CrossMark

POPULATION ECOLOGY - ORIGINAL RESEARCH

Trade-offs in host choice of an herbivorous insect based on parasitism and larval performance

Shannon M. Murphy[1] · Katrina J. Loewy[1]

Abstract Herbivore diet breadth is predicted to evolve in response to both bottom-up and top-down selective pressures, including host plant abundance, quality and natural enemy pressure. As the relative importance and strength of interactions change over an herbivore's geographic range, local patterns of host plant use should change in response, altering local diet breadths. Fall webworm (*Hyphantria cunea*) is a widespread, polyphagous moth species that feeds on hundreds of plant species worldwide. Populations of fall webworm in Colorado remain polyphagous, but their diet breadth is restricted compared to other populations and thus present an ideal opportunity to test the ecological drivers of host use by a polyphagous herbivore. We investigated how host abundance, larval performance, and parasitism affect host use for fall webworm to test how these selective pressures may act individually or in concert, as well as the role of any trade-offs among fitness components, to explain diet breadth and host use. We found that host abundance was a significant predictor of host use, which suggests a selective pressure to reduce search time for oviposition sites by adult females. We also detected an important trade-off between bottom-up and top-down selective pressures: higher quality host plants also had a greater proportion of larval mortality due to parasitism. Local patterns of host plant abundance appear to narrow the set of hosts used by fall webworms in Colorado, while the trade-off between host quality and risk of parasitism helps explain the maintenance of a generalized feeding strategy within this restricted set of hosts.

Keywords Diet breadth · Plant–insect interactions · Polyphagy · Lepidoptera · Specialization

Introduction

Of the many decisions faced by an insect herbivore, choosing a host plant is among the most important. Plants provide food for the herbivore and can also potentially provide shelter and protection from natural enemies. Herbivorous insects are often categorized as specialists, which feed on only one or a few plant families, or generalists, which feed on many different plant families; more than 90 % of insect herbivores are considered dietary specialists (Price et al. 2011; Schoonhoven et al. 2005). There are clear fitness benefits gained by dietary specialization. Specialist herbivores have evolved behaviors and metabolic systems to counteract and even thrive on their hosts' physical and chemical defenses (Schoonhoven et al. 2005). Some larval lepidopterans avoid feeding on the most highly defended host structures, and some have specialized enzymatic pathways that allow them to gain nutrition from compounds that would be toxic to other herbivores (Karban and Agrawal 2002). Juvenile insect herbivores often have limited mobility, and are restricted to feeding on hosts chosen by their mothers; however, the relationship between adult preference and larval performance can be quite complex (Mayhew 1997). For Lepidoptera, the positive relationship between the host preference of an ovipositing female

✉ Shannon M. Murphy
Shannon.M.Murphy@du.edu

[1] Department of Biological Sciences, University of Denver, 2190 East Iliff Avenue, Denver, CO 80208, USA

and the performance of larvae on the same plant is stronger in specialized species than in generalized ones (Gripenberg et al. 2010). However, both specialist and generalist adults and their offspring are exposed to additional environmental conditions that may favor generalization and it is important to understand how specialization may evolve despite these selective pressures. For example, specialized females searching for rare hosts spend more time vulnerable to attack by natural enemies, and may not be able to lay a full complement of eggs. The ability to use additional hosts can reduce search time and result in more oviposition opportunities, translating into a higher percentage of eggs laid (Johansson et al. 2007). Greater resource availability may also benefit larvae that leave or fall from their original host plants (Bernays and Minkenberg 1997). Multiple host plants also allow for the possibility of diet mixing within the larval stage, which has been shown to improve larval performance for some generalist species (Karban et al. 2010).

Certain bottom-up and top-down interactions between host plants, herbivores and natural enemies may also support a generalist herbivore feeding strategy. Jeffries and Lawton (1984) defined enemy-free space as a way of living that reduces a species' exposure to parasitoids and predators. More recent research has demonstrated that host choice plays an important role in creating enemy-free space (Murphy 2004) and that trade-offs exist between enemy-free space and plant quality (Singer et al. 2004). If host plants that provide protection from natural enemies and host plants that provide high-quality food are different, the trade-off insects experience when choosing among these hosts may sustain relatively polyphagous habits within insect populations (Rodrigues et al. 2010). The existence and direction of such trade-offs are expected to vary, even when the suite of potential host plant species remains unchanged. Both biotic and abiotic factors modify a host plant's suitability throughout its range and growing season (Michaud 1990), and variation in host plant genotype may alter its quality as a food source as well (Fox and Morrow 1981). Throughout an herbivore's range, it can experience different communities of plants, natural enemies and competitors. The resulting patchwork of selective pressures variably shapes species' habits, including host use and diet breadth (Thompson 1998, 2005).

The fall webworm (*Hyphantria cunea* Drury, Erebidae) presents an ideal opportunity to test the ecological drivers of host use by a polyphagous herbivore. Worldwide, fall webworms are known to feed on hundreds of different host plant species in dozens of plant families (Warren and Tadić 1970). In North America, populations of fall webworms in the eastern US commonly feed on dozens of different species (Berger 1906; Greenblatt 1978; Mason et al. 2011). Compared with the broad array of host plants used by fall webworms throughout most of their range, host use in Colorado is relatively restricted with only 19 plant species recorded as hosts, and only three of those species accounting for over half of the records (Swain 1936; Loewy and Murphy, personal observation). Thus, while still considered dietary generalists by the common definition of feeding on plants in more than three plant families (Bernays and Graham 1988), Colorado fall webworms are relatively more specialized than other fall webworm populations and the selective pressures that could have led to this restriction in diet breadth are currently unknown.

Here we investigate three main selective pressures that may drive host use by fall webworms in Colorado and test for potential trade-offs among these selective pressures. We examined the impact of: (a) host plant abundance; (b) larval performance (survival, development time, pupal mass, and feeding efficiency); and (c) mortality from parasitoids on fall webworm host choice in the Colorado foothills through an observational field experiment as well as a manipulative split-brood experiment under controlled lab conditions. Our goal was to test how these selective pressures may act individually or in concert as well as the role of any trade-offs among fitness components to explain fall webworm diet breadth and host use.

