Mechanisms maintaining two feeding strategies in the moth *Symmetrischema lavernella*

Stephanie Cruz Maysonet
Charlottesville, Virginia

B.S., University of Puerto Rico in Bayamón, 2012

A Thesis presented to the Graduate Faculty
of the University of Virginia in Candidacy for the Degree of
Master of Science

Department of Environmental Sciences

University of Virginia
August 2014

Abstract

Traditional explanations for specialized host use patterns by herbivores include evolving to use high quality plant hosts, avoid natural enemies and make efficient use of the most common food resource in the environment. While several studies have combined two of these hypotheses, we are still in need of understanding how an increasing number of factors interact to determine herbivores' diets. *Symmetrischema lavernella* is a phytophagous gelechiid moth whose hosts appear to be limited to the genus *Physalis* (Solanaceae). Flower buds and fruits serve as larval substrates producing budworms and frugivores, respectively, and both strategies are used in each of the 3+ generations of the moth. However, each larva can adopt only one strategy, leading to the prediction that the most profitable strategy should persist over time. Alternatively, frugivores and budworms would coexist if selective pressures render both strategies similar in costs and benefits or show enough variation to impede fixation on the most profitable strategy. This study was aimed at explaining the occurrence of these two feeding strategies in *S. lavernella* by assessing the effects of larval substrates on growth performance and survival, and resource availability through field observations and experiments. Frugivore pupal weights were found to be 33% greater than in budworms, with females being heavier for both feeding strategies. Moreover, frugivores showed greater survival than budworms in natural patches of their host plant. Parasitoid wasps and a larger frugivore acting as a predator on *S. lavernella* were rare, suggesting natural enemies are not important agents of mortality–at least in late summer, when this study was conducted. On the other hand, lab experiments showed that the feeding strategy chosen corresponds to the size of the floral bud entered: caterpillars that enter small floral buds (<4.2mm) adopt the budworm strategy, eating plant reproductive tissue and preventing the flower from opening; caterpillars that enter larger floral buds or open flowers adopt the frugivore strategy, burrowing into the ovary and eating ovules as the fruit develops around it. Together these findings indicate greater body size and survival in frugivores favor frugivory but its benefits are limited by the availability of floral buds large enough to support frugivores. Given that each fruit supports only one frugivore, *S. lavernella* faces high intraspecific competition and thus, a high opportunity cost in avoiding small buds, favoring maintenance of the budworm and frugivore strategies.

Acknowledgements

Two years of exciting research would not have been possible without the contribution of the following people. My work at the Blandy Experimental Farm was facilitated by the Blandy staff, especially Judy Masi –who managed my purchases for instruments and supplies- and Kyle Haynes –who coordinated the use of lab space and field sites. I also received help in the field from the REU 2013 program participants, Ariela Haber, Lewis Bauer, and especially from Amber Emerson, who worked closely with me during the summer of 2013 and did part of the data collection for this project. Thanks to Sangmi Lee for identifying the study moth at the beginning of this project and Robert Kula and Michael Gates for identifying parasitoid wasps in this system.

When my work was conducted at Charlottesville, Michael Pace and Karen McGlathery were key to completion of data collection by providing access to lab space and instruments at the Environmental Sciences facilities at the University of Virginia. I am also very grateful for the lab assistance provided by Susie Maben and Meg Miller and the help received from fellow graduate students, Grace Wilkinson, Jessica Gephart, Kyle Emery and Andrew Robinson. Special thanks to Rosemary Malfi who helped me at all stages of my project, from providing advice on instruments and supplies, to helping me build cages, and discussing statistical analysis.

I am also thankful for the financial support received from the Department of Environmental Sciences and Graduate School of Arts and Sciences at the University of Virginia, the Blandy Experimental Farm and the Foundation of the State Arboretum.

Certainly, my research was also advanced by the helpful contributions of my thesis research committee: T'ai H. Roulston, David E. Carr and Todd M. Scanlon. Thanks to Dave for his advice on statistics. And special thanks to my advisor, T'ai, for giving me the opportunity to pursue one of my educational goals, for all the time he dedicated to my project, his assistance in data collection, his advice on every step of the project, and his encouragement. I am very grateful for your contribution to my academic and professional growth during the past two years.

Finally, thanks to my family and friends for their support in the distance and their energizing love during my visits. To all of you who helped me reach my goal, thank you.

Table of contents

Background

Host shifts and subsequent specialization are widespread among plant-feeding insects (Jaenike, 1990; Nosil, 2002), which likely explain their exceeding diversity compared to non-phytophagous insects (Mitter et al., 1988; Farrell, 1998; Jasnz et al., 2006). More remarkably, specialists also tend to consume only one organ of their host (Hespenheide, 1991; Cook et al., 2002; Joy and Crespi, 2007). A traditional explanation for such a narrow diet breadth has been host plant quality, arguing that maximizing nutritional benefits or minimizing the effects of plant defensive compounds drives specialization (Futuyma and Moreno, 1988). Accordingly, specialists adapted to their host are expected to assimilate host plant material better, outperforming generalists on the same host (Dethier, 1954). In a study of 85 species of lepidopterans, Coley et al. (2006) found specialist caterpillars grew faster and were less affected by secondary compounds in expanding leaves than generalist species. In many lepidopterans, larval diet is especially important because it strongly determines adult fecundity: in females, total egg production may be determined during immature stages (Awmack and Leather, 2002; Hough and Pimentel, 1978; but see Fenemore, 1977 and Leather, 1988) and in males, pupal weight has been observed to affect mating frequency (Makee and Saour, 2001).

As an alternative to food quality, interspecific interactions such as predation and parasitism may serve as pressures selecting for diet specialization (Price et al, 1980; Futuyma and Moreno, 1988). A narrower diet breadth will be favored if protection is conferred through utilization of a host less trafficked by antagonists or by becoming less apparent to predators and parasitoids while using it -that is, by gaining “enemy-free space” on a particular host (Jeffries and Lawton, 1984). An example is provided by the noctuid moth *Heliothis subflexa*. This moth is a specialist on *Physalis* (Solanaceae), a genus characterized by the inflation of the calyx (i.e. collection of sepals) to cover the developing fruit. By exploiting a feeding site within the inflated calyx, *Heliothis subflexa* suffers three times less parasitism than its generalist congener *H. virescens* (Sisterson and Gould, 1999; Oppenheim and Gould, 2002).

Nutritional or protective benefits associated with specializing on a particular resource however, may only be advantageous if the resource is abundant in space (i.e., within the herbivore’s range) or time (i.e., across herbivore’s generations) (Bernays and Chapman, 1994).

Optimal foraging theory predicts that diet choices should follow abundance of food items with the greatest reward to handling time ratios (Pyke, 1984; Futuyma and Moreno, 1988). Furthermore, high ranked items should always be taken when available, precluding inclusion of lower quality items if the former are readily available (Pyke, 1984; Futuyma and Moreno, 1988). Nevertheless, because resources are likely to vary, specialist herbivores pay an opportunity-cost in avoiding lower ranked yet suitable hosts at times when their preferred host is in limited supply.

While the individual roles of food quality, enemy risk and food abundance have been shown to be important in some studies, other studies have failed to find key single drivers determining herbivores' diets (Joern, 1979; Moran, 1986; Bernays and Chapman, 1994; Singer, 2001). This conflicting evidence, along with studies combining at least two potential selective pressures, suggests an integrative approach may provide a better explanation for the evolution of diet breadth (e.g., Singer et al, 2004; Mooney et al, 2012). Further understanding the interactive associations in shaping herbivores' diets requires exploring systems in which the effects of multiple factors can be quantified (e.g., Singer et al, 2004; Mooney et al., 2012). Ideally, such a system would have limited, discrete food options that pose either differential risks to the same antagonists or different antagonists associated with different feeding strategies.

Symmetrischema lavernella is a phytophagous gelechiid moth whose hosts appear to be limited to the genus *Physalis* (Solanaceae). Caterpillars colonize individual flower buds and open flowers to feed on immature floral tissues (i.e., anthers and ovary) or the ovules inside a developing fruit. Because each larva uses only one structure for development, caterpillars develop on one of these larval substrates and thus become either a budworm or frugivore. Frugivores may result from the colonization of open flowers and large flower buds that are close to opening and will therefore produce a fruit soon, while budworms may arise from the colonization of small flower buds (Fig.1). Because some *Physalis* species continuously produce flowers and fruits throughout the summer, both substrates are available simultaneously for most of the season (June - September). Both feeding strategies are observed in each of the 3+ generations of the moth (pers. obs.).

