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Dietary Parental Effects in a Generalist Heribivore

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Dietary Parental Effects in a Generalist Heribivore

Abstract

The environment or experiences of a parent generation can impact the fitness of the next generation, a phenomenon known as parental effects. The parental diet, for example, can have consequences for their offspring who may perform better or worse on the same diet. Dietary specialists are often the focus of studies of parental effects due to diet because a narrow diet breadth suggests that the offspring environment may be predictable. Dietary generalists, in contrast, are less often studied regarding parental effects and this may be because their wide diet breadth makes the future environment less predictable.

We investigated whether parental effects exist in a generalist herbivore, fall webworm (*Hyphantria cunea*, hereafter FW), by testing if larval development and adult fitness depended on the host plant on which the parental generation was reared. While FW is a dietary generalist as a species, this generalism only manifests at a population level; individual larvae are functionally monophagous since they complete their development on the plant on which their mother lays her eggs. Female FW moths do not disperse far after eclosion, so oviposition likely occurs on the same host plant on which the mother developed as a larva. Therefore, FW is an ideal study system to test for parental effects in a dietary generalist. We found that FW parents reared on a low-quality diet can negatively impact offspring fitness, but that FW larval diet is more important than FW parental diet. However, we did not find any evidence that FW parents reared on a specific host plant “primed” their offspring to do well on the parent’s host plant. We provide insight into the parental effects of diet in FW and the potential implications for reduced lifetime fitness when a low-quality host plant is selected as an oviposition site.

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Abstract

The environment or experiences of a parent generation can impact the performance of the next generation, a phenomenon known as parental effects. Most studies of parental effects in insects focus on specialists, and much less is known about whether parental effects are important in generalists. We investigated whether parental effects exist in a generalist herbivore, fall webworm (*Hyphantria cunea*, hereafter FW), by testing if offspring performance depended on the host plant on which the parental generation was reared. We found that FW reared on a low-quality diet can negatively impact offspring performance and that FW reared on a high-quality diet produce offspring with higher survival, shorter development time, and higher pupal mass. However, we did not find any evidence that FW reared on a specific host plant "primed" their offspring to do well on that host plant, as other parental effects literature has found for specialist herbivores. This study provides insight into the transgenerational effects of diet in FW and the potential implications for reduced lifetime performance when a low-quality host plant is selected as an oviposition site.

Introduction

Parental effects describe the phenomenon of when the environment of a parental generation impacts the performance of the following generation. Diet and levels of stress, for example, can have negative consequences for an individual, but a parental effect is when there is a transgenerational response to these stimuli that manifests in their offspring (Mousseau and Fox 1998). Plants and vertebrates have long been subjects of studies of parental effects, and only in recent decades have invertebrates, especially insects, become popular model systems (Woestmann and Saastamoinen 2016).

Parental effects can manifest in two different ways. First, if the parental environment provides a reliable cue about the environment offspring will encounter, then some insects have evolved adaptations such that the mother can provision her offspring differently if they will experience the same environment (Fox and Mousseau 1998). For example, if a mother experiences a stressful environment, such as a low-quality host plant, she may be able to provision her eggs such that she lays fewer eggs with more resources so that her offspring can better succeed on that same low quality host plant. In Lepidoptera, it has been found that mothers can sometimes adjust resource allocation to their offspring; Hunter (2002) found that a female gypsy moth can provision eggs with nutrients from her own diet, which has the potential to prepare her offspring for a stressful diet (Hunter 2002). Dietary specialists are often the focus of studies of these kinds of parental effects due to diet because a narrow diet breadth suggests that the offspring environment may be predictable. Dietary generalists, in contrast, are less often studied regarding parental effects and this may be because their large diet breadth makes it impossible to predict the future environment. However, some dietary generalists may be generalists at a population level, but individuals feed only on a single host plant (e.g., crop pests may be generalists, but feed for consecutive generations on a single crop host). Second, it is possible that what a parental generation eats may not benefit offspring performance; feeding on a low-quality host plant may inhibit females from provisioning their offspring with beneficial resources and then the parental effect manifests in that all offspring exhibit reduced performance from having a parent reared in a stressful environment. For example, increased leaf age eaten by parental winter moths can hinder the development time of the offspring (Asch et al. 2010). Host plant quality can influence larval development, pupal mass, and adult fitness (Zielonka et al.

