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Fruit abscission by *Physalis* species as defense against frugivory

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Abstract

Fruit abscission as a response to herbivory is well-documented in many plant species, but its effect on further damage by mobile herbivores that survive fruit abscission is relatively unstudied. *Physalis* plants (Solanaceae) abscise fruit containing feeding larvae of their main frugivore, *Heliothis subflexa* Guenée (Lepidoptera: Noctuidae), a specialist moth. We tested the ability of *H. subflexa* larvae placed under the plant canopy to find and climb onto two architecturally different *Physalis* species. *Physalis pubescens* L., a low, shrub-like, spreading plant, abscises its fruit at a higher rate than *Physalis angulata* L., a tall arborescent plant. As a result, small larvae are more often dropped from *P. pubescens*. Third and fifth instars located *P. pubescens* faster and with a higher probability than *P. angulata*. Although fifth instars outperformed third-instar caterpillars at finding *P. angulata*, *P. pubescens* was located equally fast by the two instars. *Heliothis subflexa* located *Physalis* plants more successfully and more quickly than a close relative, the generalist *Heliothis virescens* Fabricius. The higher fruit abscission rates in *P. pubescens* may be an evolved response to its greater susceptibility to searching caterpillars.

Introduction

Many plants abscise leaves, flowers, and fruit damaged by herbivory. Because herbivore-damaged fruit may not develop properly, abscission may be an efficient way for a plant to minimize its losses by not investing further in the damaged fruit. When the herbivore is dislodged from the plant along with the abscised fruit, abscission can additionally be viewed as a direct defense against the herbivore. Many studies have documented the phenomenon of herbivores falling to the ground with the abscised plant part (Stephenson, 1981, and references within). However, the fate of these herbivores has rarely been investigated, in part because (1) relatively sessile stages of the herbivores may be involved (e.g., eggs, galls, and leaf miners) (Stiling et al., 1991; Pellmyr & Huth, 1994; Espirito-Santo & Fernandes, 2002), and (2) many herbivores can complete

development within the abscised plant part (Janzen, 1971; Cross, 1973; Racette et al., 1992; Toy et al., 1992; Minchinton & Dalby-Ball, 2001) (but see investigations of a few sessile insects: Dohanian, 1944; Fernandes & Whitham, 1989; Waddell et al., 2001).

Heliothis subflexa Guenée (Lepidoptera: Noctuidae) is a frugivorous specialist, feeding solely on some *Physalis* species (Solanaceae) (Brazzel et al., 1953; Bateman, 2006), and is the main frugivore of most natural North American populations of *Physalis*. *Heliothis subflexa* larvae feed on the berry-like *Physalis* fruit surrounded by a lantern-like calyx. These two parts, the calyx and the berry inside, are hereafter referred to as the *Physalis* fruit. Some plants in the genus *Physalis* drop their fruit in response to herbivory by *H. subflexa*. If the fruit abscises while the larva is within the calyx, the larva falls to the ground along with the fruit. Preliminary experiments have found that 14 and 22% of abscised fruits of *Physalis angulata* L. and *Physalis pubescens* L., respectively, contained larvae (JL Petzold, unpubl.). Because larvae must feed on multiple (ca. 3) fruit to complete development, most dislodged larvae on the ground must

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re-locate the host plant, climb back onto it, and enter a calyx. The ability of the larva to do this may be affected by (1) the architecture of the plant and its understory landscape (e.g., weeds), (2) the size of the larva, and (3) the larva's behavioral response to being on the ground, under the plant canopy.

Physalis species vary considerably in general architecture, from low spreading forms to tall arborescent forms. *Physalis pubescens* and *P. angulata* have a marked difference in architecture. *Physalis pubescens* is shrub-like, with many major branches drooped downward and much of the canopy close to and often touching the ground, while *P. angulata* is arborescent, with the stem and major branches upright. The architecture of both species is somewhat plastic, responding to density of surrounding vegetation and light competition, but the typical forms described above predominate in natural populations. Natural populations of these two species are often infested by *H. subflexa* (Sisterson, 1997; Bateman, 2006) and these two species were used preferentially by *H. subflexa* in common garden studies in North Carolina, USA, (Benda, 2007) and Jalisco, Mexico (Bateman, 2006).