Overall, if two feeding strategies are to be maintained, selective pressures should render both strategies similar in costs and benefits or show enough variation in outcome to impede fixation on either strategy. Preliminary data on *S. lavernella* suggested that *S. lavernella* grows bigger while feeding in fruit (Moorhouse, unpublished), as would be generally expected for this nutrient-sink structure. Nevertheless, the frugivore strategy may not always be available on a plant if all large flower buds have been occupied by other larvae. Because *Physalis* branches feature a sequence of diminishing flower bud sizes (Fig. 1), occupation of the more advanced flower buds should leave only small flower buds capable of supporting budworms instead. On the other hand, frugivores likely experience competition and potential predation pressure from *Heliothis subflexa,* a larger *Physalis* specialist caterpillar whose larvae consume multiple fruits during development and have been observed consuming fruits occupied by *S. lavernella* (Fig.2b). *Heliothis subflexa* has only rarely been observed feeding on flower buds (pers. obs.; Fig. 2a). Preliminary data also show that at least three parasitoid wasps attack *S. lavernella*. Given that frugivores are protected by the fruit wall and its enclosing calyx (Sisterson and Gould, 1999; Oppenheim and Gould, 2002), budworms are expected to be more susceptible to parasitoids. Furthermore, mortality risks from these antagonists may vary temporally as antagonist populations go through seasonal cycles, and spatially if antagonists respond to host plant density, as a greater concentration of resources is expected to attract and maintain a greater number of herbivores and consequently of parasitoids (Root, 1973; but see Hambäck and Englund, 2005). Thus, selection of a feeding strategy may be limited by the resources available and may entail a tradeoff between body size attained inside a developing fruit and the likelihood of being consumed by another species of moth while in that fruit, along with differential risks to parasitoids that vary with substrate.

Because this system has the potential for tradeoffs between nutritional quality, resource availability, and enemy exposure on the same individual plant, it is ideally suited for exploring how selection may either work toward a narrowing of feeding strategies over time or may be constrained from further narrowing. Thus, the goal of this study is to elucidate the mechanisms maintaining two feeding strategies in the gelechiid moth *S. lavernella* by addressing the following questions:

a) Do frugivores grow bigger and survive better than budworms?

b) Do risks from predators and parasitoids vary with feeding strategy, and do these risks change with host plant density?

c) Is adoption of a strategy dependent on the size of the bud colonized?

Methods

Study system

Symmetrischema lavernella (Chambers 1874; Gelechiidae) is a brown-colored microlepidopteran (Fig.3, inset) with host plants identified only in the genus *Physalis* (Solanaceae) (e.g., *P. viscosa*: Robinson et al., 2010). Newly hatched larvae are less than a millimeter in length while adults attain an approximate length of 7 mm. Yellow green eggs are laid singly mostly under leaves (Cruz-Maysonet, unpublished), although eggs can be found on stems, pedicels, flower buds, the surface of inflated calyxes and above leaves. Larvae hatch in ca. five days and seem to present three instars as suggested by the total number of head capsules found in the brood chamber (pers. obs). Budworms initiate pupation after feeding on the anthers and ovary of a flower bud while frugivores reach pupation after feeding on ovules of a developing fruit. Adult emergence is observed approximately two weeks after pupation starts.

Previous to this study *S. lavernella* had been reported in at least six states across the United States of America (Fig.3). In the location of the present study *S. lavernella* caterpillars develop in flower buds or fruits of the perennials *P. longifolia* var. *subglabrata* and *P. heterophylla*. Flower bud and fruit infections by *S. lavernella* have also been observed in annual species (e.g., *P.pubescens*) but abscission of these structures prevented successful larval development (pers. obs.). Because infections by *S. lavernella* are more frequent in *P.heterophylla* at the study site (pers. obs.), this study focused on this host plant species.

Physalis heterophylla, commonly known as clammy groundcherry, is a native herb widely distributed in North America (USDA NRCS, 2014). Flowering starts in May and continues until early September, with fruit initiation occurring a few days after anthesis. Indeterminate growth in this herb results in a range of bud sizes present throughout the growing season, along with open flowers and fruits.

Symmetrischema lavernella and *Physalis heterophylla,* are common at the study site, the Blandy Experimental Farm (78.065199 W, 39.063965 N; hereinafter referred to as ‘Blandy’), a field research station in Clarke County, Virginia administered by the University of Virginia. Blandy encompasses an area of 278.5 ha with a mix of land types, including old and cultivated fields, and woodlots (Lawrence and Bowers, 2002). All data collection was carried out at Blandy during the summer of 2013. During the winter, experiments were carried out in a greenhouse at Blandy and laboratory facilities at the University of Virginia (Charlottesville, VA).

Plant material, caterpillars and moths

Physalis heterophylla plants were propagated from wild-collected seeds, as well as rhizome cuttings and whole plants transplanted from the field. Seeds collected during the fall of 2012 at Blandy were refrigerated for three months and planted afterwards in 3-4 mm of potting soil to initiate germination in the greenhouse (ca. 22°C). Approximately six weeks after germination, seedlings were transplanted to individual pots with soil supplemented with slow releasing fertilizer (potting soil). Rhizome cuttings (ca. 1cm) were taken from whole root systems refrigerated in the fall, cultivated in the greenhouse (ca. 22°C) and transplanted to individual pots. All plants received liquid fertilizer (Miracle-Gro® Liquid All Purpose Plant Food Concentrate, NPK=12-4-8) two or three times during the summer, at least two weeks apart. Plants were also exposed to ladybugs (*Hippodamia convergens*) to control aphids (*Macrosiphum euphorbiae*).

Potted plants from seeds and rhizome cuttings were exposed to moths in the field and transferred to a screen house to produce a captive source population of *S. lavernella*. Additional infected plants or moths were added to the screen house throughout the season when necessary to maintain this moth population. No detrimental effect of lady bugs exposure was observed on *S.lavernella* populations.

Statistical analysis

All statistical tests were performed with SAS 9.3 (SAS Institute) using significance levels (α) of 0.05. Specific tests are described below.

a) Do frugivores grow bigger and survive better than budworms?

I used pupal weight and survival to adulthood (under exclusion of predators) as a measure of performance to compare food quality under the budworm and frugivore strategies. Twenty one potted *P. heterophylla* plants were maintained outside close to wild *Physalis* (both *P.*

heterophylla and *P. longifolia*) populations. The plants were protected by a metal cage with 1/8” x 1/8” mesh to prevent plant damage by larger herbivores but allowing infections by *S. lavernella.*

Observed infections were tagged when recognized as budworm or frugivore and monitored weekly to register the beginning of pupation. When identifying infections, frugivores were determined by presence of an entrance hole into the ovary (Fig.4a) while budworms were determined by touch (infected flower buds are hollow) or with a 30X pocket microscope (upon small separation of the calyx or corolla) (Fig.4c). Pupation is easily recognized for frugivores as caterpillars make a hole through the fruit wall and calyx right before pupating (Fig.4b) that serves as an “exit hole” for the emerged adult. Thus, infected fruits were removed from the plant at the appearance of exit holes. Budworms were removed as soon as pupation was evident upon inspection: small separation of sepals reveals presence of cocoon webbing. Removed pupae were kept in clear 50mL plastic tubes at the laboratory and monitored daily. All pupae were weighed at the appearance of dark eyes (Fig. 5) and kept until emergence. Emerged adults were sexed based on genital morphology (Fig. 6) or the number of frenula (i.e., bristle like structures that hold fore and hind wings together during flight). *Symmetrischema lavernella* females have three orange frenula while males have only one. Failure to pupate or to emerge was noted for individuals that did not reach adulthood. Parasitoid infections resulting in the death of the moth could usually be assigned to a genus of wasp. Malformations in the pupal case (e.g., bent abdomen sections) and adults (e.g., shortened wings) were also noted.

A mixed model three-way ANOVA (PROC MIXED) was used to test for effects of strategy (i.e., budworm or frugivore), sex, and the strategy-by-sex interaction (fixed effects) across plants (random effect) on body size. This analysis included only plants that had registered both budworms and frugivores (n=17). Additionally, only individuals that had been sexed were included (n=151). A “normalizing transformation” was applied to pupal weight observations using PROC RANK and the ‘blom’ ranking method (normal option).

In addition, a chi-square test of independence (PROC FREQ) was used to compare survival to adulthood (i.e., surviving or not) between frugivores and budworms, including all individuals for which survival data had been recorded (n=197).

b) Do risks from predators and parasitoids vary with feeding strategy, and do these risks change with host plant density?

Frugivores and budworms were exposed to predation and parasitism in the field under two levels of host plant density. Naturally occurring patches of *P.heterophylla* were classified as low or high density based on the number of stems within a 15 meters radius area. Patches with up to 30 stems were classified as low density and those with more than 50 as high density. The number of stems in low density patches ranged from 10 to 23 while the number of stems in high density patches ranged from 54 to over 90. Five patches per density level were used.

At the center of each patch, four potted plants (arising from a single clone, transplanted from the wild) were added. Each of these plants had received infections from the captive moth population. Four plants were used in order to include enough budworm and frugivore infections. These plants were positioned with leaves touching so that they seemed to function ecologically as a single unit, resembling *P. heterophylla*'s highly clonal growth from underground rhizomes and eliminating plant identity effects in statistical analysis. Both feeding strategies were represented across plants at each patch, although not in the same quantities. A total of 191 budworm and 462 frugivore infections were marked. Because caterpillar size is correlated with bud and fruit size (Moorhouse, unpublished), size of infected buds and fruits was recorded during tagging to provide an estimate of the stage of development of the caterpillars at the moment of exposure. Only small (n=303) and medium (n=130) buds were included in statistical analysis because older infections were exposed to field conditions for too short a time before pupation. Because small and medium structures were not equally represented across feeding strategies (chi-square test of independence: df=1 , χ^2= 4.35, P=0.037), a size-by-strategy interaction was included in the statistical analysis (see the description of the model below).