2021), but how these measures are affected by transgenerational effects in a dietary generalist is not well studied.

Fall webworm (*Hyphantria cunea*, hereafter FW) is an extreme dietary generalist species of moth, feeding on over 400 plant species worldwide (Schowalter and Ring 2017). While FW is a dietary generalist as a species, this generalism only manifests at a population level; individual larvae are functionally monophagous as they are isolated on the plant on which their mother lays her eggs. Dietary generalists typically eat several plants from different taxa within their lifetime, but FW offspring develop on one host plant for the duration of their lives. However, little is known about whether the diet of the parental generation can impact the performance of the following generation (Morris 1967). It is unclear if a parental generation reared in a stressful environment (e.g., larvae reared on a low-quality diet) will affect the performance of the next generation. Female FW moths do not disperse far, so when they emerge from their pupae, they likely often oviposit on the same host plant on which they developed as larvae; FW therefore are an ideal study system to test for parental effects in a dietary generalist.

We designed a factorial experiment to test if dietary parental effects are found in FW. For our study, we used four plants, two of which are high quality (choke cherry and black willow) and two which are low quality (thinleaf alder and narrowleaf cottonwood). The quality of these plants was defined based on previous FW studies in which FW performed better on the higher quality than lower quality host plants (Murphy and Loewy 2015). We reared FW on each of these host plants to form a parental generation and then reared their offspring on both the parental host as well as the other three host plants, allowing us to test if FW parental or larval host is most important in understanding offspring performance. If FW parents experiencing a stressful environment are able to provision their offspring to succeed in that same stressful environment, then we predicted that the offspring of parents reared in a stressful environment would exhibit greater performance in that same stressful environment than offspring whose parents were reared in a favorable environment. For example, offspring of parents reared on a low-quality host plant (e.g., thinleaf alder or narrowleaf cottonwood) should have greater performance on that same low-quality host plant than offspring of parents reared on other host plants. However, if a stressful environment lessens a mother's ability to provision her eggs with resources, then we predicted that the offspring of parents reared in a stressful environment would perform poorly in all other environments compared to offspring of parents reared in a favorable environment.

Methods

Study system

Fall webworm (*Hyphantria cunea*, hereafter FW) is a species of moth widely found in North America and some regions of Europe and Asia (Gomi and Takeda 1996, Yang et al. 2006). As a polyphagous insect, FW larvae eat a variety of plants at the population level, but individuals are functionally monophagous feeding on a single host plant throughout their larval development (Murphy and Loewy 2015). FW larvae vary considerably in performance on their different host plants, which has been documented by over a decade's worth of data (Murphy and Loewy 2015, Vidal and Murphy 2018, Vyas and Murphy 2022, unpublished data). Thus, the host plant on which a FW mother lays her eggs can have repercussions for the survival and performance of her offspring; however, whether there are long-lasting offspring performance consequences for the offspring and future generations is unknown.

For our study, we used two plant species that have been considered high-quality host plants for FW in Colorado, black willow (*Salix nigra*) and choke cherry (*Prunus virginiana*), as well as two plant species that have been considered low-quality host plants for FW in Colorado, thinleaf alder (*Alnus tenuifolia*) and narrowleaf cottonwood (*Populus augustifolia*) (Murphy and Loewy 2015, Murphy unpublished data). In 2020, we collected hundreds of FW larvae from field sites along the front range of Colorado; these larvae were collected from a variety of host plants, including the four plants used in our experiment. These larvae completed their development in the lab, overwintered as pupae, and eclosed as moths in spring 2021; the offspring of these moths formed the parental generation for our study (Figure 1). All larvae in our experiments were reared on one host plant species for the entire duration of their development until pupation, as larvae would do in the wild.