In addition to differences in plant architecture, these two *Physalis* species differ in their rates of fruit abscission. *Physalis pubescens* shed fruit more readily in response to frugivory than *P. angulata* (JL Petzold, unpubl.). *Physalis pubescens* also abscise ripe fruit more quickly than *P. angulata*. These differences in abscission patterns lead to much younger (and hence, smaller) larvae being dropped by *P. pubescens* than by *P. angulata* (ML Bateman, unpubl.). In general, *P. pubescens* also produce more abscised, intact fruit per plant than *P. angulata*.

To determine the effectiveness of the abscission response at reducing herbivore impact in *P. angulata* and *P. pubescens*, we examined the ability of *H. subflexa* larvae to re-locate and climb onto both plants. Although the two *Physalis* species may differ in various traits that may affect herbivore performance (e.g., chemistry, color, and pubescence), we hypothesized that their divergent architecture would play a major role in plant re-discovery by dislodged larvae. We therefore compared the ability of third and fifth *Heliothis subflexa* instars to locate *P. angulata* and *P. pubescens* plants. *Heliothis subflexa* fifth instars are 29–35 mm long, which is 2–2.5-fold larger than third instars. If *H. subflexa* larvae are better able to re-locate and infest the shrub-like *P. pubescens* than the upright *P. angulata*, higher abscission rates and investment in more, smaller fruit by *P. pubescens* may represent a direct defense against *H. subflexa*. In this scenario, because many dislodged larvae perish on the ground, *P. angulata* would be able to reduce the number of larvae on the plant by abscising fewer fruit. Because other intact fruit are protected, *P. angulata* would need to produce

fewer fruit total to produce the same number of progeny as *P. pubescens*.

Moreover, if third instars experience greater difficulty locating *Physalis* than fifth instars, then earlier abscission increases the effectiveness of this herbivore defense. If the difference between instars is greater when locating *P. pubescens* than when locating *P. angulata*, then the disadvantage of *P. pubescens*' architecture may be compensated by an earlier abscission leading to dropping of smaller instars. This would suggest that the interaction of the host-location abilities of the frugivore with plant architecture may select for different abscission patterns.

Because *H. subflexa* is a specialist on *Physalis* species, and shows a number of host plant-specific behaviors (such as using the plant as shelter against parasitoids, and oviposition preference for *Physalis*) (Oppenheim & Gould, 2002; Benda, 2007), we assessed whether *H. subflexa* would be more adept at re-locating *Physalis* plants than a related generalist herbivore. *Heliothis virescens* Fabricius larvae feed on leaves and fruits of species in more than 14 plant families, including Solanaceae, but not *Physalis*. Although *H. virescens* becomes dislodged when cotton fruit is abscised (Adkisson et al., 1964), *H. virescens*, unlike *H. subflexa*, also readily feeds on leaves on most of its host plants. Therefore, we hypothesized that *H. subflexa* larvae have adapted to *Physalis* fruit abscission with enhanced abilities to re-locate the plant than have *H. virescens* larvae.

Materials and methods

Laboratory-reared insects

Laboratory-reared *H. subflexa* and *H. virescens* third and fifth instars were tested in 2004 and 2005. The *H. virescens* laboratory colony (YDK strain) was established using eggs from flowering tobacco in Yadkin County, NC, USA, in 1988 (Gould et al., 1995). The *H. subflexa* laboratory colony (Lab strain) was established using larvae collected from natural populations of *Physalis* in Florence and Barnwell Counties, SC, USA, in 1996 (Sheck et al., 2006). *Heliothis subflexa* and *H. virescens* were reared as outlined by Sheck & Gould (1993).

Larvae used in field bioassays were marked with a spot of either writer's corrective fluid (white or pink), or permanent marker (blue or red), to distinguish the two species. Larvae were transported to the field in a cooler and kept at 26–28 °C until testing.