Frugivores and budworms were exposed to field conditions for three weeks, starting in mid-August (late summer). After exposure, all plants were isolated in a screen house and advanced infections were removed and kept in clear 50mL plastic tubes. Less advanced infections were allowed extra days to reach pupation to avoid interference with parasitoid development, if any was present. Emergence of moths or cause of mortality was noted for all infections. Mortality was attributed to failure to emerge, failure to pupate, or attack by the larger frugivore *H. subflexa* or parasitoids. Parasitoid identity was determined based on emerging parasitoid adults, and/or pupal case (Fig. 7). For buds or fruits that dropped off the plant, found along with the tag or the tag alone, the caterpillar was assumed to have not survived. The same was assumed if a bud or fruit was found to have typical *S. lavernella* damage but no larva was present (i.e., abandonment of fruit or bud). An unexpected finding was to observe several buds that had been tagged as budworms to be seen hosting frugivores after the three weeks exposure (9.6% of all marked infections). These were excluded from analyses because it was not possible to determine whether these were the original individual that shifted strategy, a subsequent colonization after the original failed, or represented dual initial infections that subsequently lost the budworm.

A generalized linear mixed model (PROC GLIMMIX) was used to determine the influence of feeding strategy (i.e., budworm or frugivore), host plant density (i.e., high or low), and bud size (i.e., small or medium) on survival outcome (i.e., yes or no). The model also evaluated the density-by-strategy and size-by-strategy interactions. I used a binary distribution with a logit link function for this test, identifying infection type, host plant density, and bud size as fixed effects. Patch identity, nested within density, was included as a random effect.

In order to determine if parasitoids were more common in budworms and whether parasitoid abundance varied with *P. heterophylla* density, I used a three-way ANOVA to compare the proportion of non-parasitized budworms and frugivores per patch among density levels. Due to the low frequency of parasitoids, proportion of non-parasitized individuals was preferred over proportion of parasitized individuals. These observations were arcsine transformed. For this mixed model (PROC MIXED) I identified density, strategy, and the density-by-strategy interaction as fixed effects while controlling for the nested effect of patches within density. Specific comparisons of budworms and frugivores within density levels were achieved with contrasts.

No further statistical analysis was pursued on the effect of *H. subflexa* given its rare occurrence.

c) Is adoption of a strategy dependent on the size of the bud colonized?

I evaluated the effect of bud size colonized on the occurrence of budworms and frugivores by transferring 1-2 days old caterpillars to *P. heterophylla* branches across 23 plants. On a plant, one or multiple adjacent branches were used to present a sequence of bud sizes, ranging from very small buds to open flowers. For closed buds, size was measured as the length from the base of the calyx to the longest point at the tip. Open flowers and buds that were visible but too small to measure were observed as well and their outcome recorded, but these were excluded from regression analysis as these could not be measured.

Larvae were transferred in excess relative to buds available –usually two times the number of buds- to ensure infections over the range of bud sizes. Caterpillars were placed on small pieces of paper and transferred to leaves at the top of branches. This method was preferred over direct transfer of larvae to avoid injuries by trichomes. Migration of caterpillars to non-target branches was prevented by removing leaves as necessary and by applying a sticky, non-drying adhesive (Tanglefoot®) at the base of each target branch.

This experiment was performed during the winter, with plants maintained in a greenhouse (ca. 22°C) at Blandy or a growth chamber (Conviron 4030 Model PGR15; Conviron) at the University of Virginia. Plants in the greenhouse were exposed to 16 hours of light daily (natural light supplemented with sodium vapor lights). Plants in the growth chamber were under the same photo:scotophase period, using fluorescent light only (level 2) at 22°C. An open container with approximately two gallons of water was kept inside the chamber to prevent dry conditions given that control of chamber humidity was not available.

Probability of adopting a frugivore (P=1) or budworm (P=0) strategy in response to bud size was analyzed with a logistic regression (PROC LOGISTIC). Accordingly, the analysis included all measured structures that had been colonized (n=170) and excluded those that were not occupied or that had fallen off the plant. The original model for this analysis controlled for location of trials (i.e., Blandy and University of Virginia) and the nested effect of plants within locations. However, none of these had a significant effect (location: Wald's χ^2=0.03, P=0.86; plant-within-location: Wald's χ^2=6.40, P=0.99). Additionally, this model resulted in a quasi-complete separation of data, producing suspect maximum likelihood estimates. Therefore, a reduced model combining observations across locations and plants was used for the final analysis.

The size of unoccupied buds (n=22) was compared to that of occupied buds (n=61) with a two-way ANOVA (PROC MIXED). This model controlled for plant and the plant-by-occupancy (i.e., occupied or not) interaction as random effects. For this test, only trials that had been conducted in the laboratory at the University of Virginia were considered because only those trials were monitored closely enough to assure that unoccupied buds did not represent developmental failures of young caterpillars.

Results

a) Do frugivores grow bigger and survive better than budworms?

Pupal weights at the appearance of dark eyes ranged from 2.5 to 9.0 mg in budworms, with a mean of 6.6 mg. Frugivores exhibited greater variation in pupal weights, recording both the minimum and maximum values of all: 2.0 and 13.5mg, respectively. The mean pupal weight for frugivores was 8.8mg.

Female budworm pupae were 8.6% heavier than male budworm pupae on average (Fig. 8). Similarly, female frugivores were recorded as having a mean pupal weight 12.2% greater than that of male frugivores (Fig. 8). These differences in mean pupal mass were significant, indicating frugivores grow bigger than budworms (ANOVA: $F_{1,131}$=73.11, P<0.0001) and females are the heaviest for both feeding strategies ($F_{1,131}$=7.47, P=0.0071). Neither plant identity (covariance parameter= 0) nor the interaction between feeding strategy and sex ($F_{1,131}$=0.00, P=0.8868) had an effect on pupal weights.

Survival to adulthood was similar for budworms and frugivores, with 89.7% and 85% emerging as adults, respectively (chi-square test: df=1, χ^2=0.9778, P=0.3227). Only four parasitoids were recorded in this experiment, all from the same species (*Bracon* sp., Hymenoptera: Braconidae) (Fig.7a) and occurring in the same frequency across feeding strategies. Malformations in the pupal or adult stage occurred in 5.8% of the individuals, on five frugivores and six budworms. All malformed adults (4) presented shortened wings.

b) Do risks from predators and parasitoids vary with feeding strategy, and do these risks change with host plant density?

Budworms suffered higher mortality (75.4%) than frugivores (64.3%) ($F_{1,419}$=5.72, P=0.0172) across patches of *P. heterophylla* (Table 1). Size of buds and fruits also had an important effect on survival: caterpillars in small-sized buds or fruits (i.e., the youngest caterpillars) exhibited a lower survival when compared to those in medium-sized structures ($F_{1,419}$=18.59, P<0.001; Table 1). There was no significant effect of a size-by-strategy interaction ($F_{1,419}$=1.75, P=0.1861). Neither patch density ($F_{1,8}$=0.44, P=0.5262) nor the strategy-by-density interaction ($F_{1,419}$= ;P=0.6582) had a significant effect on mortality (Table 1). More failures of caterpillars (125 out of 286) were associated with uncertain circumstances (e.g., buds dropped or seemingly abandoned by the caterpillar) than any single cause. The second most common cause was failure to emerge (119 out of 286) (Fig. 9).

Two parasitoid wasp species were recovered from *S.lavernella* exposed to field conditions, belonging to the Braconidae and Chalcididae families (Fig.7). The braconid wasp *Bracon* sp. (Fig.7a) was observed 25 times, all but one in frugivores. Larvae of this species would kill late instar *S.lavernella* and pupate outside the caterpillar. The chalcid wasp *Conura* sp. (Fig.7b) was only recorded in one budworm. Larvae of this species completed development inside *S.lavernella*'s caterpillars and emerged as adults from *S.lavernella*'s pupal case. It must be noted that additional parasitoids were observed in advanced infections that were not analyzed as mortality factors in this experiment due to their proximity to pupation when the experiment began. *Conura* sp. was observed in eight non-target budworms while a third parasitoid wasp species, in the Ichneumonidae family (*Cryptinae* sp., Fig.7c), was observed in one non-target budworm. This ichneumon parasitoid also pupated inside *S. lavernella*'s pupal case.

The proportion of parasitized *S. lavernella* caterpillars did not vary overall with feeding strategy (ANOVA: $F_{1,8}$=2.23, P=0.17) or host plant density ($F_{1,8}$=0.02, P=0.89) but the interaction between these factors was significant ($F_{1,8}$=7.39, P=0.026): parasitoids killed more frugivores in low density patches (contrast: $F_{1,8}$=8.87, P=0.018) while producing similar mortality among strategies in patches of high *P.heterophylla* density (contrast: $F_{1,8}$=0.75, P=0.41).

The larger frugivore *H. subflexa* was recorded on 23 fruits and one bud. No mortality could be directly attributed to *H. subflexa* in any of these instances (i.e., a predation event), yet 48% of the frugivores that developed in fruits partially eaten by *H. subflexa* failed to pupate or emerge. Only one of these caterpillars hosted a parasitoid (*Bracon* sp.).

c) Is adoption of a feeding strategy dependent on the size of the bud colonized?