Materials and methods

Study system

The fall webworm is a moth native to North America and invasive in Europe and Asia (Gomi and Takeda 1996; Jasič and Macko 1961; Yang et al. 2006). The moths were unintentionally introduced to Hungary and Japan in the 1940s and spread to other parts of Europe and Asia in the following decades (Tadić 1963; Yang et al. 2008). In China, fall webworms feed on 175 host tree species, including cultivated crops, and are considered a pest of economic importance (Yang et al. 2006).

In North America, fall webworms range across the US and are found in parts of Canada and Mexico (Masaki and Ito 1977). The taxonomic status of fall webworm is not well resolved and there may be genetically distinct "races" or forms in North America (Jaenike and Selander 1980) that are capable of interbreeding to produce fertile offspring (Masaki and Ito 1977; Oliver 1964). Morphologically, the only distinguishing feature between the two forms is larval head capsule coloration (black or red); within our study area in Colorado, we find only the red-headed form (Loewy et al. 2013).

Adults have been recovered in most Colorado counties, and relatively dense populations can be found in the foothills of the Colorado Rocky Mountains (Ferguson et al.

2000). Females lay all of their eggs in one batch and the gregarious larvae spin extensive webs for protection (Ito 1977) and thermoregulation (Morris and Fulton 1970; Rehnberg 2002), usually on the outer branches of deciduous trees. Fall webworm larvae are highly polyphagous in that they may feed on hundreds of species from dozens of plant families throughout their range (Warren and Tadić 1970), but individual larvae are functionally monophagous because they are confined to the host plant that the female chose as an oviposition site. However, their diet is limited regionally; in Colorado, we have observed them on 19 woody tree species representing 11 different genera from eight plant families. Fall webworms in Colorado can completely defoliate trees during outbreaks (Swain 1936) but the larvae and their expansive webs are usually more unattractive than harmful.

Study sites

Along the Colorado Front Range, fall webworm populations are concentrated in the canyon-carved foothills of the Rocky Mountains, as well as in the adjacent plains (Loewy et al. 2013). Fall webworm females preferentially lay their eggs along open edges (e.g., roads, streams), which make larvae easy to locate after they have built a web. We collected larvae from multiple field sites near the cities of Boulder (Boulder County, 40.090013, -105.359962), Fort Collins (Larimer County, 40.5852602, -105.084423), and Idledale (Jefferson County, 39.746944, -105.210833) 1557–2023 m in elevation in both 2010 and 2011. Fall webworms in these populations emerge as adults in midsummer and larval webs can be found from mid July up to and including the end of September (Loewy et al. 2013).

Host plant abundance

To quantify the abundance of host plants available to ovipositing female moths, we haphazardly chose 72 trees that had fall webworm webs in 2010 and 82 in 2011 to serve as focal trees for our study. For each host plant, we established a 30-m transect. 15 m to either side of the host, parallel with the habitat edge (e.g., road or stream) and approximately 5 m wide. For each tree along the transect, we recorded the species' identity and stem diameter at breast height, excluding plants that rarely serve as fall webworm hosts [we never observed webs on trees <1.5 m in height or gymnosperms, but see Oliver (1964) and Warren and Tadić (1970)]. We collected voucher specimens for all host plants as well as any plant species that we were unable to identify in the field for later identification (host plant voucher specimens are deposited in the Kathryn Kalmbach Herbarium at the Denver Botanic Gardens). If any trees within the transect had additional fall webworm webs, we also recorded

the number of webs in each tree, assuming that each web represented the offspring of a single mother (a brood) as suggested by Jaenike and Selander (1980) (host plants in Colorado are generally isolated and we currently have no evidence of larvae moving between plants).

Prior to analysis, we lumped several host plant species into higher taxonomic categories because of challenges with consistent identification and low sample size (Table 1). For example, "elm" included Siberian and Scotch elms (*Ulmus pumila* and *Ulmus glabra*), and "willow" included black willows, peachleaf willows, and other less common willow species (*Salix nigra* and *Salix amygdaloides*). Apple (*Malus domestica*) is distinguished from the many species of crabapple (all crabapple species are lumped as *Malus* spp.). We split chokecherry into two groups: chokecherry with green leaves (*Prunus virginiana*) and an ornamental variety with purple leaves, Schubert chokecherry (*Prunus virginiana* var. Schubert). The remaining hosts were narrowleaf cottonwood (*Populus angustifolia*), plains cottonwood (*Populus deltoides*), quaking aspen (*Populus tremuloides*), Lombardy poplar (*Populus nigra*), box elder (*Acer negundo*), green ash (*Fraxinus pennsylvanica*), thinleaf alder (*Alnus tenuifolia*), plum (*Prunus americana*), white oak (*Quercus alba*), black walnut (*Juglans nigra*), and viburnum (*Viburnum* sp.).

Plant communities in the canyon areas (designated "wild") were generally distinct from those of the cultivated residential developments. Larimer and Boulder Counties contained both wild and cultivated transects while all transects within Jefferson County were classified as wild. To quantify the similarity between wild and cultivated sites in 2010 we calculated a Jaccard coefficient (Gotelli and Ellison 2004). We pooled all species recorded on transects in wild areas into a "wild" site type and all species recorded on transects in cultivated areas into a "cultivated" site type. A Jaccard coefficient (or similarity index) is calculated as $C/(A + B + C)$ in which A = number of species only in wild sites, B = number of species only in cultivated sites, and C = number of species both site types have in common. The coefficient is expressed as the percentage of species shared between the two types of sites.

We calculated relative host use as the number of webs on a single species divided by the total number of webs in a site type (cultivated versus wild). We calculated relative abundance as the number of times a host species was present on transects divided by the total number of trees, both host and non-host, recorded on transects within a site, following Mason et al. (2011). We defined host species as any species observed with one or more webs during the study. Surveys took place when webs were most visible, from 7 August 2010 up to and including 26 September 2010 and 21 July 2011 up to and including 22 August 2011.

