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PERFORMANCE OF WESTERN TENT CATERPILLAR (*MALACOSOMA CALIFORNICUM*) ON TWO COMMON HOST PLANTS, INCLUDING A NEW HOST PLANT RECORD

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ABSTRACT. Tent caterpillars are generalists across their full host range, but display local host plant preferences. We present evidence for a new host plant record, wax currant (*Ribes cereum*), for western tent caterpillars (*Malacosoma californicum*) along the Colorado Front Range. We tested the suitability of wax currant as a host plant for western tent caterpillars as compared to chokecherry (*Prunus virginiana*), an abundant and commonly used host plant. We measured the density of tent caterpillar tents in areas where both host plants occur to assess host plant use. We reared tent caterpillar larvae on both host plants and measured fitness effects due to host plant quality (survival, pupal mass) and natural enemies (parasitism). We did not find a relationship between host plant abundance and use by tent caterpillars and found no evidence for a preference for either host plant. We found that western tent caterpillars do not differ in pupal mass when reared on chokecherry and on wax currant in a laboratory setting, but did vary in survival with greater survival on wax currant. We found no difference in parasitism rate for larvae collected from chokecherry or wax currant. Our results suggest that wax currant is a suitable yet previously unrecorded host plant for tent caterpillar larvae.

Additional key words: novel host record, host plant use, host plant preference, *Ribes cereum*, *Prunus virginiana*

The host plants that an adult female insect selects for oviposition can determine the fitness and even survival of her offspring (Thompson 1988, Renwick 1989, Jaenike 1990). Although generalist insects have a wider range of potential host plant choices available to them than specialist insects, larval fitness for generalists is still impacted by bottom-up (e.g. host plant secondary compounds, nutrient content) and top-down (e.g. predators, parasitoids) selective pressures (e.g. Greenblatt and Barbosa 1981, Shiojiri et al. 2002, Agrawal 2005). Some generalist female insects are still choosy in their host plant selection and may even act as specialists at a local level (Fox and Morrow 1981, Thompson 2005). Female insects that lay their eggs in batches and/or have larvae with limited mobility early in development are predicted to be under strong selection to be choosy in host plant selection. For species with larvae that are restricted to the plant where their mother laid them, poor host plant choice could lead to the loss of all of an individual's progeny (Knolhoff and Heckel 2014).

Western tent caterpillars, *Malacosoma californicum* Packard (Lasiocampidae), are generalists when considered across their full geographic range, but frequently show strong host plant preferences at a local level (Powell and Opler 2009). In midsummer, tent caterpillar adult females oviposit all of their eggs in one group on a tree branch (Fitzgerald 1995). The eggs overwinter on the branch and hatch in the early spring. Although it has not been verified, it is believed that the larvae primarily stay on the host plant that their mother selects (Fitzgerald 1995). It is therefore important that she select a plant that will allow her offspring to thrive. Tent caterpillars feed gregariously as larvae through their penultimate instar before dispersing. Larvae construct silk tents that last through the summer and, occasionally, into the next year. While tent caterpillars can have large-scale impacts on tree health, they rarely kill their host plants (Cooke et al. 2012).

Western tent caterpillars are commonly found on *Prunus* spp. (Fitzgerald 1995, Powell and Opler 2009) and are frequently found feeding on chokecherry (*Prunus virginiana* L. (Rosaceae)) on the eastern slope of the Rocky Mountains of Colorado (personal observation). Here we report on an additional common, but previously unrecorded, tent caterpillar host plant: wax currant, *Ribes cereum* Dougl. (Grossulariaceae). Whether wax currant is as commonly used as chokecherry or a high quality host plant has not been previously tested. Host plant preference may be revealed in the relationship between the relative abundance of a host plant in an area and the proportion of that host plant used by the herbivore (Fig. 1).