A total of 53 budworms and 117 frugivores resulted from caterpillar transfers. Colonization was observed across the entire range of bud sizes available, from very small buds that could not be measured to large buds and open flowers. Strategy was strongly tied to bud size, with the adoption of the frugivore strategy in buds larger than 4.2 mm and the budworm strategy in buds smaller than 4.2 mm (logistic regression: Wald's χ^2= 32.22, P<0.0001; Fig.10). Accordingly, all the smallest buds (i.e., visible but not measured) that were colonized hosted budworms and all the open flowers that were colonized hosted frugivores.

The difference in the mean size of unoccupied buds (4.6 mm) and that of occupied ones (6.3 mm) was marginally non-significant (ANOVA: $F_{1,5}$=5.82, P= 0.061).

Discussion

a) Do frugivores grow bigger and survive better than budworms?

Consistent with preliminary observations on this system, frugivores were found to have an advantage in performance by attaining average pupal weights 33% greater than that of budworms. Higher pupal weights may have important fitness consequences if they translate into adult body sizes and ultimately mediate reproduction and survival. Generally, fecundity in insects is related to female body size (Honěk, 1993), a well documented relationship exemplified by Lepidoptera species such as the spruce budworm (*Choristoneura fumiferana*; Lorimer and Bauer, 1983), the diamondback moth (*Plutella xylostella*; Niu et al., 2013), *Streblote panda* (Calvo and Molina, 2005), and *Dirphia araucariae* (Zenker et al., 2013). Among males increased body size can result in higher mating frequencies (e.g., Makee and Saour, 2001) and production of larger spermatophores (Royer and McNeil, 1993). Greater body sizes may also allow for greater overwintering success if individuals overwinter as pupae (e.g., Liu et al., 2007) or adults. Flight performance can also be positively affected by pupal weight (e.g., Wu et al., 2006).

Despite the differences in pupal weight, survival to adulthood in the first experiment was high for both feeding strategies, ranging from 85-90%, and showed no effect of larval diet under protection from predators. This unexpected finding suggests larval nutrition may have a lower effect on survival to adulthood than other factors influencing survival such as predation or mechanical plant defenses (e.g., abscission of early infections), although predation was also found to be of little importance in this study.

b) Do risks from predators and parasitoids vary with feeding strategy, and do these risks change with host plant density?

Development inside of flower buds and fruits was predicted to provide differential protection from parasitoids due to the different thickness of the tissues. Accordingly, budworms were expected to receive most attacks from parasitoids while fruits were expected to provide enemy-free space to frugivores. Contrary to expectations, parasitoids were not an important source of mortality for budworms and were only important for frugivores in low density patches of *P.heterophylla*.

The lack of a marked difference in parasitoid attacks between strategies may be explained by the morphology of parasitoids attacking each strategy: the braconid wasp seen almost exclusively in frugivores features a long ovipositor (Fig.6a) in contrast to the chalcid wasp, seen only on budworms, that exhibits a short ovipositor (Fig.6b). Ovipositor length is considered a good indicator of host finding conditions (Price, 1972); however, this observation is not meant to imply parasitoid specialization in this system. Since successful parasitoid attacks were observed only in a small portion of the caterpillars (6%), these parasitoids may be generalists that prey upon *S. lavernella* after other hosts have declined at the end of the summer. On the other hand, higher parasitism of frugivores at low density patches is in contrast with the overall expectation that higher plant density will host more herbivores and thus, attract more carnivores (Root, 1973), but may be explained by parasitoid avoidance of high density patches if abundant plant foliage increases search time for hosts.

More importantly, the low occurrence of parasitoids for most of the summer season (based on observations of caterpillars studied for differences in performance), together with the low parasitoid prevalence during late summer, suggest these antagonists may not be an important driver of mortality for *S. lavernella*. Indeed, despite the significantly higher attack to frugivores in low density patches, parasitoids do not present a trade-off in survival given the overall lower mortality observed on frugivores.

Asymmetrical effects were also expected for the interaction of budworms and frugivores with *H. subflexa* (Moorhouse, unpublished; Emerson, unpublished). *Heliothis subflexa* typically emerges during mid-June at Blandy and exhibits high abundance for most of the summer, thus providing a small window at the beginning of the summer when budworms and frugivores are equally free of this potential source of mortality. This is followed by a period when interactions with *H. subflexa* seem more common for frugivores while budworms are expected to receive enemy-free space by utilizing an organ rarely used by *H. subflexa*. This pattern seemed to be supported by the frequency of budworm and frugivore interactions with this larger *Physalis* specialist observed here in late summer (one versus 23 times, respectively), but was unexpectedly rare overall, making *H.subflexa* an unimportant source of mortality for *S. lavernella* in this particular experiment at this time of year.

For the 23 frugivores occupying fruits partially eaten by *H. subflexa* there is a potentially high cost for the interaction, as failure to reach adulthood was observed in 48% of the frugivores (although these failures may also be related to the high mortality recorded from other sources). Surprisingly, the cost of this interaction was not related to predation events despite the observation that *H.subflexa* does prey upon *S. lavernella* (Emerson, unpublished). Instead, the apparent negative outcome in the interaction with *H.subflexa* may result from: a) facilitation of pathogen or parasite acquisition, b) injury from an aggressive encounter (i.e., interference competition), or c) reduced availability of food (i.e., exploitative competition). Although very little mortality could be attributed to *H. subflexa*, this experiment may have greatly underestimated their impact. It is possible that predation is more common when *H. subflexa* is in its late instars, a stage that was not observed on this experiment's plants as these were initially free of *H. subflexa* and would have required more than three weeks in the field to develop from eggs to late instars.

The lack of host plant density effects on overall moth survival is contrary to expectations but not surprising as host plant density does not always influence dynamics at higher trophic levels (Hambäck and Englund, 2005; Vanbergen et al., 2007). In this particular system, host plant density may not provide a good explanation for mortality due to the absence of strong responses from *H. subflexa* and parasitoids to *P. heterophylla* density. In *H. subflexa* lack of a relationship with density of this host plant may be related to preference for *Physalis longifolia* (pers. obs.).

In contrast with survival to adulthood observed in protected caterpillars studied for pupal weights, an overall low survival was observed when budworms and frugivores were exposed to field conditions. In this experiment the majority of failures were associated with circumstances for which death was assumed but not observed -including falling off the plant and abandonment of the bud- and failure to emerge. Abscission of fruits in response to caterpillar feeding is exhibited by some *Physalis* species as a defense against frugivores (Benda et al., 2009; Petzold et al., 2009) while bud abscission has been observed in response to mechanical damage (pers. obs.). Because a free roaming larva would be more susceptible to starvation and predation, it is likely that caterpillars in abscised buds and fruits, or that had abandoned a bud or fruit, would fail to survive. On the other hand, maintaining caterpillars in vials along with plant tissue may have led to some emergence failures as the tissues rot. Failure to emerge in presence of rotting tissues was noticed more frequently for frugivores but the observed higher survival of frugivores suggests this was not an important source of error.

c) Is adoption of a strategy dependent on the size of the bud colonized?

As suspected, bud size posed an important limitation to adoption of a feeding strategy, preventing development as a frugivore for larvae that encounter buds smaller than 4.2mm. While an experimental assessment of preference was not a part of this study, a mechanism is provided that explains occurrence of two feeding strategies in a scenario where preference exists for bud sizes resulting in the frugivore strategy. In a branch with a sequence of bud sizes, selection of larger buds produces frugivores initially, leaving only small buds available for late hatching larvae. Furthermore, due to the indeterminate growth of *Physalis* species, new buds available on a branch will be the small ones produced at the tip of branches, allowing caterpillars at the end of a generation to develop only as budworms. It is not until a break between generations that flower buds can grow enough to support frugivores again in the next generation. Indeed, the marginally non-significant difference in the size of occupied and unoccupied buds suggests a potential choice being made by caterpillars that warrants further study.

What maintains two feeding strategies in Symmetrischema lavernella*?*

A similar case to that of *S. lavernella* is observed in another gelechiid moth, *Frumenta nundinella*. This moth is also a specialist in a Solanaceae plant that produces flowers and fruits simultaneously throughout the summer, horsenettle (*Solanum carolinense*). Larvae feed at shoot meristems and fruits, but exploitation of these food items varies temporally, the former being used predominantly in the spring and the latter being used in the summer (Solomon, 1980). Solomon (1980) proposed that differences in mortality drove the marked separation in resource use: caterpillars in leaf capsules at meristems suffered a significantly greater mortality from predators, making its use when fruits are available highly disadvantageous.

In *S. lavernella*, such trade-off between feeding strategies is not observed; greater body size and survival of frugivores suggest this is the most profitable feeding strategy for larval development. These findings are consistent with the observation of complex behaviors in *S. lavernella* caterpillars that develop as frugivores such as induction of fruit formation and perforation of an exit hole, the latter rarely observed in buds. In *P. heterophylla* self-incompatibility (Roulston, unpublished) would present a high cost to caterpillars entering the ovary before fruit formation if flowers have not been pollinated (Solomon, 1980). Thus evolution or maintenance of behavioral and physiological mechanisms supporting this strategy implies a high benefit from frugivory. These advantages however, interact with availability of bud sizes able to support this strategy as there is a high opportunity cost in avoiding small bud sizes: since each fruit supports only one caterpillar, failure to colonize an available smaller bud would mean failure to reach adulthood. Consequently, high intraspecific competition favors the maintenance of an additional feeding strategy despite its lower performance. This opportunity cost is further increased by the variability in the strategy outcome when colonizing intermediate bud sizes around 4.2 mm (Fig. 10).