Wild larvae (2005 only)

Larvae were collected from *Physalis* fruit in the same field in Clayton, NC, USA (35°37'N, 78°26'W), where assays were conducted. Larvae were kept individually in 30-ml cups with a fresh *P. angulata* or *P. pubescens* fruit until they

reached the instar and age needed for testing (fruit was replaced as necessary). Wild *H. subflexa* larvae were not marked, because only one insect species was tested.

***Physalis* plants**

In both 2004 and 2005, *Physalis* plants were started from seeds in the greenhouse. *Physalis* seeds were from plants grown in our research field in the previous season. Seeds were originally collected from wild populations in Orangeburg County, SC, USA (33°33'N, 81°04'W) in 1998. Three-week-old seedlings were transferred into ca. 0.5-l black plastic pots and fertilized with one teaspoon of Osmocote 14-14-14 (N-P-K). After transplanting, plants were fertilized weekly with a liquid 20-20-20 foliar spray.

In mid-July 2004, 6-week-old *P. angulata* and *P. pubescens* plants were transplanted into two fields: (1) a 0.26-ha field on the NCDA/NCSC Central Crops Research Station (CCRS) (Clayton, NC, USA), and (2) a small field on the Lake Wheeler USDA-ARS research facility (Raleigh, NC, USA). In late June 2005, 10-week-old *P. pubescens* were transplanted to the CCRS field. In addition to the *P. pubescens* transplanted to the field, 'feral' *P. angulata* and *P. pubescens* from the seed bank of previous research seasons in the same field were also used for the bioassays in 2005.

Plants were used for multiple assays, both within and between days. But no plant was used more than three times, in order to incorporate natural variation within the typical architecture of the two *Physalis* species. One alteration to the architecture was made: in order to standardize the architecture of the *P. angulata* plants as distinctly different from that of *P. pubescens*, the occasional lower branch (extending from the main stem) that touched the ground was removed at the main stem of *P. angulata* plants using plant clippers.

The landscape surrounding the *Physalis* plants was composed of a relatively smooth sandy top soil and a naturally occurring population of non-solanaceous weeds, mainly sedges and nutsedges (Cyperaceae). While these weeds also occurred under the canopy of the *P. angulata* plants, the soil surface under the more densely shaded *P. pubescens* canopy was generally free of other plants. The ground under both the *P. pubescens* and *P. angulata* canopies was littered with abscised and often empty calyces.

Behavioral assay of host plant location

One *H. subflexa* and one *H. virescens* larva were simultaneously placed at the edge of the canopy of the same *Physalis* plant. Larvae were gently placed on the soil using a paintbrush to minimize disturbance. Larvae were tested in blocks of four larvae, such that one pair of larvae was placed under the *P. angulata* canopy at approximately

the same time that another pair was placed under the *P. pubescens* canopy. Plants used in the assays were 1–2.4 m away from all other *Physalis* plants. Each larva was observed until it located the *Physalis* plant or up to 45 min. Occasionally (20 out of 296 observed larvae), the observer lost track of individual larvae during the bioassay. In these instances, the other larvae in the block were still included in the analyses. Observations were recorded on a Sony TCM-353V cassette recorder (Sony Corp., Taiwan).

Two parameters were used to quantify the abilities of larvae to locate *Physalis* plants. The larvae were scored (1) binomially according to whether or not they were able to successfully locate the *Physalis* plant, and (2) quantitatively, using the time spent locating the plant. 'Location' was defined as completed when the larva had climbed onto the plant and remained there for ≥ 30 s.

Early third and fifth instars were tested in the assays. Age within instar was distinguished by the width of the head capsule relative to the body. Early third instars were used, because preliminary feeding assays showed that a newly hatched larva can develop to the third instar in a single *P. angulata* or *P. pubescens* fruit that had been manually removed from the plant. Therefore, this is an estimate of the smallest larva that might abandon an abscised fruit. This estimate errs on the side of a later, larger instar, because it assumes the larva remains inside the calyx long enough to finish feeding on the fruit. Fifth instars were used because, as the largest instar, they may be the most able to navigate the heterogeneous terrain under a plant canopy and re-locate the *Physalis* plant from which they had fallen. Early fifth instars were used to ensure that larvae were motivated to feed (since late fifth instars stop feeding and enter a wandering stage prior to pupation).