Experimental Design

During the summer of 2021, we reared larvae on one of the 4 host plant species introduced above: cherry, willow, alder, or cottonwood. These larvae pupated in fall 2021 and eclosed as moths in spring 2022. We mated these moths across matrilines (following methods outlined in Robinson-Castillo et al. 2021) and ensured that for each mating, unrelated males and females were from the same host plant treatment (i.e., a female moth from a chokecherry matriline would be mated to a male moth from a different chokecherry matriline). We aimed to have 9 matrilines for each host plant treatment (9 matrilines x 4 host plants = 36 matrilines); however, choke cherry and narrowleaf cottonwood each had an extra matriline that was created and kept (n=10 matrilines). The larvae produced from these matings were used for our experiments (F1 generation; Figure 1). Approximately 14 days after the eggs were laid, when head capsules were visible, we divided each egg mass into four groups and placed each group in a 0.5L deli container provisioned with a leaf from one of the four host plants. Thus, we had a total of 38 matrilines, each divided into 4 sub-groups with each sub-group feeding on one of the 4 host plants (n = total of 152 egg sub-groups).

We reared larvae using methods from Loewy et al. (2013) and Robinson-Castillo et al. (2021). Briefly, we reared larvae on their assigned host plant until they pupated or died. At least twice a week, we removed old leaves and frass from the larval containers and added fresh leaves. We reared larvae with their sub-group until they were about 2 weeks old, as mortality is increased if they are manipulated or divided before this age; we then haphazardly selected 15 individuals from each sub-group to continue rearing for performance measurements. While we aimed for 15 larvae in each treatment group, some groups had fewer larvae due to death or small clutch size (Appendix 1). Our total sample size was 2,144 larvae across all maternal lines and treatments (Appendix 1). We sexed the pupae and weighed them 30 days (±2 days) after pupation (to the nearest 0.01 mg; Mettler-Toledo XP6, Columbus, Ohio).

We recorded three larval performance measures: survival, development time, and pupal mass. We measured proportion survival as those individuals who survived to pupate out of the total number of individuals in that treatment sub-group; survival is a critical measure of fitness as an individual cannot reproduce and pass on its genes if it dies before it reaches reproductive maturity. Development time, measured as the number of days from hatch to pupation, is important for larvae in the field because those that develop more quickly may escape natural enemies and reach reproductive maturity more quickly (Price et al., 2011). Pupal mass is a predictor of lifetime fitness in most Lepidoptera including fall webworm (Loewy et al. 2013). Higher pupal mass in females is correlated with higher fecundity later in life.

Statistical Analysis

We analyzed FW larval survival using a Chi-square test, with parental host species and larval host species as our fixed effects and the interaction between these fixed effects also included in our model. We included matriline as a random effect. We analyzed FW larval development time and pupal mass with two separate mixed-model ANOVAs, each of which included parental host plant, larval host plant, and sex as fixed effects and we also included the interaction between the parental host and larval host fixed effects. We included matriline as a random effect for both models. All variables met assumptions for normality and equality of variances. We performed all statistical analyses with JMP Pro 15.2.0 (SAS Institute, Cary, NC).

Results

For survival, we found a significant effect of larval host ($\chi^2_3 = 455.2$, $P < 0.0001$), parental host ($\chi^2_3 = 17.0$, $P < 0.001$), and matriline ($\chi^2_{34} = 228.6$, $P < 0.0001$) (Figure 2). Overall, parents reared on low-quality hosts decreased the survival of offspring. We did not find a significant interaction between larval host and parental host ($\chi^2_9 = 18.7$, $P = 0.028$). For development time, we found a significant effect of the interaction between larval host and parental host ($F_{9, 1016} = 8.3$, $P<0.0001$), and larval host ($F_{3, 1017.8} = 900.8$, $P<0.0001$), but no effect of sex ($F_{1, 999.6} = 0.072$, $P=0.7889$) or parental host ($F_{3, 36.7} = 2.6$, $P=0.0649$) (Figure 3). Lower-quality parental hosts overall increased larval development time. For pupal mass, we found a significant effect of the interaction between larval host and parental host ($F_{9, 1015} = 4.4$, $P<0.0001$), larval host ($F_{3, 1017} = 393.9$, $P<0.0001$), and sex ($F_{1, 997} = 126.8$, $P<0.0001$), but no effect of the parental host ($F_{3, 34.4} = 1.1$, $P= 0.3596$) (Figure 4). Higher-quality hosts resulted in greater pupal mass, but a high-quality parental host benefited offspring slightly as well.

