



Time-lagged intraspecific competition in temporally separated cohorts of a generalist insect

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Abstract

Competition can have far-reaching consequences for insect fitness and dispersion. Time-lagged interspecific competition is known to negatively affect fitness, yet time-lagged intraspecific competition is rarely studied outside of outbreak conditions. We tested the impact of competition between larval cohorts of the western tent caterpillar (*Malacosoma californicum*) feeding on chokecherry (*Prunus virginiana*). We reared larvae on host plants that either had or did not have feeding damage from tent caterpillars the previous season to test the bottom-up fitness effects of intraspecific competition. We measured host-plant quality to test potential mechanisms for bottom-up effects and conducted field oviposition surveys to determine if female adult tent caterpillars avoided host plants with evidence of prior tent caterpillar presence. We found that time-lagged intraspecific competition impacted tent caterpillar fitness by reducing female pupal mass, which is a predictor of lifetime fitness. We found that plants that had been fed upon by tent caterpillars the previous season had leaves that were significantly tougher than plants that had not been fed upon by tent caterpillars, which may explain why female tent caterpillars suffered reduced fitness on these plants. Finally, we found that there were fewer tent caterpillar egg masses on plants that had tent caterpillars earlier in the season than plants without tent caterpillars, which suggests that adult females avoid these plants for oviposition. Our results confirm that intraspecific competition occurs among tent caterpillars and suggests that time-lagged intraspecific competition has been overlooked as an important component of insect fitness.

Keywords Plant-mediated competition · Amensalism · Lepidoptera · *Malacosoma californicum* · *Prunus virginiana*

Introduction

Competition is a powerful force shaping communities that can alter fitness, species dispersion, and population size (Gurevitch et al. 1992; van Veen et al. 2006; Svanbäck and Bolnick 2007; Kaplan and Denno 2007). There is little debate that time-lagged interspecific competition is common (e.g., Schultz and Baldwin 1982; Kaitaniemi et al. 1998, 1999; Nykanen et al. 2004) and is most often mediated through long-term changes to plant secondary compounds and physiology induced by herbivore damage (Faeth 1986; Awmack and Leather 2002). Given that time-lagged

interspecific competition is relatively common and that there is no reason to believe that intraspecific competition should be less common than interspecific competition, we argue that the frequency of occurrence and importance of time-lagged intraspecific competition may be underestimated. Despite much compelling evidence regarding the effects of concurrent intraspecific competition on fitness and dispersion (Bultman and Faeth 1986; Griffith and Poulson 1993; Awmack and Leather 2002; Svanbäck and Bolnick 2007), few studies investigate the effects of intraspecific competition among temporally separated generations outside of outbreak conditions. The aim of these studies is often to predict insect outbreak cycles but, given the great variability in their reported effects, the impact of time-lagged intraspecific competition on insect outbreak patterns remains unclear (Klomp 1964; Schultz and Baldwin 1982; Kaitaniemi et al. 1999; Myers and Cory 2013). An understanding of the effects and importance of time-lagged intraspecific competition in stable populations could shed light on resource use patterns (Svanbäck and Bolnick 2007) and on some of

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the unexplained variation in models of population fluctuation (Schultz and Baldwin 1982; Ginzburg and Taneyhill 1994; Sun et al. 2015). In addition, little consideration has been given to the impact of time-lagged intraspecific competition on insect behavior (Cory and Myers 2004) despite the potential of behavioral changes to alleviate competitive pressures. For these reasons, we tested the impact of time-lagged intraspecific competition on the fitness and behavior of a generalist herbivore during non-outbreak years in both a field and lab setting.

Time-lagged intraspecific competition should be mediated through the same mechanisms as interspecific competition. Interspecific competition in herbivorous insects most commonly takes place indirectly via induced responses in a shared host plant or natural enemies (Kaplan and Denno 2007). When organisms compete indirectly, they do not need to overlap physically or temporally, since their competitive interaction is mediated by another trophic level (Kaplan and Denno 2007). For example, when herbivorous insects feed, they trigger defenses that spread throughout the whole plant (e.g., Faeth 1986; Redman and Scriber 2000; Bezemer et al. 2003; van Dam et al. 2005), and these induced plant defenses affect other insects feeding on that plant (e.g., Faeth 1986; Abdala-Roberts et al. 2012; Uesugi et al. 2016). Since these changes in host-plant quality can endure for months or even a year (Kaitaniemi et al. 1998, 1999), the negative effects from herbivore damage may even extend between cohorts of the focal herbivore. In cases of between-season competition, it is impossible for a later cohort to have any impact on a previous cohort and thus this asymmetric interaction might more accurately be termed amensalism (an interaction between two organisms that is negative in one direction and neutral in the other); we use the term competition, however, due to its prevalence in the literature to describe this type of interaction (e.g., Redman and Scriber 2000; Van Zandt and Agrawal 2004; Long et al. 2007; Valdovinos et al. 2013).