Conclusion

A remarkable pattern in host plant use by specialist herbivores is the consumption of a single organ (Hespenheide, 1991; Cook et al., 2002; Joy and Crespi, 2007). Exceptions to this pattern include the *Physalis* specialist *Symmetrischema lavernella*, whose caterpillars develop as budworms or frugivores as they feed on flower buds or fruits, respectively. Nevertheless, by assessing the effect of larval substrates on growth performance and survival, this study showed that these larval feeding strategies are not equally profitable. Frugivores attain greater pupal masses and survive better. Interestingly, greater survival is observed despite the greater interaction of frugivores with natural enemies. Furthermore, this study revealed that the adoption of a feeding strategy is dependent on the size of the flower bud colonized. Thus, the maintenance of two feeding strategies is not explained by trade-offs between performance and survival. Rather, high intraspecific competition for large buds probably drives the use of small buds that lead to a budworm strategy and impede a further narrowing of *S. lavernella*'s diet breadth.

The findings of this study suggest a more extensive use of a pluralistic approach would advance our understanding of the forces interacting to shape herbivores' diets, especially those with intermediate diet breadths between high specialization or generalization. This is particularly important as specialization in plant-feeding insects has been the focus of studies aimed at explaining evolution of diet breadth in this group, neglecting much of the diet variation that also occurs and making necessary studies that evaluate other levels of host specificity along its broad spectrum (Singer 2008).

Future research

The results of the present study suggest additional aspects of the foraging ecology of *S. lavernella* that should be explored. While a positive relationship between pupal weight and adult weight has been observed in *S. lavernella* (T.H. Roulston, pers. com.), it is still unknown how adult weight may influence reproduction. Uncertainties about the effect of body size warrant further study of the adult stage to determine if reproductive output is dependent on resources acquired during the larval or adult stage and thus, if body size mediates fitness consequences of the budworm and frugivore feeding strategies. Understanding the interaction with the larger frugivore will require studies aimed at clarifying how feeding by *H. subflexa* may facilitate acquisition of internal parasites or pathogens or induce mortality through interference or exploitative competition. Future studies should also clarify whether predation on *S. lavernella* is more likely by *H. subflexa* late instars. Additionally, assessment of preference for bud sizes will complement our knowledge on the effects of bud sizes and may reveal specific choices made during oviposition and/or colonization. In the future, attention should also be paid to plant defenses against colonization by *S. lavernella*, as abscission may be an important driver of mortality of caterpillars.

References

Awmack, C.S., and Leather, S.R. 2002. Host plant quality and fecundity in herbivorous insects. Annual Review of Entomology. 47: 817-844.

Benda, N.D., Brownie, C., Schal, C., and Gould, F. 2009. Fruit abscission by *Physalis* species as a defense against frugivory. Entomologia Experimentalis et Applicata. 130: 21-27.

Bernays, E.A. and Chapman, R.F. 1994. Evolution of host range, pp. 258-263. *In* Host Plant Selection in Phytophagous Insects. Chapman and Hall, New York, NY.

Calvo, D. and Molina, J.Ma. 2005. Fecundity-body size relationship and other reproductive aspects of *Streblote panda* (Lepidoptera: Lasiocampidae). Annals of the Entomological Society of America. 98: 191-196.

Coley, P.D., Bateman, M.L., and Kursar, T.A. 2006. The effects of plant quality on caterpillar growth and defense against natural enemies. Oikos. 115: 219-228.

Conviron. Conviron 4030 Model PGR15. North Dakota, USA.

Cook, J.M., Rokas, A., Pagel, M., and Stone, G.N. 2002. Evolutionary shifts between host oak sections and host-plant organs in *Andricus* gallwasps. Evolution. 56: 1821-1830.

Dethier, V.G. 1954. Evolution of feeding preferences in phytophagous insects. Evolution. 8: 33-54.

Farrell, B. D. 1998. “Inordinate fondness” explained: Why are there so many beetles? Science. 281: 555-559.

Fenemore.1977. Oviposition of potato tuber moth, *Phthorimaea operculella* Zell. (Lepidoptera: Gelechiidae); fecundity in relation to mated state, age, and pupal weight. New Zealand Journal of Zoology. 4:187-191.

Futuyma, D.J., and Moreno, G. 1988. The evolution of ecological specialization. Annual Review of Ecology and Systematics. 19: 207-233.

Hambäck, P.A. and Englund, G. 2005. Patch area, population density, and the scaling of migration rates: the resource concentration hypothesis revisited. Ecology Letters. 8: 1057-1065.

Hespenheide, H. 1991. Bionomics of leaf-mining insects. Annual Review of Entomology. 36: 535-560.

Honěk, A. 1993. Intraspecific variation in body size and fecundity in insects: A general relationship. Oikos. 66: 483-492.

Hough, J.A. and Pimentel, D. 1978. Influence of host foliage on development, survival, and fecundity of the gypsy moth. Environmental Entomology. 7: 97-102.

Jaenike, J. 1990. Host specialization in phytophagous insects. Annual Reviews of Ecology and Systematics. 21: 243-273.

Jeffries, M.J., and Lawton, J.H. 1984. Enemy free space and the structure of ecological communities. Biological Journal of the Linnean Society. 23: 269-286.

Joern, A. 1979. Feeding patterns in grasshoppers (Orthoptera: Acrididae): Factors influencing diet specialization. Oecologia. 38: 325-347.

Joy, J.B., and Crespi, B.J. 2007. Adaptive radiation of gall-inducing insects within a single host-plant species. Evolution. 61: 784-795.

Laether, S.R. 1988. Size, reproductive potential and fecundity in insects: things aren't as simple as they seem. Oikos. 51: 386-389.

Lawrence, A.P. and Bowers, M.A. 2002. A test of the ‘hot’ mustard extraction method of sampling earthworms. Soil Biology and Biochemistry. 34: 549-552.

Liu, Z., Gong, P., Wu, K., Wei, W., Sun, J., and Li, D. 2007. Effects of larval host plants on over-wintering preparedness and survival of the cotton bollworm, *Helicoverpa armigera* (Hübner) (Lepidoptera: Noctuidae). Journal of Insect Physiology. 53: 1016-1026.

Lorimer, N, and Bauer, L.S. 1983. Spruce budworm weight and fecundity: means, frequency distributions, and correlations for two populations (Lepidoptera: Tortricidae). The Great Lakes Entomologist. 16: 153-156.

Makee, H., and Saour, G. 2001. Factors influencing mating success, mating frequency, and fecundity in *Phthorimaea operculella* (Lepidoptera: Gelechiidae). Environmental Entomology. 30: 31-36.

Mitter, C., Farell, B. and Wiegmann, B. 1988. The phylogenetic study of adaptive zones: Has phytophagy promoted insect diversification? The American Naturalist. 132: 107-128.

Mooney, K.A., Pratt, R.T., and Singer, M.S. 2012. The tri-trophic interactions hypothesis: Interactive effects of host plant quality, diet breadth, and natural enemies on herbivores. PlosOne. Vol. 7, Article ID e34403, 11 pages.

Moran, N. 1986. The benefits of host plant specificity in *Uroleucon* (Homoptera: Aphididae). Ecology. 67: 108-115.

Nosil, P. 2002. Transition rates between specialization and generalization in phytophagous insects. Evolution. 56: 1701-1706.

Oppenheim, S.J. and Gould, F. 2002. Behavioral adaptations increase the value of enemy-free space for *Heliothis subflexa*, a specialist herbivore. Evolution. 56: 679-689.

Petzold, J., Brownie, C., and Gould, F. 2009. Effect of *Heliothis subflexa* herbivory on fruit abscission by *Physalis* species: role of mechanical damage and chemical factors. 34: 603-613.

Price, P.W. 1972. Parasitoids utilizing the same host: Adaptive nature of differences in size and form. Ecology. 53: 190-195.

Price, P.W., Bouton, C.E., Gross, P., McPheron, B.A., Thompson, J.N., and Weis, A.E. 1980. Interactions among three trophic levels: Influence of plants on interactions between insect herbivores and natural enemies. Annual Review of Ecology and Systematics. 11: 41-65.

Pyke, G.H. 1984. Optimal foraging theory: A critical review. Annual Review of Ecology and Systematics.15: 523-575.

Robinson, G.S., Ackery, P.R., Kitching, I.J., Beccaloni G.W., and Hernández, L.M. 2010. HOSTS - A Database of the World's Lepidopteran Hostplants. Natural History Museum, London. http://www.nhm.ac.uk/hosts

Root, R.B. 1973. Organization of a plant-arthropod association in simple and diverse habitats: The fauna of collards (*Brassica oleracea*). Ecological Monographs. 43: 95-124.

Royer, L., and McNeil, J.N. 1993. Male investment in the European corn borer *Ostrinia nubilalis* (Lepidoptera: Pyralidae): impact on female longevity and reproductive performance.

SAS Institute. SAS 9.3. SAS Institute Inc., Cary, North Carolina, USA.

Singer, M. S. 2001. Determinants of polyphagy by a woolly bear caterpillar: a test of the physiological efficiency hypothesis. Oikos. 93: 94-104.