We had three research objectives. First, we assessed the frequency of host plant use by tent caterpillars for both chokecherry and wax currant by establishing transects and recording all plants with tent caterpillar tents. In addition, we counted the number of tents per plant and used these data in association with host plant abundance to assess host plant preference. Second, we

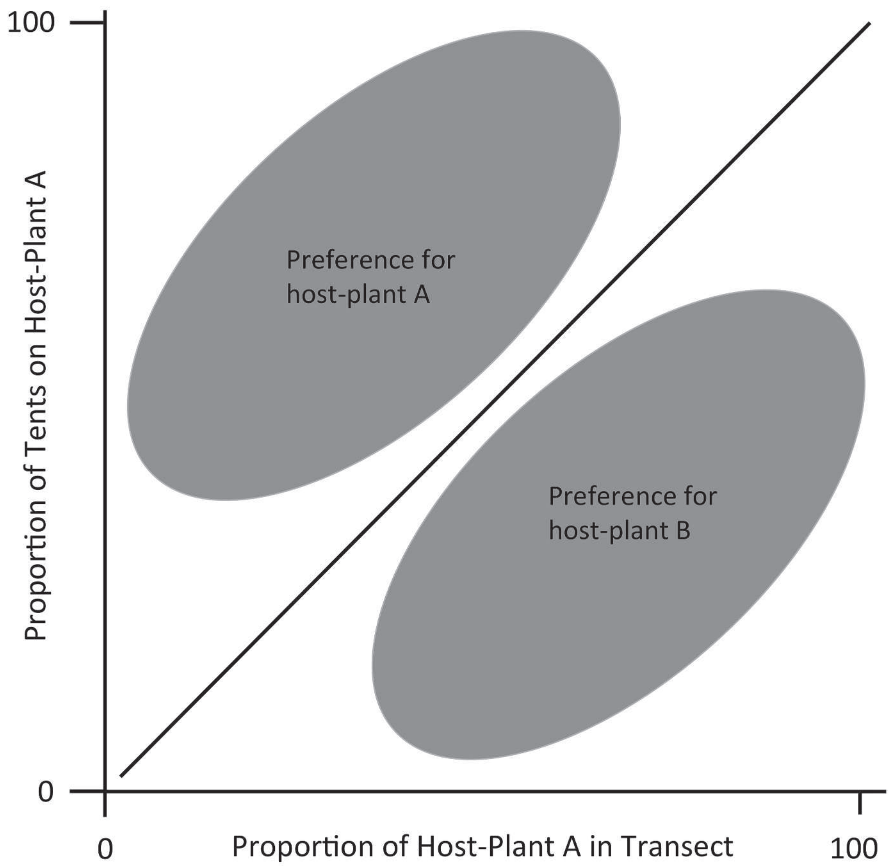

FIG. 1. Potential outcomes of host plant surveys testing host plant preference of tent caterpillars. We predicted that host plant preference would be reflected by the proportion of a species of host plant available in a transect (number of individuals of a focal plant species in a transect divided by the total number of potential host plant individuals in that transect) compared to the proportion of larvae that use that host plant (number of tent caterpillar tents on the focal host plant species divided by the total number of tent caterpillar tents in a transect). For example, if there is a low proportion of host plant A (wax currant) available compared to host plant B (chokecherry) and a high proportion of tent caterpillar tents found on host plant A, then a preference is demonstrated for host plant A because it is selected even when it is uncommon. However, if there is a high proportion of host plant A available and a low proportion of tent caterpillar tents found on host plant A, then this result suggests that host plant B is preferred. If there is no preference and tent caterpillars use plants in relation to their relative abundance, then we expect all data points to fall on the line (slope = 1). If female tent caterpillars express variation in host plant preference, then we would expect a random distribution of data with some individuals/populations preferring host plant A and others preferring host plant B.

measured tent caterpillar larval fitness on wax currant to test the quality of this newly-recorded host plant compared to a known tent caterpillar host plant, chokecherry. Third, we measured parasitism rate for tent caterpillars on the two host plants by recording the number and kind of parasitoids that emerged from larvae collected from each plant. Together this information allows us to determine whether wax currant is a superior-, inferior-, or equal-quality host plant for tent caterpillar larvae compared to the previously recorded host plant, chokecherry.