An incomplete block design was implemented, where insect species and plant species were tested within each block, and instar and insect origin (laboratory-reared and wild) were tested between blocks. Block accounted for differences between each blocked set of larvae tested [i.e., climatological factors, field site, individual plants, and marking system used (writer's corrective fluid or permanent marker)]. Assays were conducted between 09:30 and 20:00 hours, from 30 July–12 October 2004 and from 10 August–3 October 2005. Air temperature at 5 cm above soil level was 30.4 ± 0.4 °C during these assays [mean \pm SE, temperature was measured for 136 plants during the 75 blocked assays (two plants per block)]. Assay blocks occasionally overlapped, such as when a second block of assays was initiated before the 45-min-long observation of the first block had ended. Fixed variables that differed between blocks (instar and insect origin) were regularly dispersed across date and time of day (i.e., not all wild fifth instars were tested on the same day).

Data analysis

To determine whether the successful location of the *Physalis* plant (success) was affected by plant species, insect species, instar, and interactions, we conducted an analysis using Proc GLIMMIX in the statistical program SAS 9.1.3 (SAS, 2003), assuming a binomial distribution and a logit link, where block was treated as random and all other variables were treated as fixed. GLIMMIX is a procedure designed for specific non-normal distributions such as the dichotomous distribution. Block was treated as a random variable, because it was a source of replication, and all other variables were treated as fixed. The resulting least squares means (LS means) were used to calculate success probabilities and standard errors.

This analysis was conducted using three data sets. (1) Laboratory-reared larvae on *P. angulata* and *P. pubescens*. Year was also included in this analysis, as a fixed variable. (Statistical model: success = year | plant species | insect species | instar). (2) Wild larvae on *P. angulata* and *P. pubescens*. Only *H. subflexa* fifth instars were tested. (Statistical model: success = plant species). (3) Wild and laboratory-reared larvae on *P. angulata* and *P. pubescens*. Only *H. subflexa* fifth instars were tested. Insect origin (laboratory-reared vs. wild) was also considered in this analysis, as a fixed variable (Statistical model: success = plant species | insect origin).

The same three data sets and statistical models for success were also applied to analyze the number of minutes to locate the *Physalis* plant (minutes to location). To determine whether minutes to location was affected by plant species, insect species, and instar, and interactions, we conducted a factorial analysis of variance (ANOVA) using Proc MIXED (SAS, 2003), where block was treated as random and all other variables were treated as fixed. Time values were log-transformed to reduce heterogeneity among the within-treatment variances and to improve normality. Larvae that were unsuccessful in locating the host plant were excluded from further analysis. Although exclusion of unsuccessful larvae reduced sample size and may have incorrectly assumed that larvae will never locate the plant after 45 min, inclusion of these unsuccessful larvae overestimated larval success, inflated the time estimate, and made its distribution more bimodal. Tukey–Kramer adjustment for multiple comparisons (of LS means) was applied as necessary.

Results

Location of *Physalis* plants by laboratory-reared *Heliothis subflexa* and *Heliothis virescens* larvae

When year was included as a factor in the regression model for laboratory-reared larvae and this model was analyzed using Proc GLIMMIX, the model did not converge because

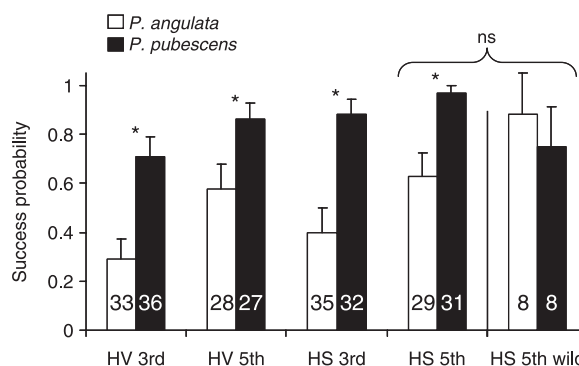


Figure 1 Mean (+ SE) probability of success of *Heliothis subflexa* (HS) and *Heliothis virescens* (HV) larvae locating the *Physalis* plant per block. Values were calculated across years. All bars represent laboratory-reared larvae ('3rd' or '5th' instars) except the pair labeled 'wild'. Numbers on the histogram bars indicate the number of larvae tested. Asterisks indicate a significant difference ($P < 0.05$) between paired bars.