If the performance of juvenile insects is negatively affected by a host plant, there may then be evidence of altered oviposition behavior by the adult females in their host-plant selection (Thompson 1988). Insects in their adult stage have a range of cues available to them that can provide information about the host plant, not just about the plant species, but also a focal plant's history of herbivory and health (Awmack and Leather 2002; Wink 2010). For example, visual and chemical cues indicate the degree to which a plant has been damaged by other herbivores. Insects can detect physical (through touch or vision) and chemical cues (through olfaction or gustation) that provide them with information about the quality of a host plant. For many insects, vision is imperfect at a distance (Schoonhoven et al. 2005; Sponberg et al. 2015), but at close range they can differentiate between plants by their shape (pattern), size (dimensions), and color (spectral quality) (Prokopy and Owens

1983; Renwick 1989; Reeves 2011; McCormick et al. 2012; Nelson and Jackson 2014). Insects that construct elaborate shelters, like tents and webs, leave behind additional evidence of their presence beyond leaf damage cues (Fitzgerald 1995). These visual cues may act as proxies for the degree of activation of host-plant defenses and thereby indicate the food quality of the plant (Prokopy and Owens 1983), and although they are not the sole determinant of host-plant choice, these cues contribute to oviposition choice in many herbivorous insects (Awmack and Leather 2002). We therefore expect that if larvae compete through changes in host-plant quality, adult females will use visual and chemical cues to avoid low-quality host plants for their offspring.

We investigated the effect of between-season intraspecific competition on both larval fitness and oviposition choice of a gregarious herbivore: the western tent caterpillar (*Malacosoma californicum*; Packard, Lepidoptera: Lasiocampidae). Tent caterpillars have a single generation per year; larvae hatch from their egg masses in early spring, typically construct their tents on their natal host plant, and only venture to other plants to forage if they exhaust their food supply. After pupation in early summer, adults eclose and lay their eggs in midsummer (Powell and Opler 2009). Tent caterpillars construct silk tents that last through the summer and, occasionally, into the next year. However, little is known about the cues that adults use to assess oviposition sites beyond the diameter of shrub stems (Schmid et al. 1981; Cadogan and Scharbach 2005; Barnes et al. 2016). We measured the effect of previous-season tent caterpillar presence on tent caterpillar fitness to assess the impact of competition between larval cohorts. We also tested a possible mechanism for these fitness effects by measuring how previous-season tent caterpillar presence affected host-plant quality. To test if competition plays a role in oviposition choice, we surveyed host plants for tent caterpillar eggs to determine whether adult tent caterpillar females use signs of early season tent caterpillar presence (e.g., tents, leaf damage) as cues to reject a plant as an oviposition site.

Methods

Study system

We tested the effects of between-season intraspecific competition with western tent caterpillars (*Malacosoma californicum*) that feed on chokecherry (*Prunus virginiana*). Western tent caterpillars build tents on their host plants and feed gregariously as larvae through their penultimate instar before dispersing. In midsummer, adult females oviposit all of their eggs in a single egg mass on a branch (Fitzgerald 1995). It is unknown if female moths use host-plant volatile cues to guide their oviposition choices (Fitzgerald 1995), only that

part of their oviposition decision is based on branch diameter (Schmid et al. 1981). The eggs overwinter and hatch in the early spring. Although it has not been verified, it is believed that most larvae stay primarily on the host plant that their mother selects (Fitzgerald 1995); it is therefore important that an ovipositing female select a plant that will allow her offspring to thrive. Multiple tent caterpillar colonies may share a single plant, but we only included plants with a single colony in our experiments. Tent caterpillar larvae are generalists when considered across their full geographic range, but frequently specialize at a local level (Powell and Opler 2009).

We conducted our study on the eastern slopes of the Rocky Mountains in Colorado, where tent caterpillars feed most frequently on chokecherry and wax currant (*Ribes cereum*) (Barnes et al. 2016). We chose study sites in open edge habitats along roads, foot paths and bike paths as tent caterpillars prefer these areas (Fitzgerald 1995, Barnes personal observations). We used four field sites: Betasso Preserve (N40°1'28", W105°20'19"), Boulder Canyon Trail (N40°0'49", W105°18'35"), Walker Ranch (N39°56'36", W105°20'56"), and Centennial Cone Park (N39°45'42", W105°20'32"). All four sites are near streams in canyons in the foothills of the Rocky Mountains. At each site, chokecherry shrubs grow wild and are dispersed throughout a mix of wooded areas and meadows. We could not determine the age of the chokecherry plants in our experiment, but we only used healthy, mature plants that were capable of producing fruit, and at least 80 cm tall.