Singer, M. S. 2008. Evolutionary Ecology of Polyphagy *In* Specialization, Speciation, and Radiation: The Evolutionay Ecology of Insects. Chapter 3: pps 29-42. University of California Press, Berkeley, California USA.

Singer, M.S., Rodrigues, D., Stireman III, J.O. and Carrière, Y. 2004. Roles of food quality and enemy-free space in host use by a generalist insect herbivore. Ecology. 85: 2747-2753.

Sisterson, M.S., and Gould, F.L. 1999. The inflated calyx of *Physalis angulata*: A refuge from parasitism for *Heliothis subflexa*. Ecology. 80: 1071-1075.

Solomon, B.P. 1980. *Frumenta nundinella* (Lepidoptera: Gelechiidae): Life history and induction of host parthenocarpy. Environmental Entomology. 9: 821-825.

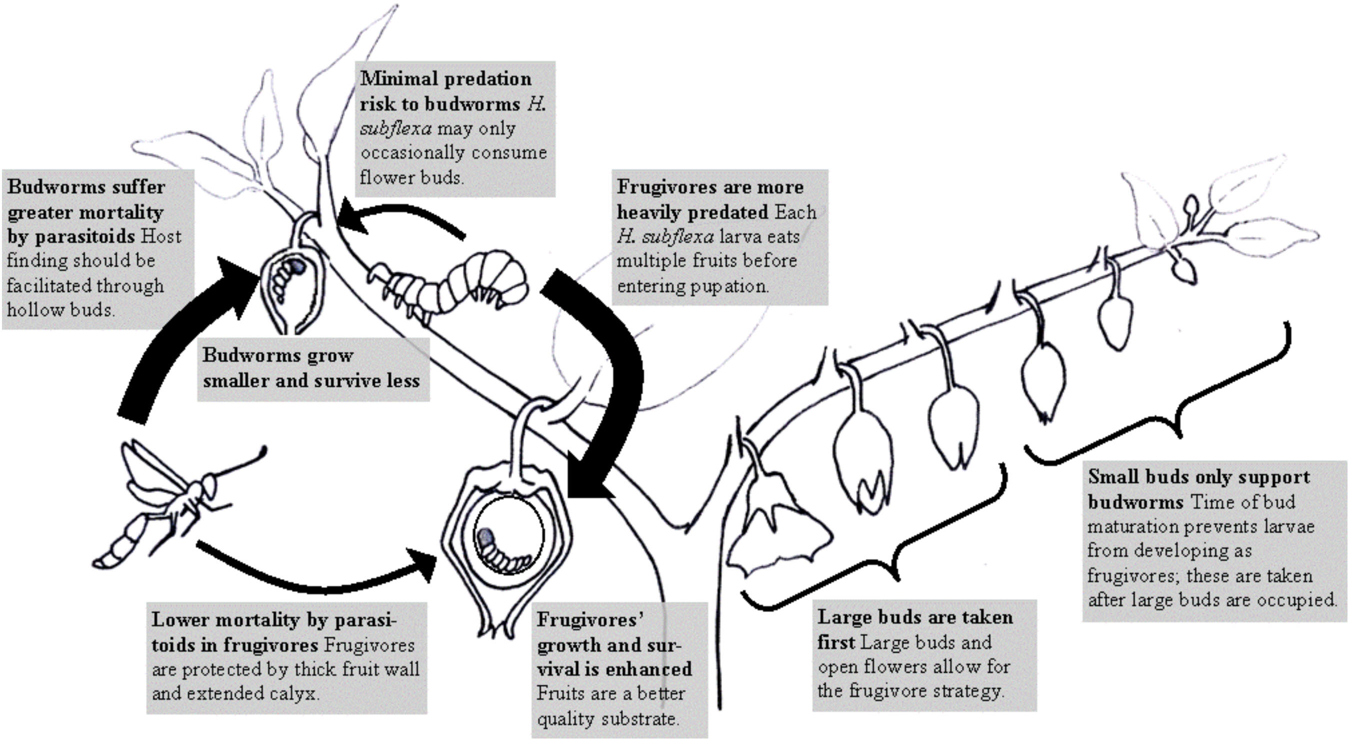
USDA, NRCS. 2014. *Physalis heterophylla* Nees, Clammy groundcherry. The PLANTS Database (http://plants.usda.gov). National Plant Data Team, Greensboro, NC 27401-4901 USA.

Vanbergen, A.J., Jones, T.H., Hails, R.S., Watt, A.D., and Elston, D.A. 2007. Consequences for a host-parasitoid interaction of host-plant aggregation, isolation, and phenology. Ecological Entomology. 32: 419-427.

Wu, H., Wu, K., Wang, D., and Guo, Y. 2006. Flight potential of pink bollworm, *Pectinophora gossypiella* Sanders (Lepidoptera: Gelechiidae). Environmental Entomology. 35: 887-893.

Zenker, M.M., Spechdt, A., Fronza, E., Poletto, G., Marcon, F., Formentini, A.C., and Gedoz, M. 2013. Biology and life table of *Dirphia araucariae* (Lepidoptera: Saturniidae): a herbivore high impact on *Araucaria angustifolia*. Zoologia. 30: 143-150.

Figures



Minimal predation risk to budworms *H. subflexa* may only occasionally consume flower buds.

Budworms suffer greater mortality by parasitoids Host finding should be facilitated through hollow buds.

Frugivores are more heavily predated Each *H. subflexa* larva eats multiple fruits before entering pupation.

Budworms grow smaller and survive less

Small buds only support budworms Time of bud maturation prevents larvae from developing as frugivores; these are taken after large buds are occupied.

Lower mortality by parasitoids in frugivores Frugivores are protected by thick fruit wall and extended calyx.

Frugivores' growth and survival is enhanced Fruits are a better quality substrate.

Large buds are taken first Large buds and open flowers allow for the frugivore strategy.

Figure 1. Predicted effects of interspecific interactions for each of *Symmetrischema lavernella*'s feeding strategies. Thickness of arrows indicate the predicted magnitude of the interaction.

Figure 2. *Heliothis subflexa* a) early instar feeding on flower bud and b) late instar eating a *Physalis longifolia* fruit inside its calyx (photo: T'ai H. Roulston).

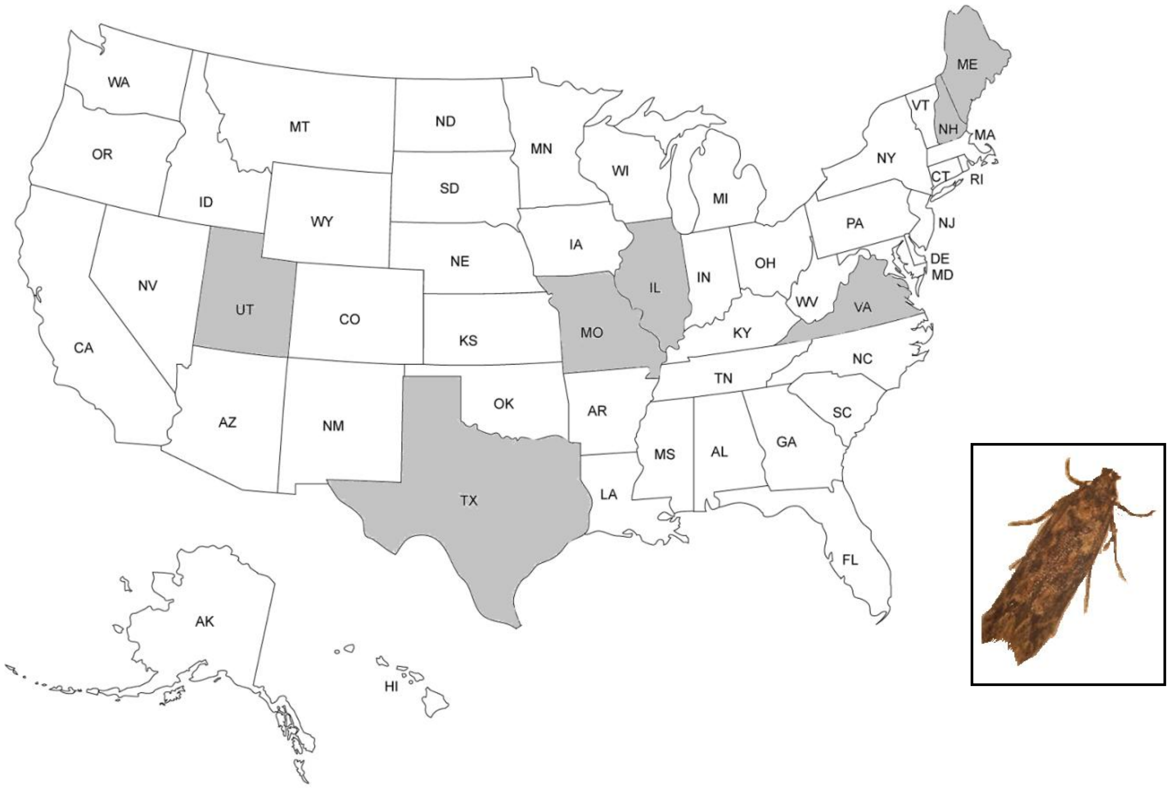


Figure 3. States in the United States of America that have reported presence of *Symmetrischema lavernella* (inset). Reports were taken from online data bases and the current study.