Table 1 Fall webworm host plants recorded in wild and cultivated sites in Colorado and in the eastern US

Wild[a, b]	Cultivated[a, b]	Eastern US[c]
1 *Acer negundo*[d] (6)	0 *Acer negundo*[d] (5)	*Acer negundo*[d]
Alnus tenuifolia (28)	*Alnus tenuifolia* (1)	*Ailanthus altissima*
2 *Fraxinus pennsylvanica*[d] (4)	2 *Fraxinus pennsylvanica*[d] (11)	*Alnus rubra*
Malus domestica (12)	*Malus domestica* (12)	*Betula nigra*
Populus angustifolia (191)	*Populus angustifolia* (2)	*Betula pendula*
Populus deltoides[d] (54)	*Populus deltoides*[d] (21)	*Betula populifolia*
1 *Prunus americana* (7)	0 *Prunus americana* (7)	*Carya glabra*
Prunus virginiana (124)	*Prunus virginiana* (6)	*Carya* sp.
Salix spp.[d] (37)	*Salix* spp.[d] (6)	*Castanea pumila*
3 *Ulmus* spp.[d] (15)	0 *Ulmus* spp.[d] (16)	*Cephalanthus occidentalis*
		Cercis canadensis
	1 *Juglans* sp. (1)	*Diospyros virginiana*
	Malus spp. (29)	*Fagus grandifolia*
3 *Populus nigra* (11)		*Fraxinus pennsylvanica*[d]
	1 *Populus tremuloides* (56)	*Lonicera japonica*
	Prunus virginiana	*Lonicera* sp.
	var. Schubert (50)	*Morus alba*
	1 *Quercus alba* (1)	*Morus rubra*
1 *Viburnum* sp. (3)		*Nyssa sylvatica*
		Platanus occidentalis
		Populus deltoides[d]
		Prunus pensylvanica
		Prunus serotina
		Rhus trilobata
		Salix fragilis
		Salix nigra
		Salix spp.[d]
		Tilia americana
		Ulmus rubra
		Ulmus sp.[d]

The sample size (*n*; *in parentheses*) associated with each genus or species is the number of times we recorded a tree of that type in a transect during the study, whether or not it served as a host

[a] The number before the species name indicates how many times we found that genus or species used as a host (we collected a web from it) if the number was three or fewer

[b] Host plants in Colorado are listed alphabetically, although hosts that co-occur in wild and cultivated sites are listed first

[c] Host plants used by fall webworm populations in the eastern US (Mason et al. 2011) are listed alphabetically

[d] Plants observed as hosts in Colorado and the East Coast

Larval performance

In 2010 and 2011, we cut branches containing fall webworm webs with a tree pruner (4.9-m Jameson poles, Marvin pruner head; Sherrill Tree, Greensboro, NC) and removed from five to 15 fall webworm larvae from each web. We brought all caterpillars found in the field back to the lab to complete development on their natal host plant and monitored them for parasitoid emergence. For each larval container, we replaced old food plants with fresh foliage and removed frass at least biweekly, but more often if needed [for rearing methods, see Loewy et al. (2013)]. The single growth performance measure for field collected fall webworms among the different host plants was pupal mass. We weighed all pupae exactly 30 days after pupation (to the nearest 0.01 mg using a Mettler-Toledo XP6 microbalance, Mettler-Toledo, Columbus, OH; larvae were monitored for pupation daily). We analyzed male and female pupal mass separately; the impact of male pupal mass on lifetime fitness is more equivocal than that of female pupal

mass, which correlates positively with potential fecundity for Lepidoptera generally (Calvo and Molina 2005; Davis and Landolt 2012; Loewy et al. 2013).

In order to control for maternal effects and to record performance measures that we could not obtain from field-collected individuals (e.g., development time), we conducted a split-brood experiment in 2011 with the offspring of fall webworms we collected in 2010. We selected four hosts to use in the controlled experiment that varied in quality. Host quality was determined by pupal masses of field-collected individuals in 2010; larvae on high-quality plants produce heavier pupae (Loewy et al. 2013). We chose two high-quality host plants (narrowleaf cottonwood and chokecherry) and two low-quality host plants (crabapple and alder). We haphazardly chose ten egg masses from our colony [see Loewy et al. (2013) for details on colony maintenance] that were laid within a 5-day period, 12-17 July 2011, to diminish the effect of foliage age on larval fitness. We then cut each egg mass into four sections, one to be reared on each host plant. After 21 days, we culled the larvae to ten per host per mother for a total of 400 individuals. At that point, the larvae were transferred to individual containers and moved to a climate-controlled growth chamber at temperatures and day lengths appropriate for Boulder, Colorado in mid August (light 14 h:day 10 h and 27:19.5 °C day:night temperature) (Loewy et al. 2013). We measured larval performance on host plants in four ways: survival to pupation, development time to pupation, pupal mass, and feeding efficiency. We measured development time as the number of days from hatching to pupation; shorter development time is generally correlated with higher fitness because of reduced exposure to natural enemies in the wild (Price et al. 1980). We weighed all pupae exactly 30 days after pupation (same methods as above). We also calculated an overall fitness score for all surviving individuals that incorporated both pupal mass and development time. To calculate the fitness score for each individual we divided its pupal mass (milligrams) by its development time (days), which allowed us to test whether host plant abundance and relative percent use affect overall larval performance as a single measure. We measured feeding efficiency as the slope of the line of best fit in a correlation of frass mass (fecal mass) by pupal mass. This measure of feeding efficiency controls for larvae that eat different amounts; efficient feeders convert a greater portion of the food they consume into biomass and leave less waste than less efficient feeders (Mason et al. 2011). We collected frass from each larva from 21 days of age until pupation, dried the frass in a drying oven for a week at 40 °C and weighed it. Highly efficient larvae should have higher body masses relative to the amount of food eaten (represented by the mass of their waste).

Mortality from parasitoids

Although we observed insect predators attacking and eating fall webworm larvae in the field, we limited our measurements of top-down control to parasitoids. We recorded parasitoid emergences for all field-collected larvae. The majority of parasitoid flies and wasps emerged prior to pupation, but some emerged from the pupal cases after overwintering. To estimate the influence of fall webworm ontogeny (a proxy for exposure time) on parasitoid host use, we recorded the body length of one representative fall webworm from each web upon collection from the field (we measured body length to the nearest 0.1 mm using 150 mm/0.1 mm Super Poly Fiberglass Dial Caliper, Swiss Precision Instruments, Garden Grove, CA).