METHODS

We surveyed riparian areas in the foothills of the eastern slope of the Colorado Rocky Mountains. We conducted our experiments at four sites in Colorado: Betasso Preserve (N40°1'28", W105°20'19"), Boulder Canyon Trail (N40°0'49", W105°18'35"), Red Rocks (N39°39'56'', W105°12'21''), and Centennial Cone Park (N39°45'42.3", W105°20'32.6"). At each site, chokecherry and wax currant bushes are dispersed throughout a mix of wooded areas and meadows. We selected these sites because they contain both focal

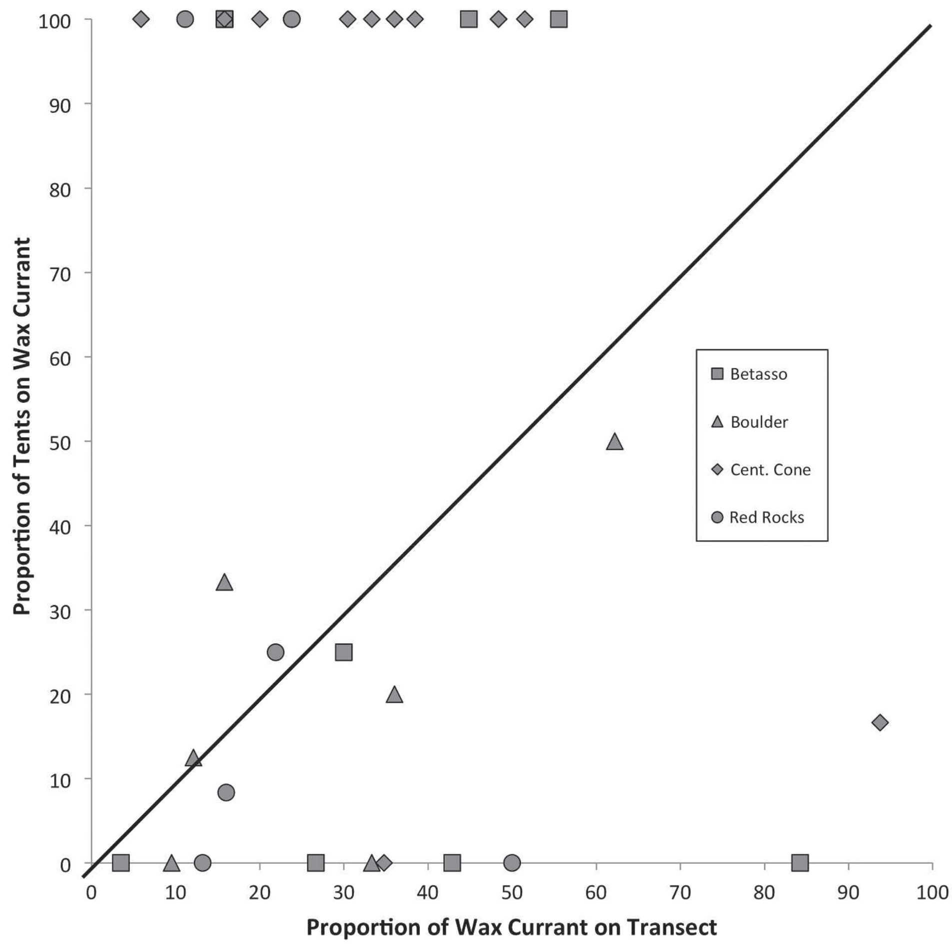

Fig. 2. Relationship between the proportion of wax currant available and the proportion tent caterpillar tents found on wax currant (χ^2 = 1.4, *df* = 1, N = 35, P = 0.23). Site are represented with the following symbols: Betasso Preserve: square, Boulder Canyon: triangle, Centennial Cone Park: diamond, and Red Rocks: circle.

plant species and numerous western tent caterpillar tents. We surveyed all sites from April to May 2015 after tent caterpillar larvae had constructed their tents.

Objective 1: Survey of Host Plant Use. To measure the abundance of chokecherry and wax currant at each site and the frequency that tent caterpillar larvae use each plant species as a host, we conducted plant surveys in the summer of 2015. Our transects were 20 m by 2 m and were centered at a focal chokecherry or wax currant plant with at least one tent caterpillar tent. We surveyed 18 transects with chokecherry as the focal species (Red Rocks: n=6, Centennial Cone: n=2, Boulder Canyon: n=7, Betasso Preserve: n=3), and 23 transects with wax currant as the focal species (Red Rocks: n=3, Centennial Cone: n=12, Boulder Canyon: n=3, Betasso Preserve: n=5) for a total of 41 transects. No transects overlapped and were at least 20m apart. For all chokecherry and wax currant plants within the transect area, we recorded the species, distance from focal tree, and the presence or absence of tent caterpillar tents; if tents were present on a plant, we also counted the number of tents.