of insufficient variation in subsets of the data (all but one *H. subflexa* fifth instar located *P. pubescens*). However, Proc MIXED can better handle data with this characteristic. The same model, analyzed using Proc MIXED, found no effect of year ($F_{1,62} = 0.01$, $P = 0.9430$) or any interactions involving year ($P = 0.0765$ – 0.9984), so plant location was analyzed across years (using Proc GLIMMIX). The probabilities of *H. subflexa* and *H. virescens* larvae (across instars) successfully locating *P. pubescens* plants were 0.94 ± 0.03 and 0.79 ± 0.06 , respectively (means \pm SE, throughout results). These were greater than the success probabilities of larvae locating *P. angulata* (0.51 ± 0.07 and 0.43 ± 0.07 , respectively; effect of plant species: $F_{1,179} = 31.93$, $P < 0.0001$) (Figure 1). *Heliothis subflexa* and *H. virescens* fifth instars were 1.3- and 1.4-fold more successful, respectively, than third instars (effect of instar: $F_{1,64} = 6.90$, $P = 0.0108$). The probability of *H. subflexa* larvae (across instars) successfully locating *Physalis* plants (across plant species) was 0.80 ± 0.05 , and was greater than the success probability of *H. virescens*, which was 0.63 ± 0.06 (effect of insect species: $F_{1,179} = 5.17$, $P = 0.0241$). There were no significant interactions of the three independent variables ($P = 0.1745$ – 0.8751).

Location of *Physalis* plants by wild *Heliothis subflexa* larvae

Wild *H. subflexa* fifth instars located the two *Physalis* species equally well (effect of plant species: $F_{1,6} = 0.52$, $P = 0.4994$) (Figure 1). There was also no significant difference in success probabilities of laboratory-reared and wild *H. subflexa* fifth instars ($F_{1,37} = 0.20$, $P = 0.6558$). There was a significant interaction of plant species and insect origin ($F_{1,35} = 4.75$, $P = 0.0361$). A Tukey-adjusted

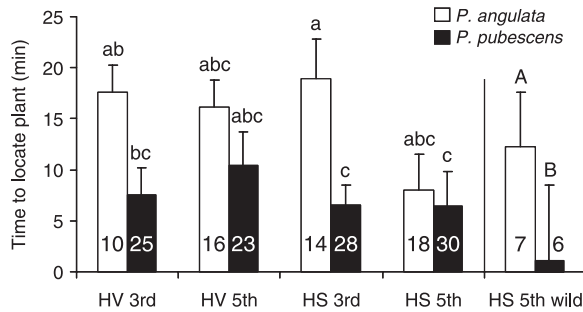


Figure 2 Mean (+ SE) number of minutes that *Heliothis subflexa* (HS) and *Heliothis virescens* (HV) larvae took to locate the *Physalis* plant per block (where unsuccessful larvae were excluded from the analysis). Values were calculated across years. All bars represent laboratory-reared larvae ('3rd' or '5th' instars) except the pair labeled 'wild'. Regarding the laboratory-reared larvae only, histogram bars capped with different letters are significantly different ($P < 0.05$) using a Tukey-adjusted t-test of least squares means. Numbers on the histogram bars indicate the number of larvae that successfully located the *Physalis* plant.

t-test of LS means revealed that this interaction was due to a difference in success probability of laboratory-reared *H. subflexa* fifth instars between plant species. Within each plant species, there were no significant differences in success probabilities between laboratory-reared and wild *H. subflexa* (Tukey t-test: $P = 0.3264$ – 0.9114).