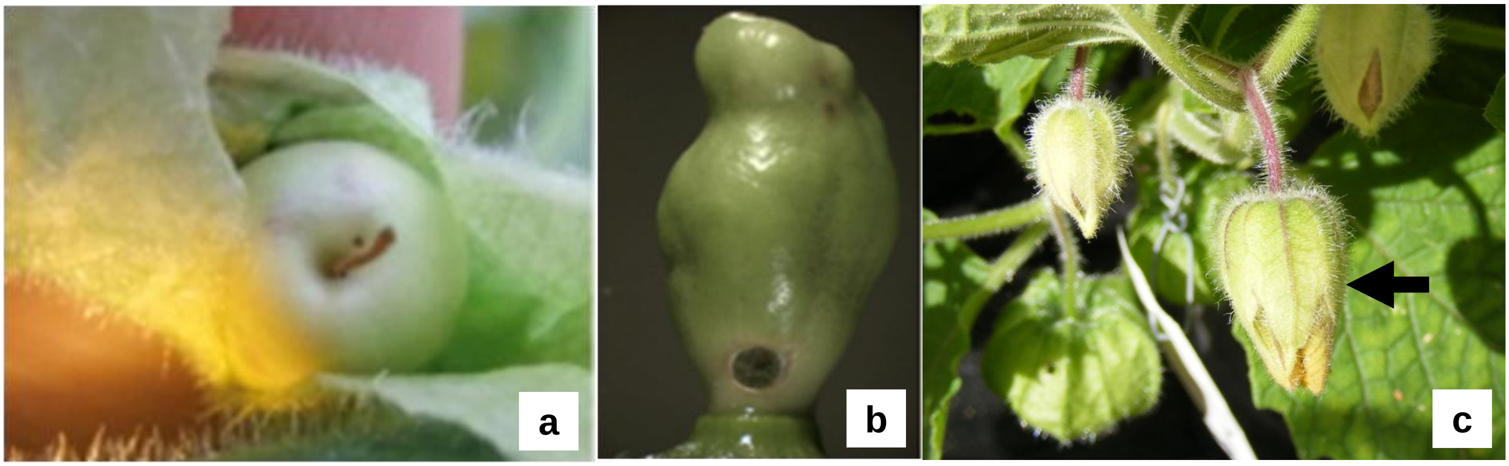


Figure 4. *Symmetrischema lavernella* frugivore and budworm infections diagnosis. a) A red dot indicates the point of entry of a larva into the ovary, usually at the apex, prior to fruit formation. b) Frugivores bore an exit hole through the fruit wall and calyx (not shown) before the onset of pupation. c) Budworm infections are inconspicuous initially; infection is obvious for large buds that remain closed as the one pointed out by the arrow. (Photos: T’ai H. Roulston)

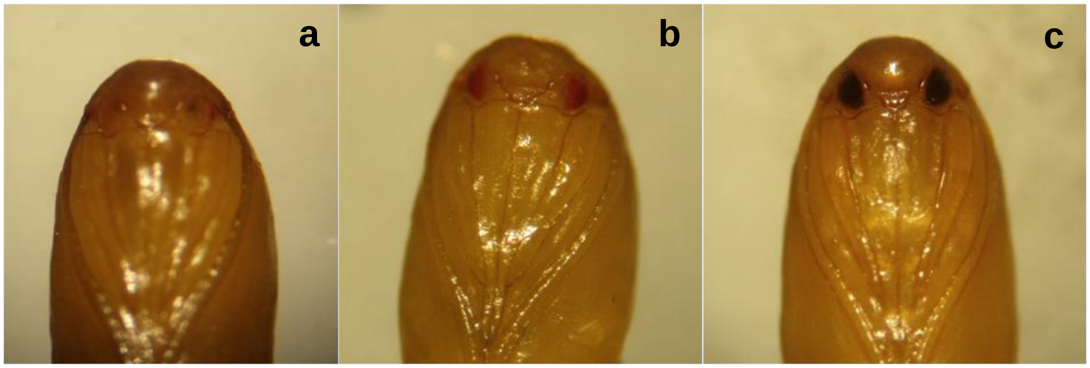


Figure 5. Eye pupal stages in *Symmetrischema lavernella*. Initially no coloration is evident in the eye area (a). Later red pigmentation is visible (b) and gradually becomes a distinct dark area (c).

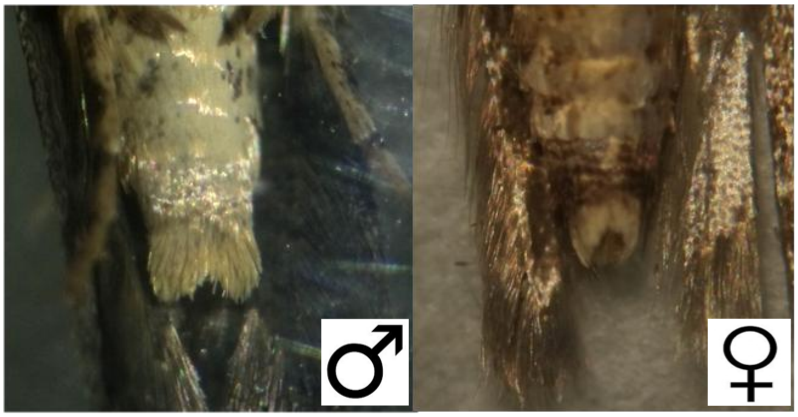


Figure 6. Genital morphology of males (left) and females (right) in *Symmetrischema lavernella*.

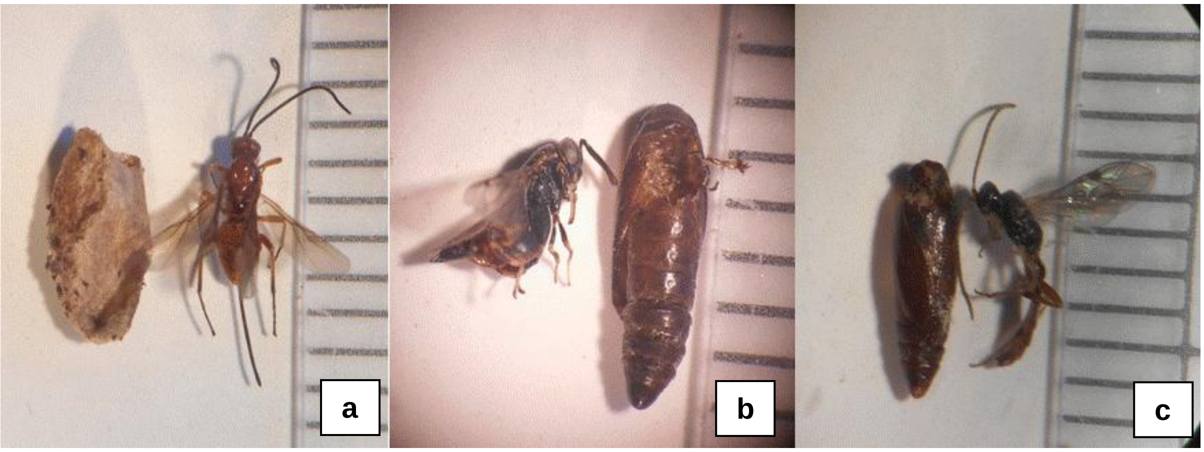


Figure 7. Parasitoid wasps found on *Symmetrischema lavernella*'s budworms and frugivores exposed to field conditions for three weeks in late summer. a) *Bracon* sp. (Braconidae), found almost exclusively on frugivores, next to its pupal case. b) *Conura* sp. (Chalcididae), found only on budworms, pupates inside *S. lavernella*'s pupal case (to its right). c) *Cryptinae* sp. (Ichneumonidae), found in one budworm, also pupates inside *S. lavernella's* pupal case (to its left). Divisions in the ruler indicate millimeters.