Objective 2: Effects of Host Plant Quality on Tent Caterpillar Fitness. To test the effect of host plant quality on tent caterpillar fitness, we reared larvae on chokecherry and wax currant. In April, we collected 5–10 larvae in their second or third instar from 27 tents for a total of 235 larvae (Red Rocks: n= 71 larvae, Boulder Canyon: n=122 larvae, Betasso Preserve: n=42 larvae). We collected larvae from 16 chokecherry tents and 11 wax currant tents. We divided each tent into two groups; we reared half of the larvae from each tent on chokecherry, and half on wax currant. Thus, from each tent, half of the larvae were reared on their natal host

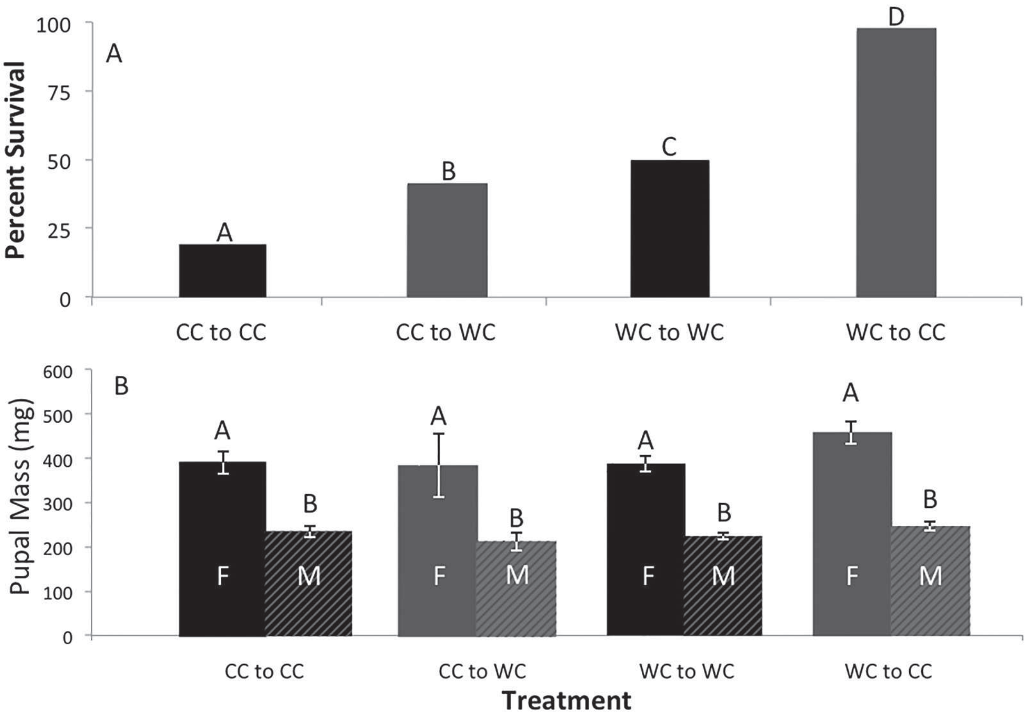

FIG. 3. Larval performance of tent caterpillar larvae reared on the four host plant treatments (chokecherry remaining on chokecherry (CC to CC), chokecherry switched to wax currant (CC to WC), wax currant remaining on wax currant (WC to WC), and wax currant switched to chokecherry (WC to CC) measured by A) larval survival (χ^2 = 66.29, *df* = 3, N = 235, P < 0.0001), B) mean female pupal mass (ANOVA: $F_{3,33}$ =1.75, P = 0.18) and mean male pupal mass (ANOVA: $F_{3,59}$ =2.01, P = 0.12). Female pupal mass is indicated with solid bars and the letter F. Male pupal mass is indicated with stripes and the letter M. Black bars indicate host plant treatments in which larvae remained on their natal host for the duration of the experiment and gray bars indicate host plant treatments in which larvae switched host plants mid-development. Error bars show ±1 standard error. Letters indicate the treatments that are significantly different.

