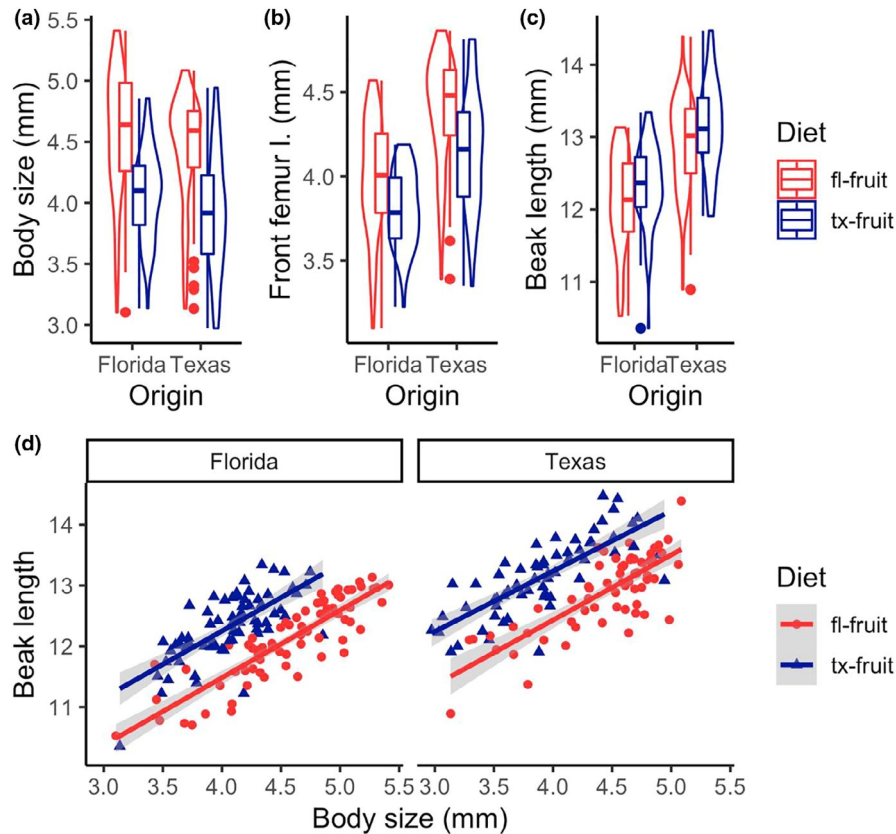


FIGURE 3 (a). Insects developed larger body sizes (box plots and violin plots—raw data) when raised on Florida fruit (Table 1). (b). Front femurs (box plots and violin plots) were longer on bugs raised on Florida fruit and longer on bugs from the Texas population. (c) Beaks (box plots and violin plots) were longer when insects were raised on Texas fruit, and insects originating from Texas had the longest beaks. (d) Beak length was longer (higher elevation/intercept) for any given body size, when bugs were raised on Texas fruit (Table 2). Only female are data shown here for brevity; males exhibited similar patterns (Figure S3). Regression lines (95% confidence intervals) represent the allometry (scaling relationship) of beak length versus body size. Equations for static allometry between beak length and body size [\log_{10} - \log_{10}]: Florida bugs/tx-fruit, $y = 0.86 + 0.37x$, $R^2 = 0.52$, Florida bugs/fl fruit, $y = 0.82 + 0.40x$, $R^2 = 0.75$, Texas bugs/tx-fruit $y = 0.94 + 0.29x$, $R^2 = 0.60$, Texas bugs/fl fruit $y = 0.88 + 0.35x$, $R^2 = 0.62$

Soapberry bugs, like *N. femorata*, feed with straw-like mouthparts on developing seeds and nearby tissues. Carroll et al. (1997, 2005) have demonstrated that soapberry bugs are capable of rapid evolutionary (genetic) changes in beak length in response to differences in fruit structure. These insects have provided powerful examples of how host switching can lead to morphological adaptation and genetic divergence across populations, but the soapberry bug work is not a story of developmental plasticity. The difference in responses between *N. femorata* and soapberry bugs is likely due to their ecological context and life histories. In particular, soapberry bug juveniles and adults feed differently. All ages of soapberry bugs feed on mature seeds located in full-size fruit. However, juveniles are small enough to climb into the core of fallen fruits to feed directly on seeds, thereby avoiding having to reach through the fruit wall (S.P. Carroll, *personal communication*). In contrast to soapberry bug feeding, both juveniles and adults of *N. femorata* must reach through the cactus fruit wall to reach the core (Figure 1a and Figure S1a), a process that may facilitate the evolution of developmental plasticity.