Discussion

We found that parental effects play an important role for FW in that a parental generation reared in a stressful environment (low-quality host plant) produced offspring that performed poorly in all other environments compared to offspring of parents reared in a favorable environment (high quality host plant). Having a parent reared on a low-quality diet (e.g., thinleaf alder) had an overall negative impact on the performance of the next generation on all four of the host plants, while having a parent reared on a high-quality diet (e.g., black willow) increased the performance of all offspring regardless of diet. We did not find any support for the hypothesis that FW parents experiencing a stressful environment (low quality host plant) are able to provision their offspring to succeed in that same stressful environment. FW reared on a low-quality diet did not exhibit greater performance when their parents were also reared on that diet, but having parents reared on a high-quality diet can increase the performance of all offspring also reared on different diets.

We found that larval host, parental host, and matriline were all important in determining the survival of the F1 generation, but there was no significant interaction between the larval and parental host. Our results suggests that the larval host plant and matriline are the most important factors, but the host plant of the parent generation also can positively or negatively affect survival. We observed this especially in thinleaf alder where survival rates were overall lower for larvae on some host plants (e.g., willow, cottonwood) when their parents were reared on alder (Figure 2). However, because there was no interaction between parental and larval host plant, that means that the relative survival of larvae on any single host plant does not vary depending on which host plant the parental generation used.

In contrast to our results for survival, we found significant interactions between larval host plant and parental host plant for both other performance measures, development time and pupal mass. We found that the time of larval development was affected by the interaction between the larval and parental host as well as the larval host; however, sex and parental host on their own did not affect development time (Figure 3). Similarly, for pupal mass we also found a significant interaction between larval and parental host, as well as significant effects of larval host and sex, but parental host was not important (Figure 4). These results suggest that for these two performance measures (development time and pupal mass) larval host plant played the largest role in determining performance, but the interaction with parental host plant indicates that larval performance varies across host plants depending on the parental host. This is most striking when larvae feed upon alder as individuals feeding on alder generally had a low pupal mass compared to other host plants, but larvae whose parents had fed on cherry had an even lower pupal mass compared to larvae with parents reared on any of the three other host plants. Ultimately, the most important indicator of overall larval performance is the host on which they are reared, not the host plant of the parental generation.

While we did not observe a positive parental effect of FW mothers on stressful diets, we did observe an overall effect of parental host plant on the next generation. We found support for our second hypothesis for which we predicted that the offspring of parents reared in a stressful environment would perform poorly on all diets compared to offspring of parents in a favorable environment. It could be that dietary generalists have not adapted to be able to provision extra resources in stressful environments as seen in some parental effects literature for specialists because of their more unpredictable environments. Notably we found that offspring of parents reared in a favorable environment (willow) performed better than offspring from other parents in all environments, suggesting that parental provisioning depends on parents being in favorable environments where they have adequate resources. In the future, it would be helpful to test specifically for egg provisioning on different host plants by measuring clutch egg mass and size from FW females reared on a low-quality diet and how they compare to clutches of FW reared on high-quality host plants. For offspring reared on the same host plant as their parents, we see that consistent host plant environment is not necessarily advantageous in the case of a low-quality diet.