plant while the other half were reared on the alternate host plant for a total of four treatments (chokecherry remaining on chokecherry, chokecherry switched to wax currant, wax currant remaining on wax currant, and wax currant switched to chokecherry); if we had only reared larvae on their natal host plant, any differences in larval performance between host plants could have been attributed to maternal effects since maternal lines would have been confounded with host plant. We reared larvae in deli containers in ambient conditions according to the methods outlined in Loewy et al. (2013). Larvae were reared in groups of 5–10 per container. We fed all of the larvae every three days or as needed with host plant that we collected from Betasso Preserve and Boulder Canyon Trail. All larvae were fed leaves from both field sites to control for variation in host-plants between sites.

We measured two proximate measures of fitness: pupal mass and survival. Pupal mass is a measure of fitness for Lepidoptera as heavier female pupae produce more eggs (including for *Malacosoma* spp.; Parry et al. 2001, Loewy et al. 2013). Survival is an important component of fitness because larvae that do not reach pupation are unable to reproduce. We measured pupal mass to the nearest 0.01 mg eight days after pupation using a using a Mettler-Toledo XP6 microbalance (Mettler-Toledo, Columbus, OH). We monitored all larvae daily for emergence. We used these fitness measurements to test the relative quality of each host plant type for tent caterpillars.

Objective 3: Tent Caterpillar Mortality from Parasitoids. To measure tent caterpillar mortality from parasitoids, we monitored the tent caterpillar larvae and pupae in Objective 2 for parasitoid emergence in the laboratory. We collected all parasitoids that emerged and have preserved them for future identification. We allowed parasitoids six months to emerge before the pupa was recorded as dead by other causes. We categorized parasitoids as either Diptera or Hymenoptera.

Data Analysis

For Objective 1, we analyzed results from the host plant survey by comparing the proportion of wax currant in each transect (number of wax currant plants in a transect divided by the total number of potential host plants in that transect) to the proportion of wax currant used by tent caterpillar larvae (number of tents on wax currant in a transect divided by the total number of tents in that transect). We plotted the results according to our prediction graph (Fig. 1) and counted the number of points that fell above and below the one-to-one line and performed a chi square test to determine if there was a preference for one host plant. We did not include any transects that only contained wax currant or chokecherry in this analysis as we were only interested in transects where the female moths had a choice between species of host plant. For Objective 2, we analyzed larval survival using a chi square test with host plant treatment as the independent variable and survival (yes/no) as the dependent variable. We analyzed the results from the lab fitness trial using an ANOVA with host plant treatment as the independent variable, and pupal mass was the dependent variable. The pupal mass data were normally distributed for both male and female pupae. For Objective 3, we collected too few parasitized larvae to analyze statistically and so report descriptive statistics. All data was analyzed using JMP Pro 11.0.0.

RESULTS

Objective 1: Survey of Host Plant Use. We found no significant relationship between relative host plant use and abundance for either wax currant (R^2 = 0.083, N= 27, P = 0.14) or chokecherry (R^2 = 0.056, N = 21, P = 0.29). We found no significant relationship between the proportion of wax currant in each transect and the proportion of wax currant used by tent caterpillar larvae (Fig. 2; χ^2 = 1.4, *df* = 1, N = 35, P = 0.23). Compared to our prediction graph (Fig. 1), we found that our data points were dispersed randomly.

Objective 2: Effects of Host Plant Quality on Tent Caterpillar Fitness. We found a significant difference in larval survival between the four host plant treatments with larval survival in the wax current to chokecherry treatment 5 times greater than larval survival in the chokecherry to chockcherry treatment (Fig. 3 A; χ^2 = 66.29, *df* = 3, N = 235, P < 0.0001). We found no significant difference in the mean pupal mass between the four host plant treatments for females (Fig. 3B; ANOVA: $F_{3, 33}$ =1.75, P = 0.18) or for males (Fig. 3B; ANOVA: $F_{3, 59}$ =2.01, P = 0.12).