Statistical analyses

We analyzed pupal mass and development time using a mixed-model ANOVA, with host species, sex and origin (lab reared or field collected) as main effects as well as interactions between host species with sex and origin; brood (the egg clutch from a given female) was analyzed as a random effect. When significant, ANOVAs were followed by post hoc Tukey's honest significant difference (HSD) tests. We used contingency tables to analyze variation in survival (yes/no) by host plant (Pearson's χ^2 value is reported); for analysis within year, we removed plant species that were only recorded as being a host for fall webworms once in our data set, but we reinserted them for the pooled analysis. We analyzed parasitism using an ordinal logistic regression with parasitism (yes/no) as the dependent variable and host species and web as independent predictor variables. We used Student's t-test to determine if the type of parasitoid (wasp or fly) that emerged from the fall webworms was predicted by the caterpillar's body length (a proxy for developmental stage) when collected. To determine the selective factors with the highest impact on natural patterns of host use, we tested for correlations between relative host use and relative host abundance, survival, development time and pupal mass. We also tested for correlations between percent parasitism and performance measures, excluding feeding efficiency. We analyzed feeding efficiency with an analysis of covariance, in which significant interactions between the slopes of different host plants indicate variation in feeding efficiency (Mason et al. 2011). Means are given ±SE. All statistical analyses were performed with JMP Pro 9.0.0 (SAS Institute, Cary, NC).

Fig. 1 Patterns of natural host use by fall webworms in Colorado measured by relative percent use in wild and cultivated sites, ordered from least to most commonly used host plants in wild sites. *Relative % use* is the number of webs on a host species divided by the total number of webs in the site. Data are pooled from 2010 ($n = 273$ webs) and 2011 ($n = 244$ webs). *Black bars* represent host species in wild sites ($n = 378$ webs) and *gray bars* represent host species in cultivated sites ($n = 139$ webs). Host plants *without bars* were not used by fall webworms within the site type
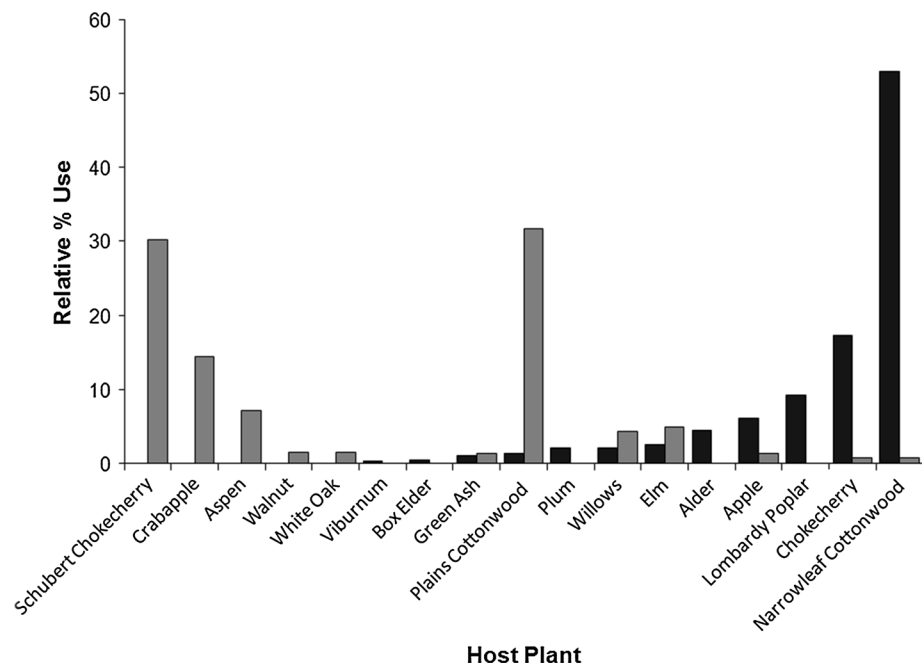
Results

Host plant abundance

Host plant use by fall webworms varied between wild and cultivated sites (Fig. 1). However, in both wild and cultivated areas, fall webworm primarily used cottonwood (*Populus*) species (narrowleaf cottonwood in wild and plains cottonwood in cultivated), followed by chokecherry (*P. virginiana* in wild and *P. virginiana* var. Schubert in cultivated). In both types of sites, host plant abundance strongly predicted host plant use (Fig. 2a; wild, $R^2 = 0.82$, $n = 17$, $p < 0.0001$; Fig. 2b; cultivated, $R^2 = 0.43$, $n = 17$, $p < 0.005$). Host abundance was a stronger predictor in wild sites, where potential hosts made up 85 % of total trees recorded, than in cultivated sites where potential hosts comprised 70 % of total woody, broadleaf trees. However, the significant trend of abundance predicting host use in wild sites was due to the effect of a single species; narrowleaf cottonwood was both far more abundant and more commonly used than other host plant species. When we removed narrowleaf cottonwood from the wild-site analysis, the relationship between host abundance and use by fall webworm disappeared ($R^2 = 0.02$, $n = 16$, $p > 0.5$).

The geographic area encompassed by our transects spanned ~125 km north to south, yet we found that plant communities in canyons (wild sites) in Jefferson and Larimer Counties were similar to those in Boulder County (69 % of canyon plants in Jefferson County and 64 % in Larimer County were also found in Boulder County). Furthermore, we found that wild plant communities differed

from plant communities in cultivated areas; over all transects in 2010, only 25.5 % of plants, both fall webworm hosts and non-hosts, were recorded in both wild and cultivated sites.

Larval performance

For fall webworm larvae that we collected from the field, pupal mass varied by sex ($F = 73.87$, $df = 1$, $p < 0.0001$), brood ($F = 6.35$, $df = 73$, $p < 0.0001$), and host species ($F = 7.18$, $df = 12$, $p < 0.0001$) when larvae from both sites and years were combined (Fig. S1 in ESM). There was no interaction between host species and fall webworm sex ($F = 1.29$, $df = 15$, $p = 0.2$).