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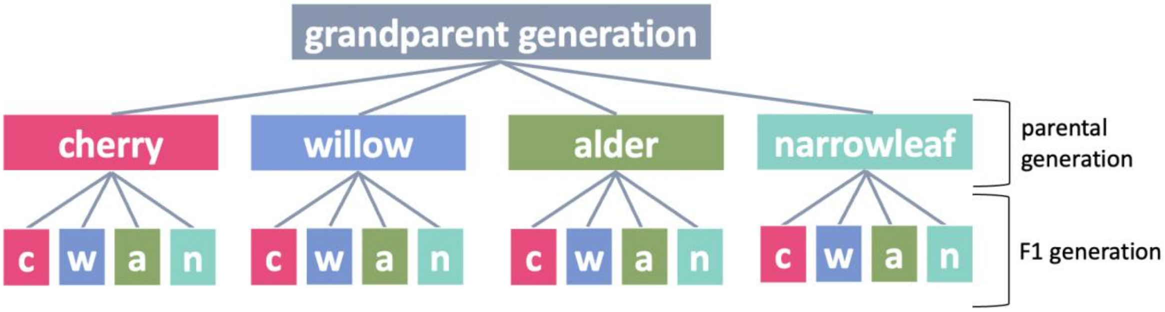

Figure 1. Experimental design of diet treatments. The grandparent generation was collected as larvae during the summer of 2020 from the field, with moths eclosing in spring 2021. The parental generation was then reared during the summer of 2021 on one of four host plants: cherry (red), willow (blue), alder (green), narrowleaf cottonwood (aqua). Moths of the parental generation eclosed in spring 2022, were mated and their offspring are the F1 generation. A total of 38 matrilines were created (Appendix 1) and these matrilines produced our F1 generation, which were reared on the same four host plants (abbreviated by first letter of the host plant, colors same as above).