Lab fitness trial

We reared tent caterpillar larvae on chokecherries with and without previous-season tent caterpillar presence to test the effect of foliar damage by tent caterpillars on tent caterpillar fitness. We reared larvae in 2015 on leaves collected from chokecherry plants that we tagged and recorded during the previous season at our four field sites (April–June 2014) as either having or not having tent caterpillars present (40 shrubs/treatment). None of these plants had tent caterpillars feeding on them during the rearing trial in 2015. In April 2015, we collected first-instar larvae from ten tent caterpillar maternal lines in Boulder Canyon and divided each clutch into two groups of about 15 larvae each. First-instar larvae are small, delicate, and often tightly entwined in their tents and are therefore difficult to separate for an exact count without compromising their survival. In the lab in ambient conditions, we reared the larvae in a split-clutch design with half of the larvae on leaves from chokecherry with tent caterpillars absent in the previous season (maternal lines $n = 10$, ~ 15 individuals/maternal line, total larvae $n = 154$), and half on leaves from chokecherry with tent caterpillars present in the previous season (maternal lines $n = 10$, ~ 15

individuals/maternal line, total larvae $n = 159$). We collected host plants fresh from the field each day that we fed the experimental larvae in the lab and fed the larvae at least twice per week or as often as needed. We collected leaves from multiple shrubs and fed them to the larvae in a haphazard fashion so that larvae were fed leaves from specific treatments, but not from specific shrubs. We recorded two measures of fitness that allowed us to test the relative quality of each host-plant treatment on tent caterpillars. First, we measured larval survival to pupation (larvae pupate anytime between late May and mid June), which is a prerequisite to reproduction. Second, we measured pupal mass, which is positively correlated with the number of eggs a female will produce (Loewy et al. 2013). We sexed pupae and measured pupal mass 14 days after pupation using a Mettler-Toledo XP6 microbalance (to the nearest 0.01 mg; Mettler-Toledo, Columbus, OH).

Host-plant quality

We quantified multiple measures of host-plant quality including leaf toughness, %water, %N, %C, and cyanogenic glycoside concentration. We collected leaf samples in early June 2016 from chokecherry shrubs with and without larval tent caterpillars the previous season (tent caterpillars present $n = 26$ shrubs; tent caterpillars absent $n = 30$ shrubs) from Boulder Canyon and Betasso Preserve. We collected the leaves while tent caterpillars were feeding on nearby shrubs to ensure that we collected leaves during a phenologically appropriate time, but none of the shrubs that we sampled had tent caterpillars feeding on them during the 2016 growing season when we collected the leaves. We randomly collected a total of 15 leaves from each plant by picking every fifth leaf starting at a branch randomly selected using a die. We immediately placed the leaves in a cooler in the field and froze them immediately upon returning to the lab. We kept the leaves flat to ensure that they were not bent or broken.

We measured leaf toughness and %water by randomly selecting five leaves per plant that were larger than 3 cm by 2 cm. We thawed the leaves, rinsed them in water to remove dirt, and allowed them to dry for 10 min at room temperature (~ 21 °C). Next we weighed the leaves as a group (fresh mass) and then measured toughness and the dimensions of each leaf individually. We measured the length of each leaf from the tip of the leaf along the central vein to the base of the stem and measured width across the widest section of the leaf. We measured toughness using a modified version of the sand-pouring method described by Feeny (1970). We attached a safety pin through the leaf 1.5 cm up from the tip of the leaf along the central vein and 0.5 cm from the central vein. The safety pin was attached to a cup by a string. We poured sand into the cup until the safety pin broke all the way through the leaf and weighed the sand. After measuring

toughness, we dried all 5 leaves from each plant for 4 days at 60 °C and then weighed them once dry. We calculated %water by subtracting dry mass from fresh mass and dividing by fresh mass. For %water and toughness measures on individual leaves, we calculated a mean value per plant and used these means in the analyses. We performed all %water and leaf toughness mass measurements using a Scout Pro Ohaus Balance (Ohaus Corporation, Pine Brook, NJ, USA).