Here, we have shown that insects from distant populations exhibit immediate developmental responses to novel food challenges

TABLE 2 GLMM testing for the effects sex, population origin, diet (host plant) and their interactions on beak length on *Narnia femorata* adults from Texas and Florida (Figure 3d and Figure S3); using body size as a covariate and family as a random factor but are otherwise not reported. Statistically significant effects are highlighted in bold

Factor	F	p
Body size (PW)	1,051.57	<.0001
Origin (df = 1,23)	181.98	<.0001
Sex	329.20	<.0001
Diet	392.62	<.0001
Sex*Origin	0.97	.326
Origin*Diet	0.25	.616
Sex*Diet	4.75	.030
df = 1,471		

in the directions that we predicted. Those developing on the larger fruit with thicker walls grow longer beaks, while those developing on the smaller fruit with shallower pulp grew shorter beaks. These

findings indicate that some native fauna may be able to respond more rapidly than predicted to the introductions of novel plants (van Kleunen et al., 2015). They also suggest a mechanism by which insect pests may be able to quickly tolerate new foods (Via, 1990) until they evolve the ability to thrive upon them (Rauscher, 1982).

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

PEA and CWM conceived the research idea. PEA and QC conducted the research. PEA and CWM analysed the data. PEA wrote the first draft of the manuscript. QC and CWM contributed to the editing of multiple manuscript versions and approved the final version for submission.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.13766>.

DATA AVAILABILITY STATEMENT

The dataset supporting this article has been uploaded to Dryad Digital Repository (<https://doi.org/10.5061/dryad.rn8pk0p8s>).