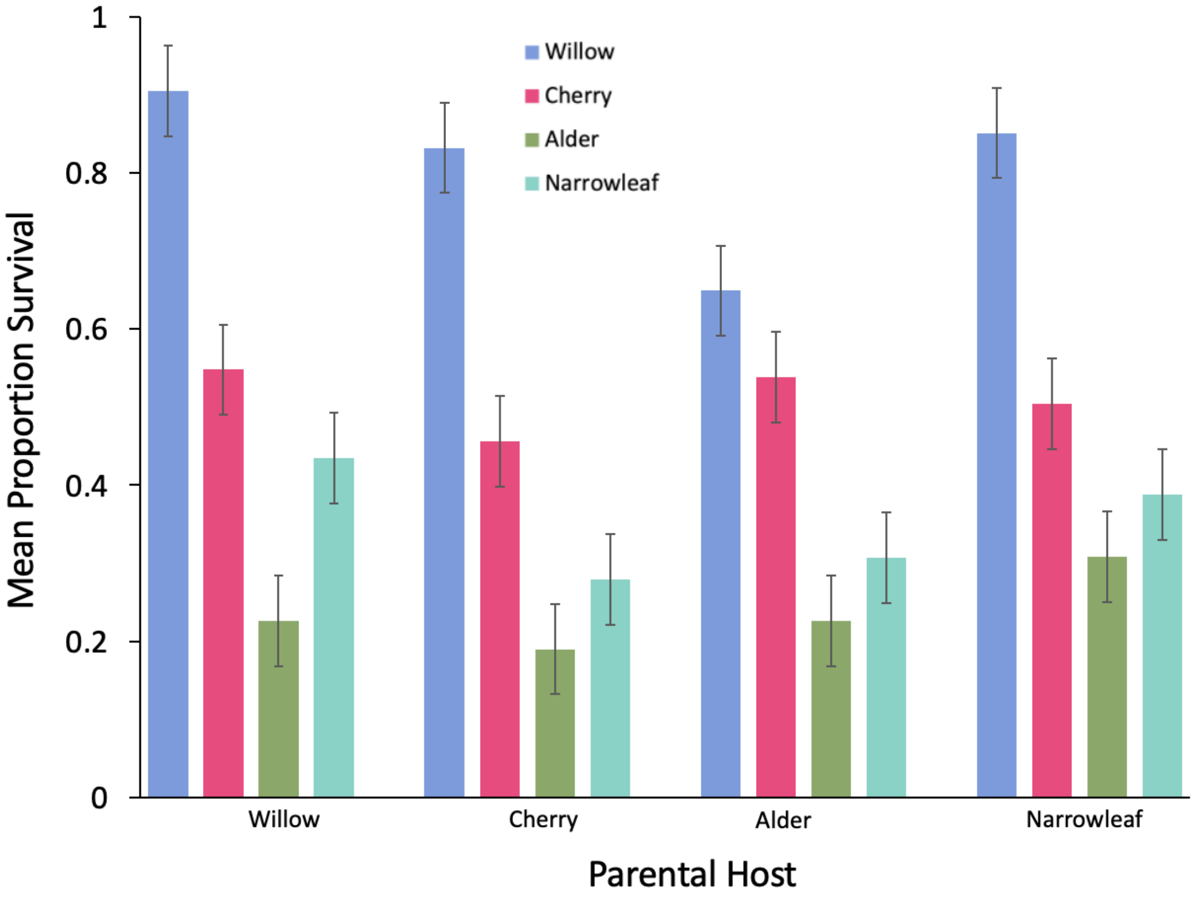

Figure 2: Mean proportion survival of larvae reared on each larval host plant treatment nested within each parental host plant treatment. Larval host plant colors are represented in the figure legend and the same as Figure 1. Means are given ± SE.

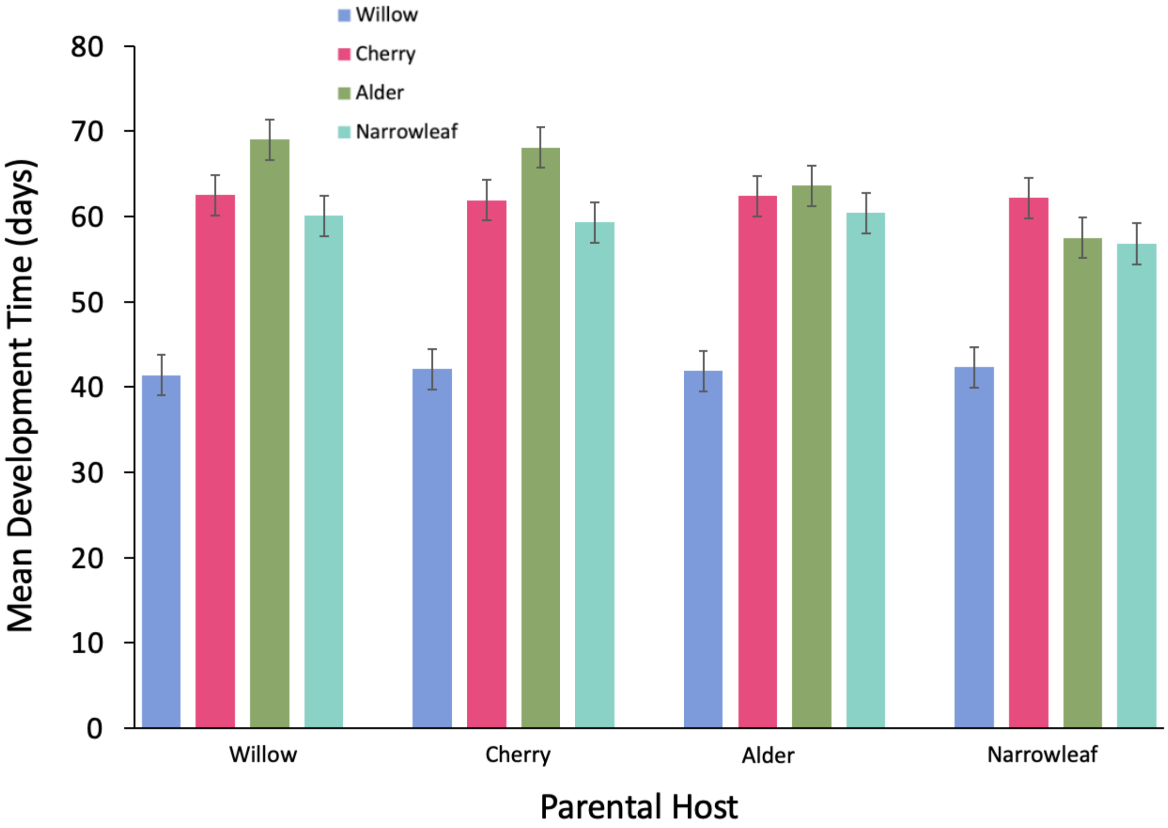

Figure 3: Mean development time of larvae reared on each larval host plant treatment nested within each parental host plant treatment. Larval host plant colors are represented in the figure legend and the same as Figure 1. Means are given ± SE.