Chokecherries are defended by cyanogenic glycosides (Majak et al. 1981). To measure cyanogenic glycoside content and percent carbon (C) and nitrogen (N), we laid out all leaves we collected and counted to the fifth leaf to select three additional leaves that were at least 3 cm by 2 cm in size (these were not the same leaves used to measure toughness and %water). We measured cyanogenic glycoside as hydrogen cyanide (HCN) released from the leaves using a picrate paper kit method containing all materials needed to test HCN (Protocol E, Konzo Prevention Group, Research School of Biology, Australia National University). We cut a section approximately 2 cm by 1 cm out of each of the three leaves, ground them together with a pestle, and measured 100 mg of subsample of the ground leaf material. We quickly poured the leaf material into an airtight tube containing a sheet of linamarase and phosphate buffer paper and covered it with 1 mL of water. We placed a test strip soaked in picrate solution in the container so that it would not touch the leaf material or water, sealed the container and allowed it to sit for 22 h. We compared the color of the test strip to a color chart to determine the concentration of HCN in the leaves. We placed the remaining leaf material in the drying oven at 60 °C for 4 days to obtain material for measuring %C and %N. We combined all three dry leaves and ground them using a Retsch MM 400 Model mixer mill (Retsch GmbH, Haan, Germany), weighed them using a Mettler-Toledo XP6 microbalance (Mettler-Toledo, Columbus, OH), and rolled them into tin capsules (Elementar Americas). We sent the samples to Cornell University Stable Isotope Laboratory to be analyzed for %N and %C using an elemental analyzer-stable isotope ratio mass spectrometer system (Thermo Delta V Advantage IRMS and Carlo Erba NC2500 EA systems).

Survey of tent caterpillar egg masses

We surveyed chokecherry shrubs for tent caterpillar egg masses to assess the oviposition preferences of tent caterpillar adult females. In midsummer 2013 (May–July), we tagged chokecherry shrubs with and without larval tent caterpillars at Boulder Canyon Trail (tent caterpillars present $n = 19$ shrubs; tent caterpillars absent $n = 22$). Shrubs with tent caterpillar damage but no tent caterpillar tents were not included in the survey. In fall 2013, we again surveyed these shrubs for tent caterpillar egg masses after chokecherry shrubs had dropped their leaves and thus it was easier to

visually inspect the plants for eggs masses. We surveyed each chokecherry shrub for 5 min, carefully inspecting each branch for egg masses, and we recorded the presence or absence of tent caterpillar egg masses.

Data analysis

For the lab fitness trial, we determined whether percent larval survival to pupation differed between host-plant treatments using an ANOVA with treatment as a fixed effect and maternal line as a random effect. We analyzed pupal mass using an ANOVA with host-plant treatment, sex, and their interaction as fixed effects; we treated maternal line as a random effect. We analyzed chokecherry %water, toughness, %N, %C and hydrogen cyanide (HCN) content using an ANOVA with host-plant treatment and collection site as fixed effects. We used a post hoc Tukey's HSD test to determine which means were significantly different from one another. We assessed whether adult tent caterpillars avoid ovipositing on shrubs with early season tent caterpillar presence using a Chi-squared test with host-plant treatment and the presence of eggs (eggs present vs. eggs absent) as classifying variables. All data were analyzed using JMP Pro 10.0.0.

Results

Lab fitness trial

We found a significant interaction between the effects of host-plant treatment and sex on tent caterpillar pupal mass ($F_{2,49} = 9.78$, $p = 0.0032$; Fig. 1); female larvae reared on

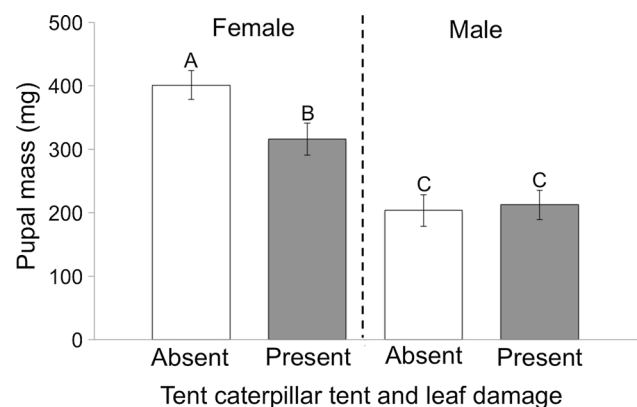


Fig. 1 Pupal mass for tent caterpillars (*Malacosoma californicum*; Packard, Lepidoptera: Lasiocampidae) reared on chokecherry (*Prunus virginiana*) plants that either did (“present”) or did not (“absent”) have previous-season tent caterpillar tents or damage. Significant differences between means are indicated with letters, and error bars show ± 1 SE