For larvae reared in the lab as part of the split-brood experiment, survival varied by host plant (Fig. 3a; $\chi^2 = 57.85$, $df = 3$, $p < 0.0001$). Fall webworms reared on chokecherry had 1.5 times more survivors than those reared on alder. Larval development time also varied by host plant (Fig. 3b; $F_{3,329} = 14.8$, $p < 0.0001$). Larvae reared on narrowleaf cottonwood had shorter development times than those on alder by ~2.7 days and larvae on chokecherry developed more quickly than those on both alder and crabapple by ~3.7 and ~2.1 days, respectively (Tukey's HSD test, $p < 0.05$). Female pupal mass varied among host plants (Fig. 3c; $F_{3,163} = 4.91$, $p < 0.005$); larvae fed crabapple had significantly lower mean pupal mass than larvae fed narrowleaf cottonwood and chokecherry (Tukey's HSD test, $p < 0.05$). The mean female pupal mass of larvae fed on alder was not significantly different from that of any other host plant. Male pupal mass did not differ
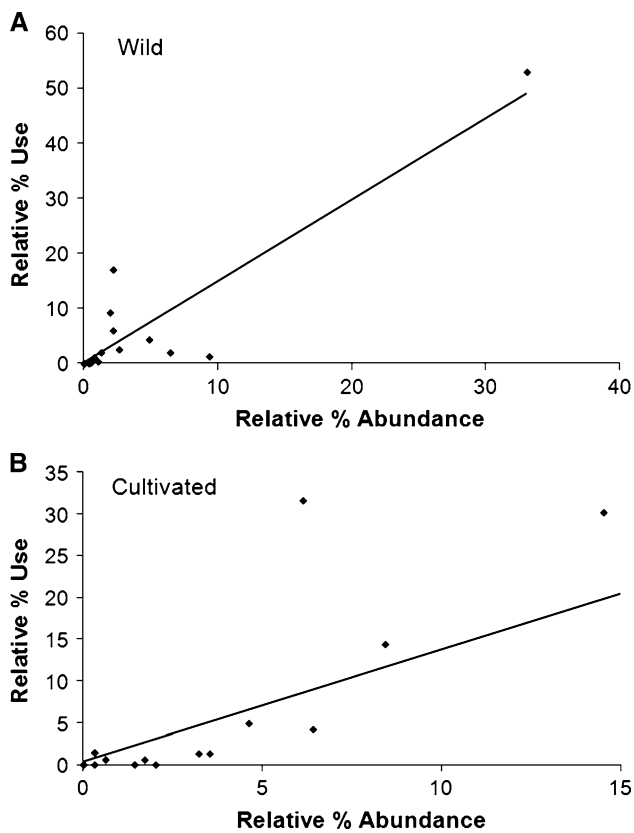
Fig. 2 **a** The relationship between fall webworm relative percent use (number of webs per host/all webs) and relative percent abundance of potential hosts in wild sites. The most abundant tree species at our sites was narrowleaf cottonwood, and when it is included in the analysis host plant abundance predicts host plant use ($R^2 = 0.82$, $n = 17$, $p < 0.0001$), but the relationship disappears when this most abundant species is removed from the analysis ($R^2 = 0.02$, $n = 16$, $p > 0.5$). **b** The relationship between fall webworm relative percent use (number of webs per host/all webs) and relative percent abundance of potential hosts in cultivated sites ($n = 17$, $p < 0.005$). Data are pooled for 2010 and 2011 and *each point* represents a host species

Fig. 3 Larval performance, measured by **a** survival ($\chi^2 = 57.85$, $df = 3$, $p < 0.0001$), **b** development time ($F_{3,329} = 14.8$, $p < 0.0001$) and **c** pupal mass ($F_{3,163} = 4.91$, $p < 0.005$) on four host plants in the split-brood experiment. Fall webworms of both sexes are included in graphs of survival and development time. Only female fall webworms are included in the graph of pupal mass. *Bars* represent mean ± SE. Treatments with the *same letter* are not significantly different

significantly among host plants ($F_{3,151} = 0.096$, $p = 0.96$; data not shown). Fall webworms reared from eggs in controlled lab conditions had higher mean pupal mass than fall webworms collected from the field, but only when reared on alder and narrowleaf cottonwood ($F_{3,504} = 6.16$, $p < 0.0004$).

Fitness score, which incorporates both development time and pupal mass, varied by host plant ($F_{3,166} = 11.00$, $p < 0.0001$). Mean larval fitness scores for larvae reared on chokecherry (5.1 ± 0.07) and narrowleaf cottonwood (5.0 ± 0.07) were significantly higher than the mean fitness scores for larvae reared on both crabapple (4.6 ± 0.08) and alder (4.7 ± 0.09) (Tukey's HSD test, $p < 0.05$).

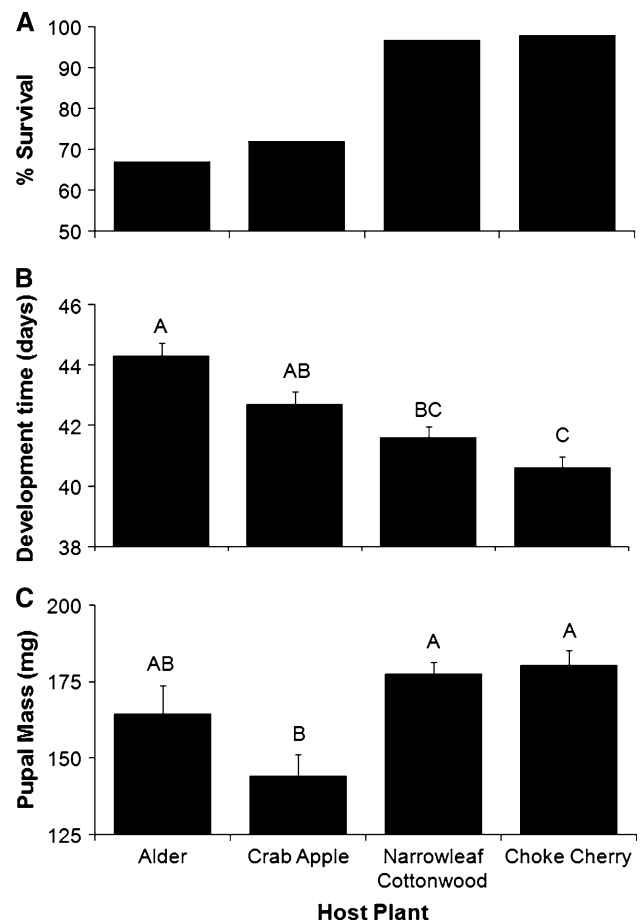Feeding efficiency, the slope of the linear relationship between pupal mass (both sexes lumped) and frass mass, was greatest on chokecherry (slope = 0.19, $R^2 = 0.6$, $n = 96$, $p < 0.0001$), followed by crabapple (slope = 0.15, $R^2 = 0.33$, $n = 69$, $p < 0.0001$) and then alder (slope = 0.1, $R^2 = 0.13$, $n = 62$, $p < 0.005$) (Fig. S2, ESM). The slope of feeding efficiency for larvae fed on narrowleaf cottonwood was not significantly different from zero (slope = 0.02, $R^2 = 0.01$, $n = 96$, $p = 0.3$).