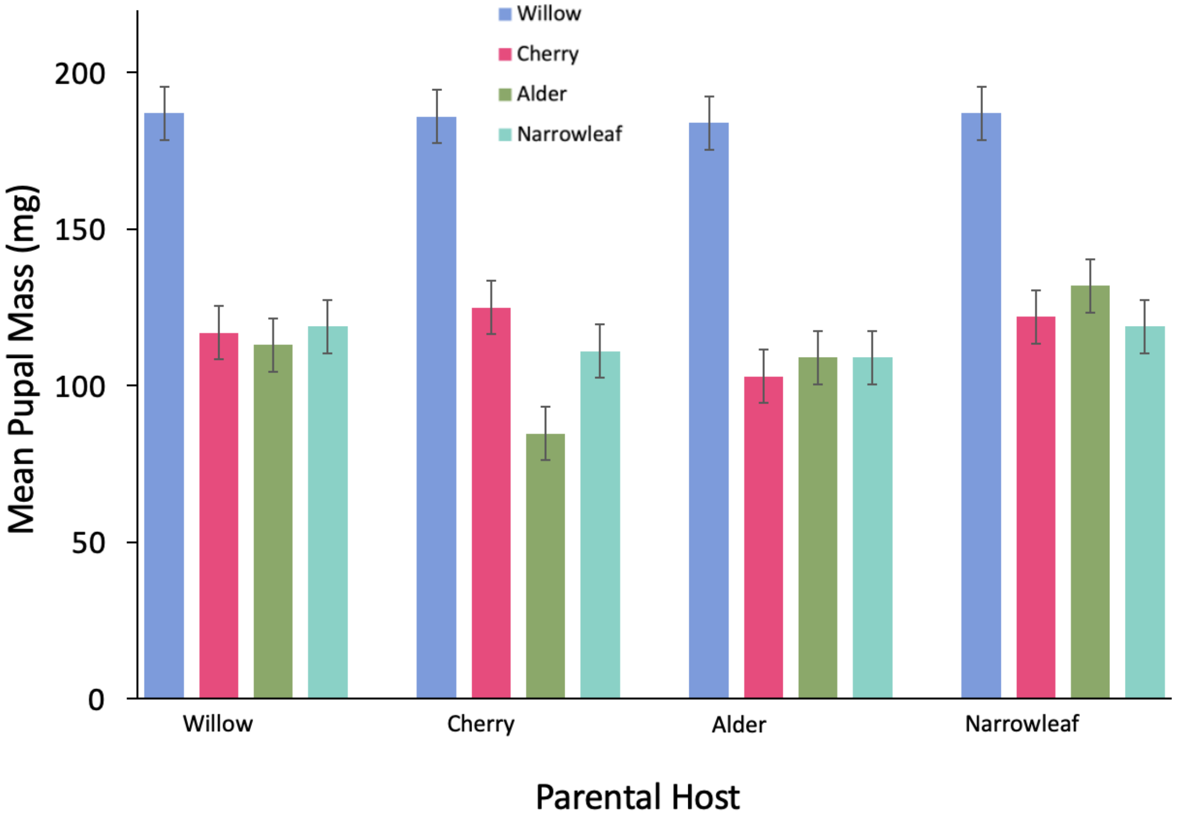

Figure 4: Mean pupal mass of larvae reared on each larval host plant treatment nested within each parental host plant treatment. Larval host plant colors are represented in the figure legend and the same as Figure 1. Means are given ± SE.

Appendix 1: Number of larvae reared in each larval host and parental host treatment.

	Parental Host (# of matrilines)				
Larval Host	Cherry (10)	Willow (9)	Alder (9)	Narrowleaf (10)	Total
Cherry	136	135	117	139	**527**
Willow	149	126	134	148	**557**
Alder	147	117	133	133	**530**
Narrowleaf	140	124	127	139	**530**
Total	**572**	**502**	**511**	**559**	**2144**