Objective 3: Tent Caterpillar Mortality from Parasitoids. We recorded 6 parasitoid emergences from the 235 larvae that we collected: 3 Diptera (1 collected and reared from a larva on chokecherry; 2 collected and reared from larvae on wax currant) and 3 Hymenoptera (all collected from chokecherry; 2 reared from larvae on chokecherry and 1 reared from a larva on wax currant). The two flies recorded from wax currant both emerged from a single larva. Thus, while our sample size is too small to analyze statistically, we found 1 parasitized larva on wax currant (of the 125 that we collected; parasitism rate = 0.8%) and 4 parasitized larvae on chokecherry (of the 110 that we collected; parasitism rate = 3.6%).

DISCUSSION

Our results demonstrate that tent caterpillars neither preferentially use wax currant or chokecherry overall, nor use host plants in relation to their abundance. Instead, our results suggest that females vary in their host plant preference, with some individuals preferring chokecherry and some wax currant. We found no pattern in the relationship between the proportion of wax currant in each transect and the proportion of wax currant on which tent caterpillars tents were found. It is possible that because we counted established tents and not egg masses, we may have missed some early season mortality due to top-down (e.g. predation or parasitism) or bottom-up (e.g. host plant quality or host-larval asynchrony) factors. At our field sites, however, chokecherry and wax currant produce leaves at approximately the same time in the spring, limiting the possible influence of asynchrony between larvae hatching and bud burst (Barnes, personal observations). If the presence of tent caterpillar tents accurately reflects adult females oviposition, our findings suggest that females may select their host plant based on host plant traits or environmental effects not included in this study and that are currently unknown. For instance, perhaps intra-host variation in foliar quality for tent caterpillars is larger than inter-host variation. Furthermore, we currently know very little about the natural enemy communities associated with either of these host plants and how predators and parasitoids may affect tent establishment. Future research may help us to understand if tent caterpillar females have any preferences within or among their host plants, but our results currently suggest that they use wax currant and chokecherry equally.

Our larval fitness results demonstrate that adult tent caterpillar females do select wax currant for oviposition, and also that tent caterpillar larvae can thrive on wax currant even though it has never previously been recorded as a host plant. We found survival differences between chokecherry and wax currant, with wax currant being a higher quality host plant for tent caterpillars. Out of the four treatment groups, larvae reared on chokecherry had the lowest survival which was unexpected as it suggests that chokecherry is an inferior host plant despite chokecherry being well-known as a tent caterpillar host (Fitzgerald 1995, Powell and Opler 2009). Notably, we found that more larvae survived to pupation in the host plant treatments where we switched their host plants mid-development (wax currant switched to chokecherry and chokecherry switched to wax currant) than in the host plant treatments where we reared larvae on their natal host (chokecherry remaining on chokecherry and wax currant remaining on wax currant). This finding is interesting because switching hosts mid-development typically lowers or has a neutral effect on larval fitness in Lepidoptera (Bernays et al. 1994), with a few exceptions such as larvae that switch hosts for self-medication (e.g. Singer et al. 2009). Finally, we found no difference in pupal mass between host plants, which suggests that females from either host plant will be able to produce similar numbers of eggs.

Although we did not directly measure top-down fitness in our study, we found that 3.6% of the larvae collected on chokecherry were parasitized compared to only 0.8% of the larvae collected from wax currant. Although the sample size of these results is too small to form any concrete conclusions, this finding suggests that there may be differences in larval mortality from natural enemies between the two host plants. Further field trials to test top-down pressures will be required to determine if this pattern in differential mortality is broadly observed.

Our results suggest that wax currant is an adequate and frequently used host plant for tent caterpillars and our host-plant survey results do not show a clear preference between wax currant and chokecherry. Despite *Prunus* spp. being a well established tent caterpillar host plant (Fitzgerald 1995, Powell and Opler 2009), we found no evidence that chokecherry is a more suitable host plant in terms of larval fitness due to bottom-up (leaf quality) or top-down (parasitism rate) factors. Additional work should assess the fitness of larvae on both host plants in the field and test whether mortality from natural enemies such as predators varies between the hosts. Our results establish wax currant as a suitable host-plant for western tent caterpillars.

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