None of the bottom-up performance measures, either from field-collected larvae or those in the split-brood experiment, was predictive of relative host use. Lumping all sites and both years, the correlation of pupal mass of larvae collected from the field and relative percent host use was not significant ($R^2 = 0.14$, $n = 16$, $p = 0.15$). Neither survival ($R^2 = 0.56$, $n = 4$, $p = 0.25$), nor fitness score ($R^2 = 0.42$, $n = 4$, $p = 0.35$) was significantly related to fall webworm percent host use.

Mortality from parasitoids

About one quarter (24 %) of all field-collected larvae died as a result of parasitism; to be conservative, we did not include individuals that died from pathogens or unknown causes in our estimate of mortality from parasitism. Fall webworms that perished due to causes other than parasitism constituted 7.5 % of deaths in 2010 and ~19 % of deaths in 2011. The proportion of larvae parasitized differed significantly among host plants for both years in wild ($\chi^2 = 79.5$, $df = 10$, $p < 0.001$) and cultivated ($\chi^2 = 30.0$, $df = 8$, $p = 0.002$) sites and also when host plants from all sites were analyzed together (Fig. S3, ESM; $\chi^2 = 117.8$, $df = 15$, $p < 0.0001$). The web of origin was a significant factor only for larvae from the wild sites ($\chi^2 = 52.4$, $df = 1$, $p < 0.001$). There was no relationship between percent parasitism and relative host use within wild sites ($R^2 = 0.27$, $n = 7$, $p = 0.19$) or cultivated sites ($R^2 = 0.001$, $n = 5$, $p = 0.95$).

Parasitized fall webworm larvae ranged from 6.0 to 31.7 mm in body length on the day we collected them from the field. The mean length-at-collection of larvae parasitized by tachinid flies was 23.4 mm (± 0.75 mm), which is ~60 % longer than the mean length of larvae parasitized by wasps (14.7 mm ± 0.46 mm) ($t_{262} = 9.78$, $p < 0.0001$).

Trade-offs

For host plants where larval survival in the controlled lab experiment was high, the percentage of larvae parasitized on that host in the field was also high (Fig. S4a, ESM; $R^2 = 0.99$, $n = 4$, $p < 0.005$). There was also a significant, positive relationship between fitness score and percent parasitism (Fig. S4b in ESM; $R^2 = 0.97$, $n = 4$, $p < 0.02$). When the analysis includes all host plants, the linear relationship between mean pupal mass of field collected larvae and percent parasitism remained significant (Fig. 4; $R^2 = 0.38$, $n = 16$, $p < 0.02$). We identified no other trade-offs; there was no relationship between host relative percent abundance and percent parasitism ($R^2 = 0.15$, $n = 16$, $p > 0.1$), pupal mass ($R^2 = 0.13$, $n = 16$, $p > 0.1$) or fitness score ($R^2 = 0.76$, $n = 4$, $p > 0.1$).

Discussion

Of the three selective pressures that we measured, host plant abundance, larval performance and percent parasitism, only abundance predicted patterns of fall webworm host use in Colorado. Host plant quality and mortality from parasitoids are major selective pressures on herbivorous insects (Price et al. 2011; Schoonhoven et al. 2005), but neither predicted host use in our study populations. For
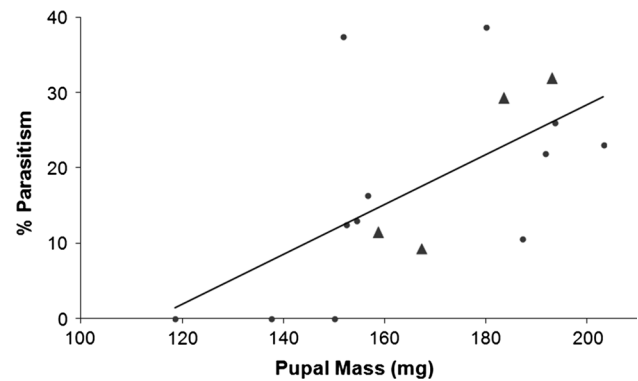
Fig. 4 The relationship between mean pupal mass (mg) and percent parasitism among field-collected fall webworms over the course of the study ($R^2 = 0.38$, $n = 16$, $p < 0.02$). Both sexes and fall webworms of unknown sex are included. *Each point* represents a single host species. *Triangles* represent the four host species also used in the controlled experiment. Data were pooled for all sites and both field seasons

instance, two high-quality host plants, chokecherry and narrowleaf cottonwood, were the most commonly used host plants in wild areas, but we did not find any evidence that plant quality, as measured by larval performance, predicted overall patterns of local host use. Mortality from parasitoids varied among host plants, but also did not predict overall patterns of host use.

Although fall webworms did not show a preference for host plants that provided better larval performance, their parasitoids did. Fall webworm larvae on the highest quality host plants also experienced the highest levels of mortality due to parasitism whereas larvae on poor-quality host plants suffered reduced fitness in terms of pupal mass and development time, but also incurred relatively low rates of parasitism. A trade-off between food quality and enemy-free space may reinforce polyphagy (Mira and Bernays 2002; Murphy 2004; Singer 2008; Singer et al. 2004). If the fitness benefits of experiencing less parasitism on low-quality host plants offset the benefits of feeding on a high-quality plant, then low-quality host plants may be maintained in the diet when specialization on high-quality hosts would otherwise be expected. This fitness trade-off for fall webworm larvae in Colorado may help to explain why a population that has a relatively restricted diet breadth compared to other populations has not evolved to specialize on the highest quality host plants and instead maintains a generalist diet breadth, albeit a rather restricted one.