ORCID

Pablo E. Allen  <https://orcid.org/0000-0001-9126-7111>

REFERENCES

- Allen, P. E., Dale, A. G., Diyaljee, S. I., Ector, N. J., Petit-Bois, D., Quinn, J. T., Ranieri, A. C., Sanchez, J. A., Smith, H. M., Tran, D. X., Winsor, A. M., & Miller, C. W. (2018). One and done: long-term sperm storage in the cactus-feeding bug, *Narnia femorata* (Hemiptera: Coreidae). *Annals of the Entomological Society of America*, *111*, 271–277. <https://doi.org/10.1093/aesa/say017>
- Allen, P. E., & Miller, C. W. (2017). Novel host plant leads to the loss of sexual dimorphism in a sexually selected male weapon. *Proceedings of the Royal Society B: Biological Sciences*, *284*, 20171269.
- Allen, P. E., & Miller, C. W. (2020). The hidden cost of group living for aggregating juveniles in a sexually dimorphic species. *Biological Journal of the Linnean Society*, *131*, 39–49. <https://doi.org/10.1093/biolinnean/blaa090>
- Anderson, P. S., Renaud, S., & Rayfield, E. J. (2014). Adaptive plasticity in the mouse mandible. *BMC Evolutionary Biology*, *14*, 85. <https://doi.org/10.1186/1471-2148-14-85>
- Bernays, E. A. (1986). Diet-induced head allometry among foliage-chewing insects and its importance for graminivores. *Science*, *231*, 495–497. <https://doi.org/10.1126/science.231.4737.495>
- Bezemer, T. M., Harvey, J. A., & Cronin, J. T. (2014). Response of native insect communities to invasive plants. *Annual Review of Entomology*, *59*, 119–141. <https://doi.org/10.1146/annurev-ento-011613-162104>
- Burghardt, K. T., & Tallamy, D. W. (2015). Not all non-natives are equally unequal: Reductions in herbivore β -diversity depend on phylogenetic similarity to native plant community. *Ecology Letters*, *18*, 1087–1098. <https://doi.org/10.1111/ele.12492>
- Carroll, S. P., Dingle, H., & Klassen, S. (1997). Genetic differentiation of fitness-associated traits among rapidly evolving populations of the soapberry bug. *Evolution*, *51*, 1182–1188. <https://doi.org/10.1111/j.1558-5646.1997.tb03966.x>
- Carroll, S. P., Loye, J. E., Dingle, H., Mathieson, M., Famula, T. R., & Zalucki, M. P. (2005). And the beak shall inherit - evolution in response to invasion. *Ecology Letters*, *8*, 944–951. <https://doi.org/10.1111/j.1461-0248.2005.00800.x>
- Cirino, L. A., & Miller, C. W. (2017). Seasonal effects on the population, morphology and reproductive behavior of *Narnia femorata* (Hemiptera: Coreidae). *Insects*, *8*, 13.
- Forbes, A. A., Devine, S. N., Hippee, A. C., Tvedte, E. S., Ward, A. K., Widmayer, H. A., & Wilson, C. J. (2017). Revisiting the particular role of host shifts in initiating insect speciation. *Evolution*, *71*, 1126–1137. <https://doi.org/10.1111/evo.13164>
- Forister, M. L., Nice, C. C., Fordyce, J. A., & Gompert, Z. (2009). Host range evolution is not driven by the optimization of larval performance: The case of *Lycaeides melissa* (Lepidoptera: Lycaenidae) and the colonization of alfalfa. *Oecologia*, *160*, 551–561. <https://doi.org/10.1007/s00442-009-1310-4>
- Fukano, Y., Thomas, C. E., Takata, M., Koyama, S., & Satoh, T. (2016). Contemporary evolution of host plant range expansion in an introduced herbivorous beetle *Ophraella communa*. *Journal of Evolutionary Biology*, *29*, 757–765.
- García-Robledo, C., & Horvitz, C. C. (2012). Jack of all trades masters novel host plants: Positive genetic correlations in specialist and generalist insect herbivores expanding their diets to novel hosts. *Journal of Evolutionary Biology*, *25*, 38–53. <https://doi.org/10.1111/j.1420-9101.2011.02401.x>
- Gil, D., Bulmer, E., Celis, P., & López-Rull, I. (2008). Adaptive developmental plasticity in growing nestlings: Sibling competition induces differential gape growth. *Proceedings of the Royal Society B: Biological Sciences*, *275*, 549–554. <https://doi.org/10.1098/rspb.2007.1360>
- Graves, S. D., & Shapiro, A. M. (2003). Exotics as host plants of the California butterfly fauna. *Biological Conservation*, *110*, 413–433. [https://doi.org/10.1016/S0006-3207\(02\)00233-1](https://doi.org/10.1016/S0006-3207(02)00233-1)
- Hughes, J., & Vogler, A. P. (2004). Ecomorphological adaptation of acorn weevils to their oviposition site. *Evolution*, *58*, 1971–1983. <https://doi.org/10.1111/j.0014-3820.2004.tb00483.x>
- Kawecki, T. J., & Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, *7*, 1225–1241. <https://doi.org/10.1111/j.1461-0248.2004.00684.x>
- Mainwaring, M. C., Dickens, M., & Hartley, I. R. (2010). Environmental and not maternal effects determine variation in offspring phenotypes in a passerine bird. *Journal of Evolutionary Biology*, *23*, 1302–1311. <https://doi.org/10.1111/j.1420-9101.2010.01997.x>
- Mainwaring, M. C., Dickens, M., & Hartley, I. R. (2012). Sexual dimorphism and offspring growth: Smaller female Blue Tit nestlings develop relatively larger gapes. *Journal of Ornithology*, *153*, 1011–1016. <https://doi.org/10.1007/s10336-012-0828-0>