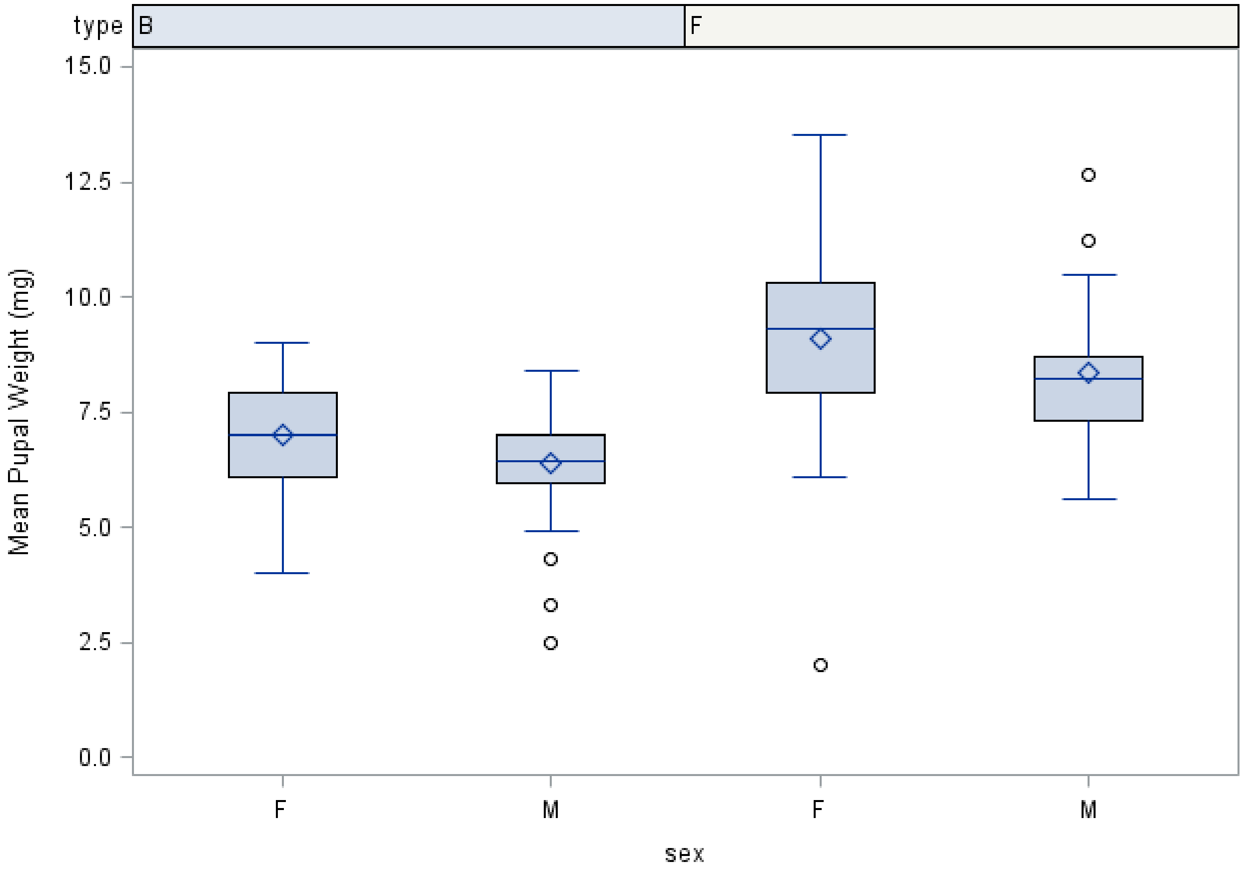


Figure 8. Mean pupal weights for females (F) and males (M) for both, budworm (B) and frugivore (F) feeding strategies in *Symmetrischema lavernella*. Frugivores grow 33% bigger than budworms (three-way ANOVA: $F_{1,131}$=73.11, P<0.0001) and females are the heaviest for both feeding strategies ($F_{1,131}$=7.47, P=0.0071).

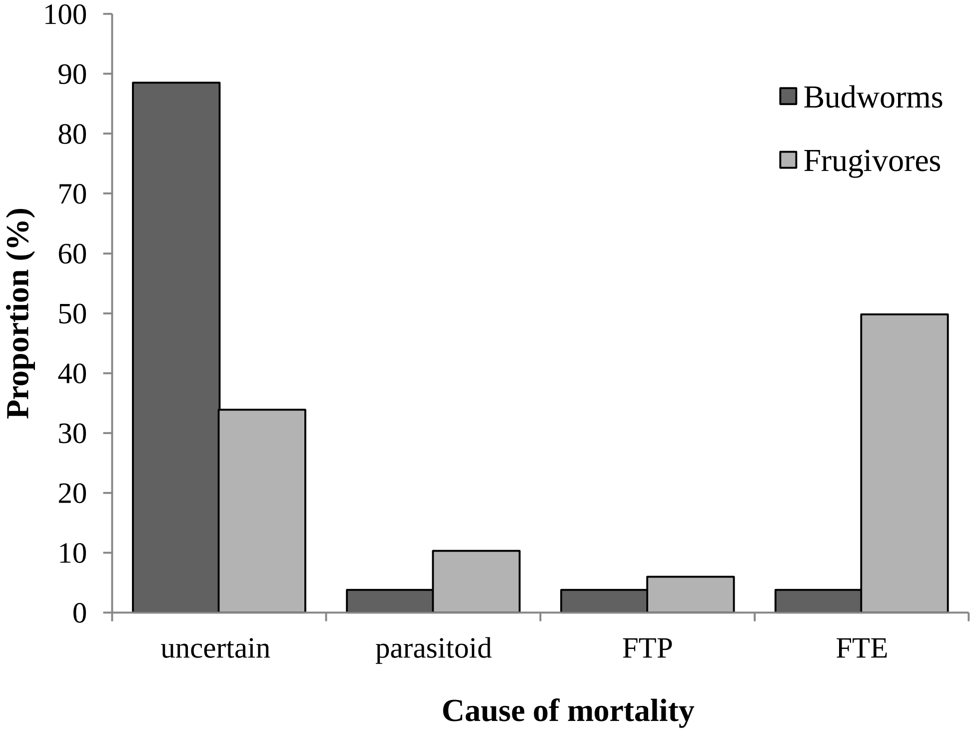


Figure 9. Mortality causes for *Symmetrischema lavernella* budworms and frugivores that failed to reach adulthood. Uncertain conditions for which death was assumed include events such as buds or fruits being dropped off the plant or abandonment of bud or fruit. FTP= failure to pupate; FTE= failure to emerge.

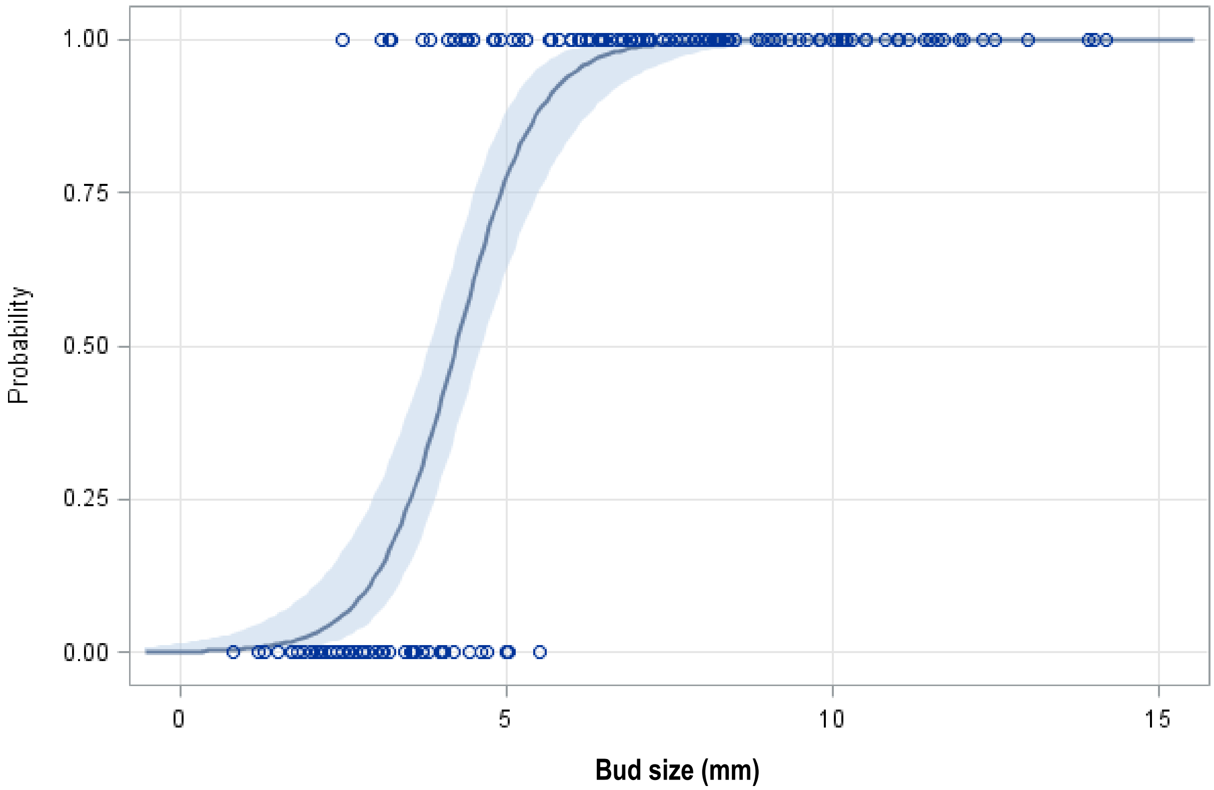


Figure 10. Logistic regression modeling probability of adopting a frugivore (P=1) versus a budworm (P=0) strategy in response to bud size at moment of colonization by *Symmetrischema lavernella*. Frugivores are more likely for buds larger than 4.2 mm. Open circles represent observed values, the solid curve represents the predicted relationship and the shaded area represents 95% confidence limits.

Tables

Table 1. Results of analysis of variance test evaluating the effect of *Physalis heterophylla* patch density, larval feeding strategy, size of bud at moment of exposure, density-by-strategy interaction and size-by-strategy interaction in overall survival of *Symmetrischema lavernella* after exposure to field conditions for three weeks. Significant effects at α=0.05 shown in bold. df=degrees of freedom.

Model term	numerator df	denominator df	F ratio	*P*
density	1	8	0.44	0.5262
strategy	1	419	5.72	**0.0172**
size	1	419	18.59	**<0.0001**
density*strategy	1	419	0.20	0.6582
size*strategy	1	419	1.75	0.1861