Time to locate *Physalis* plants by laboratory-reared *Heliothis subflexa* and *Heliothis virescens* larvae

Only four of 67 larvae that were observed for an additional 15 min (for a total of 60 min) successfully located and climbed the *Physalis* plant. Exclusion of unsuccessful larvae decreased skew in the data set and did not substantially modify the results (analysis not shown). Since most third instars did not successfully locate the *P. angulata* plant in 2004, a test of the effect of year was conducted using fifth instars only. The amount of time laboratory-reared fifth instars required to locate the *Physalis* plants did not differ by year ($F_{1,28} = 1.07$, $P = 0.3088$), nor by interactions of other main effects with year ($P = 0.1809$ – 0.6475). Therefore, time to plant location (of both instars) was analyzed across years. *Heliothis subflexa* and *H. virescens* larvae (across instars) took significantly less time to locate *P. pubescens* (6.5 ± 1.1 and 8.9 ± 1.7 min, respectively) than to locate *P. angulata* plants (12.8 ± 2.2 and 16.7 ± 2.9 min, respectively) (effect of plant species: $F_{1,97} = 17.55$, $P < 0.0001$) (Figure 2). Effects of instar and insect species were not significant ($F_{1,62} = 3.68$, $P = 0.0596$, and $F_{1,97} = 3.67$, $P = 0.0585$, respectively). The difference between plant species was larger within the third instars than the fifth instars, resulting in a significant

interaction of plant species with instar ($F_{1,97} = 7.99$, $P = 0.0057$). *Heliothis subflexa* third instars took 2.9 times longer to find *P. angulata* than to find *P. pubescens* (Tukey-adjusted t-test of LS means: $P = 0.0078$), while the time *H. subflexa* fifth instars took to locate the plant differed between plant species by a factor of only 1.3 (Tukey t-test: $P = 0.9994$). Similarly, the time *H. virescens* third and fifth instars took to locate the *Physalis* plant differed between plant species by a factor of 2.3 and 1.3 (Tukey t-test: $P = 0.120$ and 0.9857), respectively. All other interactions were not significant ($P = 0.2126$ – 0.6244) and were dropped from the analysis.

Time to locate *Physalis* plants by wild *Heliothis subflexa* larvae

Wild *H. subflexa* fifth instars were qualitatively similar to their laboratory-reared counterparts, but with a much larger difference in mean time to locate *P. angulata* plants (12.3 ± 3.7 min) relative to mean time to locate *P. pubescens* plants (1.1 ± 0.2 min) (effect of plant species on wild larvae: $F_{1,4} = 47.33$, $P = 0.0023$) (Figure 2). Analyzing across insect origin, there was a significant difference between time to locate *P. angulata* relative to *P. pubescens* (effect of plant species: $F_{1,21} = 11.40$, $P = 0.0029$). As a main effect, insect origin was not significant ($F_{1,36} = 0.01$, $P = 0.9346$), but there was a significant interaction of plant species and insect origin ($F_{1,21} = 8.67$, $P = 0.0077$). This was due to a significant difference in the amount of time wild larvae took to find *P. angulata* relative to *P. pubescens* (Tukey-adjusted t-test of LS means: $P = 0.0087$) and no other significant differences among the wild and laboratory-reared fifth instars ($P > 0.13$). As in the comparison of laboratory-reared *H. subflexa* and *H. virescens*, exclusion of unsuccessful larvae did not substantially modify the results (analysis not shown).

Discussion

When a *H. subflexa* larva is dislodged from a plant along with a fallen fruit, fruit abscission effectively reduces the impact of herbivory on the *Physalis* plant both directly and indirectly. Fruit abscission both reduces the probability of herbivory by the dropped larva on the remaining attached *Physalis* fruits, and increases the probability of morbidity and mortality of the dropped larva. We found that the effectiveness of the abscission strategy depends on plant species, behavioral specialization of *H. subflexa* in its ability to locate the *Physalis* plant, relative to *H. virescens*, and the size of the dislodged larva.