It remains unclear why parasitism pressure on fall webworms was higher on some plants than on others. The size or developmental stage of host larvae (Stoepler et al. 2011), host immune function (Schmid-Hempel 2005), host density (Lessells 1985), light environment (Stoepler and Lill 2013) and volatile cues released by herbivore-damaged plants

(Turlings et al. 1990) have all emerged as important factors in determining parasitism levels in other systems and may play a role for fall webworms as well. Tachinid fly and wasp parasitoids were responsible for nearly a quarter of the mortality that we observed. Notably, we found evidence suggesting that parasitoid wasps attack smaller fall webworm larvae than do parasitoid flies. It is important to note that we knew the size of the larval host when it was collected from the field, but not the size at which it was attacked, which would be equal or less than the size at collection [e.g., some wasp parasitoids are known to arrest the development of their host upon attack (Godfray 1994)]. The only other studies to investigate host partitioning by parasitoid communities found that parasitoid flies tend to attack larger larvae than parasitoid wasps (Murphy et al. 2014; Stoepler et al. 2011); both of these studies focused on larvae in the family Limacodidae and our similar findings for larval hosts in the family Erebidae lend additional support to the hypothesis that parasitoid flies and wasps partition hosts by size.

Our findings that host plant abundance drives plant use in fall webworms is consistent with a previous study of fall webworm populations in the eastern US (Mason et al. 2011). We found that host abundance explained 82 % (wild) and 43 % (cultivated) of variation in fall webworm host use in Colorado, while Mason et al. (2011) found that host abundance explained 54 % of host use in Connecticut and 90–96 % of host use in Maryland. In our study, the positive relationship between host abundance and host use in wild sites had more explanatory power than the relationship in cultivated sites, although that relationship was driven by the most abundant and most commonly used host, narrowleaf cottonwood. It is notable that host abundance explained more of the variation in host use in Colorado for wild sites than for cultivated sites, which are altered by human activity. Several private homeowners had attempted to control fall webworms on their properties through mechanical and chemical means (personal communication), which may have skewed fall webworm distribution towards taller trees (like plains cottonwood) and communally owned property in those areas.

The relationship between host plant abundance and host use suggests that fall webworms are under selective pressure to minimize the amount of time they spend searching for a suitable host, as was also hypothesized by Mason et al. (2011). The selective pressure of search time limitation was also important in a previous study in which gravid butterflies given access to an additional host species laid more eggs than butterflies with only one available host (Johansson et al. 2007). Since none of the selective pressures we measured other than host abundance correlated with relative percent host use, our study does not explain differences in fall webworm host breadth between Colorado and East Coast populations. However, patterns of plant availability, abundance and/or differences in host plant quality may explain variation in fall webworm diet breadth among geographic regions and should be further investigated. Apparent "local specialization" in a generalist herbivore may be due to fewer locally available host plants (Fox and Morrow 1981). Eastern forests contain more woody plant species than the riparian forests of Colorado's foothills and adjacent plains (Waring et al. 2006) and fall webworms may feed on the same proportion of potential hosts in both regions. However, this hypothesis is somewhat unsatisfactory because the plant species used as hosts by different populations varies considerably even when the same host plant species are available. For instance, many trees and shrubs, including ones common in eastern forests, are planted in Colorado residential developments (Murphy, personal observation) and are thus available to fall webworms as potential hosts and yet are either not used or only rarely (e.g., green ash). Although these plant species are available as potential host plants in Colorado, they may differ in their abundance and/or quality compared to regions where they are commonly used as hosts. For example, some host plants that are commonly used by eastern populations and that are reasonably high-quality hosts there are also fairly abundant in Colorado, such as box elder in wild sites and green ash in cultivated sites. Yet, both box elder and green ash are rarely used by fall webworms in Colorado and they are low-quality host plants as measured by larval performance. Thus, fall webworm populations in Colorado may have lost physiological adaptations that allow them to successfully feed on host plants commonly used by eastern populations or these plants may vary phenotypically in nutrient or allelochemical content and be lower quality in Colorado.

Conclusion

Host availability is the primary driver of patterns of host plant use by fall webworm populations in Colorado, which agrees with results from other populations (Mason et al. 2011) and suggests that adult females experience a selective pressure to reduce search time for oviposition sites. We found that populations of fall webworm in Colorado experience a strong trade-off between bottom-up and top-down selective pressures: higher quality host plants also had a greater proportion of larval mortality due to parasitism. Local patterns of host plant abundance appear to narrow the set of hosts used by fall webworms in Colorado, while the trade-off between host quality and risk of parasitism helps explain the maintenance of a generalized feeding strategy within this restricted set of hosts. Our results underscore the importance of understanding the geographic mosaic of selection in wide-ranging species.

References

Berger EW (1906) Observations upon the migrating, feeding, and nesting habits of the fall webworm (Hyphantria cunea Dru.). Bull Bureau Entomol USDA 80:41–65

Bernays E, Graham M (1988) On the evolution of host specificity in phytophagous arthropods. Ecology 69:886–892

Bernays EA, Minkenberg OPJM (1997) Insect herbivores: different reasons for being a generalist. Ecology 78:1157–1169

Calvo D, Molina JM (2005) Fecundity-body size relationship and other reproductive aspects of *Streblote panda* (Lepidoptera: Lasiocampidae). Ann Entomol Soc Am 98:191–196

Davis TS, Landolt PJ (2012) Body size phenotypes are heritable and mediate fecundity but not fitness in the lepidopteran frugivore *Cydia pomonella*. Naturwissenschaften 99:483–491

Ferguson DC, Opler PA, Smith MJ, Donahue JP (2000) Distribution of Arctiidae of Western North America. Moths of Western North America. C. P. Gillette Museum of Arthropod Diversity, Colorado State University, Fort Collins

Fox LR, Morrow PA (1981) Species property or local phenomenon? Science 211:887–893

Godfray HCJ (1994) Parasitoids, behavioral and evolutionary ecology. Princeton University Press, Princeton

Gomi T, Takeda M (1996) Changes in life-history traits in the fall webworm within half a century of introduction to Japan. Funct Ecol 10:384–389

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer, Sunderland

Greenblatt JA (1978) Larval feeding preferences and inducibility in the fall webworm, *Hyphantria cunea*. Ann Entomol Soc Am 71:605–606

Gripenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference-performance relationships in phytophagous insects. Ecol Lett 13:383–393

Ito Y (1977) Birth and death. In: Hidaka T (ed) Adaptation and speciation in the fall webworm. Kodansha, Tokyo, pp 101–128

Jaenike J, Selander RK (1980) On the question of host races in the fall webworm, *Hyphantria cunea*. Entomol Exp Appl 27:31–37

Jasič J, Macko V (1961) Some results of experimental study of fall webworm (*Hyphantria cunea* Drury) (Lepidoptera: Arctiidae) ecology. Publishing Office of the Slovak Academy of Science, Bratislava

Jeffries MJ, Lawton JH (1984) Enemy free space and the structure of ecological communities. Biol J Linn Soc 23:269–285

Johansson J, Bergstrom A, Janz N (2007) The benefit of additional oviposition targets for a polyphagous butterfly. J Insect Sci 7:1–8

Karban R, Agrawal AA (2002) Herbivore offense. Annu Rev Ecol Syst 33:641–664

Karban R, Karban C, Huntzinger M, Pearse I, Crutsinger G (2010) Diet mixing enhances the performance of a generalist caterpillar, *Platyprepia virginalis*. Ecol Entomol 35:92–99

Lessells CM (1985) Parasitoid foraging: should parasitism be density dependent? J Anim Ecol 54:27–41

Loewy K et al (2013) Life history traits and rearing techniques for fall webworms (*Hyphantria cunea* Drury) in Colorado. J Lepidopt Soc 67:196–205

Masaki S, Ito Y (1977) Speciation. In: Hidaka T (ed) Adaptation and speciation in the fall webworm. Kodansha, Tokyo, pp 149–172

Mason PA, Wilkes SR, Lill JT, Singer MS (2011) Abundance trumps quality: bi-trophic performance and parasitism risk fail to explain host use in the fall webworm. Oikos 120:1509–1518

Mayhew PJ (1997) Adaptive patterns of host-plant selection by phytophagous insects. Oikos 79:417–428

Michaud JP (1990) Conditions for the evolution of polyphagy in herbivorous insects. Oikos 57:278–279

Mira A, Bernays EA (2002) Trade-offs in host use by *Manduca sexta*: plant characters vs. natural enemies. Oikos 97:387–397

Morris RF, Fulton WC (1970) Models for development and survival of Hyphantria cunea. Mem Entomol Soc Can 70:1–312

Murphy SM (2004) Enemy-free space maintains swallowtail butterfly host shift. Proc Natl Acad Sci 101:18048–18052

Murphy SM, Stoepler TM, Grenis K, Lill JT (2014) Host ontogeny determines parasitoid use of a forest caterpillar. Entomol Exp Appl 150:217–225

Oliver AD (1964) A behavioral study of two races of the fall webworm, *Hyphantria cunea* (Lepidoptera: Arctiidae) in Louisiana. Ann Entomol Soc Am 57:192–194

Price PW, Bouton CE, Gross P, McPheron BA, Thompson JN, Weis AE (1980) Interactions among three trophic levels: influence of plants on interactions between insect herbivores and natural enemies. Annu Rev Ecol Syst 11:41–65

Price PW, Denno RF, Eubanks MD, Finke DL, Kaplan I (2011) Insect ecology: behavior, populations and communities. Cambridge University Press, New York

Rehnberg BG (2002) Heat retention by webs of the fall webworm *Hyphantria cunea* (Lepidoptera: Arctiidae): infrared warming and forced convective cooling. J Therm Biol 27:525–530. doi:10.1016/s0306-4565(02)00026-8

Rodrigues D, Kaminski LA, Freitas AVL, Oliveira PS (2010) Trade-offs underlying polyphagy in a facultative ant-tended florivorous butterfly: the role of host plant quality and enemy free space. Oecologia 163:719–728

Schmid-Hempel P (2005) Evolutionary ecology of insect immune defenses. Annu Rev Entomol 50:529–551

Schoonhoven LM, Van Loon JJA, Dicke M (2005) Insect-plant biology, 2nd edn. Oxford University Press, Oxford

Singer MS (2008) Evolutionary ecology of polyphagy. In: Tilmon KJ (ed) Specialization, speciation, and radiation: the evolutionary biology of herbivorous insects. University of California Press, Oakland, pp 29–42

Singer MS, Rodrigues D, Stireman JO, Carriére Y (2004) Roles of food quality and enemy-free space in host use by a generalist insect herbivore. Ecology 85:2747–2753

Stoepler TM, Lill JT (2013) Direct and indirect effects of light environment generate ecological trade-offs in herbivore performance and parasitism. Ecology 94:2299–2310

Stoepler TM, Lill JT, Murphy SM (2011) Cascading effects of host size and host plant species on parasitoid resource allocation. Ecol Entomol 36:724–735

Swain RB (1936) The biological control of the fall webworm in Colorado. Master's, Colorado State College, Fort Collins

Tadić MD (1963) Natural enemies of fall webworm (*Hyphantria Cunea* Dr.) in North America. Entomophaga 8:245–252

Thompson JN (1998) The evolution of diet breadth: monophagy and polyphagy in swallowtail butterfiles. J Evol Biol 11:563–578

Thompson JN (2005) The Geographic mosaic of coevolution. The University of Chicago Press, Chicago and London

Turlings TCJ, Tumlinson JH, Lewis WJ (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science 250:1251–1253

Waring RH, Coops NC, Fan W, Nightingale JM (2006) MODIS enhanced vegetation index predicts tree species richness across forested ecoregions in the contiguous U.S.A. Remote Sens Environ 103:218–226

Warren LO, Tadić M (1970) The fall webworm, *Hyphantria cunea* (Drury). Ark Exp Stn Bull 759:1–106

Yang Z, Wei J, Wang X (2006) Mass rearing and augmentative releases of the native parasitoid Chiuioia cunea for biological control of the introduced fall webworm Hyphantria cunea in China. Biocontrol 51:401–418

Yang ZQ, Wang XY, Wei JR, Qu HR, Qiao XR (2008) Survey of the native insect natural enemies of *Hyphantria cunea* (Drury) (Lepidoptera: Arctiidae) in China. Bull Entomol Res 98:293–302