- Miller, C. W., McDonald, G. C., & Moore, A. J. (2016). The tale of the shrinking weapon: Seasonal changes in nutrition affect weapon size and sexual dimorphism, but not contemporary evolution. *Journal of Evolutionary Biology*, *29*, 2266–2275. <https://doi.org/10.1111/jeb.12954>
- Parker, J. D., Burkepile, D. E., & Hay, M. E. (2006). Opposing effects of native and exotic herbivores on plant invasions. *Science*, *311*, 1459–1461. <https://doi.org/10.1126/science.1121407>
- Pfennig, D. (1992). Proximate and functional causes of polyphenism in an anuran tadpole. *Functional Ecology*, *6*, 167–174. <https://doi.org/10.2307/2389751>
- R Core Team (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rausher, M. D. (1982). Population differentiation in *Euphydryas editha* butterflies: Larval adaptation to different hosts. *Evolution*, *36*, 581–590.
- Relyea, R. A., & Auld, J. R. (2005). Predator- and competitor-induced plasticity: How changes in foraging morphology affect phenotypic trade-offs. *Ecology*, *86*, 1723–1729. <https://doi.org/10.1890/04-1920>
- Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, *9*, 671–675. <https://doi.org/10.1038/nmeth.2089>
- Seebens, H., Blackburn, T. M., Dyer, E. E., Genovesi, P., Hulme, P. E., Jeschke, J. M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., Bacher, S., Blasius, B., Brundu, G., Capinha, C., Celesti-Grappow, L., Dawson, W., Dullinger, S., Fuentes, N., Jäger, H., ... Essl, F. (2017). No saturation in the accumulation of alien species worldwide. *Nature Communications*, *8*, 14435.
- Snell-Rood, E. C., Kobiela, M. E., Sikkink, K. L., & Shepard, A. M. (2018). Mechanisms of plastic rescue in novel environments. *Annual Review of Ecology, Evolution, and Systematics*, *49*, 331–354. <https://doi.org/10.1146/annurev-ecolsys-110617-062622>
- Stoler, A. B., & Relyea, R. A. (2013). Leaf litter quality induces morphological and developmental changes in larval amphibians. *Ecology*, *94*, 1594–1603. <https://doi.org/10.1890/12-2087.1>
- Svensson, E. I., Goedert, D., Gómez-Llano, M. A., Spagopoulou, F., Nava-Bolaños, A., & Booksmythe, I. (2018). Sex differences in local adaptation: What can we learn from reciprocal transplant experiments? *Philosophical Transactions of the Royal Society B*, *373*, 20170420. <https://doi.org/10.1098/rstb.2017.0420>
- Thompson, D. B. (1992). Consumption rates and the evolution of diet-induced plasticity in the head morphology of *Melanoplus femurrubrum* (Orthoptera: Acrididae). *Oecologia*, *89*, 204–213. <https://doi.org/10.1007/BF00317219>
- Thompson, D. B. (1999). Genotype-environment interaction and the ontogeny of diet-induced phenotypic plasticity in size and shape of *Melanoplus femurrubrum* (Orthoptera: Acrididae). *Journal of Evolutionary Biology*, *12*, 38–48. <https://doi.org/10.1046/j.1420-9101.1999.00005.x>
- van Kleunen, M., Dawson, W., Essl, F., Pergl, J., Winter, M., Weber, E., Krefl, H., Weigelt, P., Kartesz, J., Nishino, M., Antonova, L. A., Barcelona, J. F., Cabezas, F. J., Cárdenas, D., Cárdenas-Toro, J., Castaño, N., Chacón, E., Chatelain, C., Ebel, A. L., ... Pyšek, P. (2015). Global exchange and accumulation of non-native plants. *Nature*, *525*, 100–103. <https://doi.org/10.1038/nature14910>
- Vessels, A. H. K., Bundy, C. S., & McPherson, J. E. (2013). Life history and laboratory rearing of *Narnia femorata* (Hemiptera: Heteroptera: Coreidae) with descriptions of immature stages. *Annals of the Entomological Society of America*, *106*, 575–585.
- Via, S. (1984). The quantitative genetics of polyphagy in an insect herbivore. I. Genotype-environment interaction in larval performance on different host plant species. *Evolution*, *38*, 881–895.
- Via, S. (1990). Ecological genetics and host adaptation in herbivorous insects: The experimental study of evolution in natural and agricultural systems. *Annual Review of Entomology*, *35*, 421–446. <https://doi.org/10.1146/annurev.en.35.010190.002225>
- Voje, K. L., Hansen, T. F., Egset, C. K., Bolstad, G. H., & Pélabon, C. (2014). Allometric constraints and the evolution of allometry. *Evolution*, *68*, 866–885. <https://doi.org/10.1111/evo.12312>
- Warton, D. I., Wright, I. J., Falster, D. S., & Westoby, M. (2006). Bivariate line-fitting methods for allometry. *Biological Review of the Cambridge Philosophical Society*, *81*, 259–291. <https://doi.org/10.1017/S1464793106007007>
- Watanabe, J. T., & Young, C. M. (2006). Feeding habits and phenotypic changes in proboscis length in the southern oyster drill, *Stramonita haemastoma* (Gastropoda: Muricidae), on Florida sabellariid worm reefs. *Marine Biology*, *148*, 1021–1029. <https://doi.org/10.1007/s00227-005-0152-9>
- Wund, M. A., Valena, S., Wood, S., & Baker, J. A. (2012). Ancestral plasticity and allometry in threespine stickleback reveal phenotypes associated with derived, freshwater ecotypes. *Biological Journal of the Linnean Society*, *105*, 573–583. <https://doi.org/10.1111/j.1095-8312.2011.01815.x>

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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