In general, both instars of both *Heliothis* species located *P. pubescens* more effectively than *P. angulata*. The differences we observed between the two *Physalis* species are likely due to dramatic differences in their architecture, although our

bioassays were not designed to separate architecture from other plant species-specific traits and potential *Heliothis* cues, such as chemistry, texture, and color. Nonetheless, larvae appeared to respond to all vertical shapes by reaching towards them – raising their head and thorax and waving from side to side in a stereotypical manner (i.e., ‘questing’ in Berdegue et al., 1997). Larvae then climbed the nearest vertical object, regardless of what it was – a rock, a blade of grass, or a stem or an over-hanging *Physalis* leaf. The majority of larvae that climbed onto the *Physalis* plant did so via bridges created by surrounding vegetation (*P. angulata*) or overhanging branches and leaves (*P. pubescens*), not via the main stem of the *Physalis* plant. The visual and olfactory range of lepidopteran larvae usually does not exceed a few centimeters (Cain et al., 1985; Dethier, 1989), so visual location of the main stem of a *Physalis* plant from the edge of the canopy is unlikely. Wild *H. subflexa* fifth instars exhibited the same stereotypical searching behavior as laboratory-reared larvae, and although their success probability in locating plants was similar to that of laboratory-reared *H. subflexa* fifth instars, this analysis was constrained by small sample size of wild larvae. The distribution of location times was also similar between wild and laboratory-reared insects. Most *H. subflexa* fifth instars (68–75%) found the *Physalis* plant within 15 min of being placed on the ground, regardless of insect origin or plant species.

The differences between the insect species in locating a plant (when unsuccessful larvae were included in the analysis) have at least two potential explanations. *Heliothis subflexa* may respond to host plant cues undetected or not responded to by *H. virescens* or alternatively, *H. virescens* larvae may not be as adept as *H. subflexa* larvae at locating vertical surfaces and climbing them. Cotton, a host plant of *H. virescens*, abscises fruit in response to herbivory by *H. virescens* (Adkisson et al., 1964), but the ability of fallen *H. virescens* larvae to re-establish on the cotton plant is undocumented. Testing *H. virescens* larvae on their own host plant would reveal if the advantage of *H. subflexa* larvae is due to an interaction with its host plant or an innate specialized ability. Nevertheless, for both explanations, differences in the ages of the two laboratory colonies might have also contributed to apparent species differences.

Larval size significantly affected location of the *Physalis* plant. The general searching behavior was the same for both instars, but third instars displayed greater difficulty navigating the terrain, and were often unable to reach a high perch. Third instars may also be more affected by stressors associated with re-locating the host plant than fifth instars (e.g., starvation stressors; van Dam et al., 2001).

We predicted that smaller instars would be less successful at locating plants and that this size-related difference

would be greater for larvae searching for *P. pubescens* than for larvae searching for *P. angulata*. Such a pattern would implicate a strong selection force on *P. pubescens* to drop fruit earlier than *P. angulata*, which would result in smaller larvae being dropped from the *P. pubescens* plant. However, we could not relate earlier abscission in *P. pubescens* to differences in plant-location ability between third and fifth instars. In fact, early abscission, which dislodges younger larvae from the plant, would appear to favor *P. angulata* more, because its branches infrequently contact the ground. Nonetheless, it is possible that *P. pubescens* benefits from dislodging even younger first and second instars. The two *Physalis* species differ markedly in their numerical investments in fruit and rates of abscission. In this context, it is important to consider fruit abscission as a component of an integrated life history syndrome that considers both the reproductive allocation by *Physalis* and the escalating cost to *H. subflexa* of feeding on an abscised fruit and searching on the ground for a *Physalis* plant.

These results demonstrate how plant architecture and abscission patterns may affect herbivore impact on *Physalis*. Notably, conclusive evidence that fruit abscission serves the *Physalis* plant as an herbivore defense would require determination of a difference in fitness of plants that abscised or did not abscise fruit. The results of this study demonstrate the specialized ability of *H. subflexa* to counteract fruit abscission as a defense mechanism by successfully locating the plant from the ground. It would be interesting to compare host plant location by other insect species from abscised plant parts with the location abilities of this specialized herbivore. The effects of instar and plant dispersion on other foraging lepidopteran larvae (Cain et al., 1985; Dethier, 1989) are consistent with the results of this study. However, to better understand the effectiveness and importance of abscission as a defense against herbivores, more studies of the fate of mobile larvae dislodged with abscised fruit are needed.

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