chokecherry with tent caterpillars absent the previous year had significantly greater pupal mass than those reared on chokecherry with tent caterpillars present the previous year ($F_{1,19} = 12.58, p = 0.0021$), but there was no difference between treatments for male pupal mass ($p = 0.39$). Female pupae also weighed significantly more than male pupae ($F_{1,49} = 98.8, p < 0.0001$; male mean = 208.0 ± 21.5 mg, female mean = 358.6 ± 21.7 mg). Survival did not differ between the larvae reared on chokecherry with tent caterpillars absent the previous year (mean = $18.1 \pm 8.5\%$) and those reared on chokecherry with tent caterpillars present the previous year (mean = $18.3 \pm 7.3\%$; $F_{1,19} = 0.0005, p = 0.98$).

Host-plant quality

We found that the toughness of chokecherry leaves was significantly greater on shrubs with tent caterpillars present the previous year than those with tent caterpillars absent the previous year ($F_{1,56} = 5.02, p = 0.029$; Fig. 2) and significantly greater at Betasso Preserve and Boulder Canyon than Centennial Cone Park ($F_{2,56} = 5.92, p = 0.0049$), but we found no interaction between treatment and site ($F_{2,56} = 0.28, p = 0.75$; Table 1). We found that % water was significantly lower at Centennial Cone Park than Boulder Canyon and Betasso Preserve ($F_{2,55} = 80.36, p < 0.001$) and there was an interaction between site and treatment ($F_{2,55} = 3.29,$

$p = 0.046$), but no difference between tent caterpillar treatments ($F_{1,56} = 0.11, p = 0.74$; Table 1). Site ($F_{2,55} = 1.57, p = 0.22$) and treatment ($F_{1,55} = 3.1, p = 0.081$) were not different for %N, and there was no interaction between site and treatment ($F_{2,55} = 1.62, p = 0.21$; Table 1). For %C there were no differences between tent caterpillar treatments ($F_{1,55} = 0.14, p = 0.71$) or sites ($F_{2,55} = 1.56, p = 0.22$; Table 1), nor was there an interaction between the two ($F_{2,55} = 0.49, p = 0.62$). Hydrogen cyanide was lower at Centennial Cone Park than Boulder Canyon and Betasso Preserve ($F_{2,55} = 5.77, p = 0.0057$), but there was no difference between tent caterpillar treatments ($F_{1,56} = 0.43, p = 0.51$) and no interaction between site and treatment ($F_{2,55} = 2.64, p = 0.081$; Table 1). To ensure that we had a sufficient sample size for our non-significant results, we ran post hoc power analyses with our means using the recommended statistical power of 0.8 (Cohen 1988). We found that to detect a difference between the means of our samples, we would need 2379 samples for %water, 480 for %N, 1082 for %C, and 4155 for hydrogen cyanide.

Survey of tent caterpillar egg masses

We found that chokecherry shrubs that had not been previously attacked by tent caterpillars were six times more likely to have tent caterpillar egg masses than shrubs on which tent caterpillars had been present ($\chi^2 = 7.73, df = 1, n = 41, p = 0.0054$; Fig. 3).

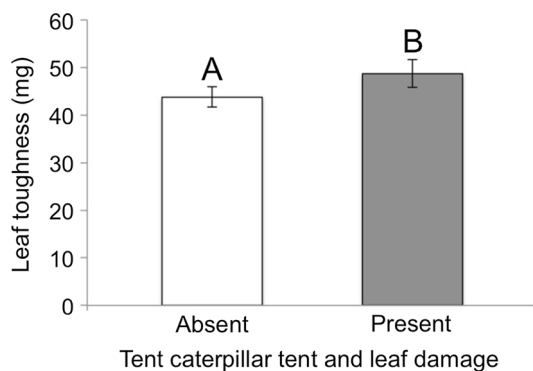


Fig. 2 Leaf toughness of chokecherry with (“present”) or without (“absent”) previous-season tent caterpillar tents or damage. Significant differences between means are indicated with letters, and error bars show ± 1 SE

Discussion

The presence of tent caterpillars on a host plant the previous season significantly reduced pupal mass for female tent caterpillars feeding on that plant the next year. Since female pupal mass is positively correlated with the number of eggs that females can lay as adults, females with greater pupal mass thus have greater lifetime fitness (Loewy et al. 2013). Interestingly, we did not find any negative consequences for male tent caterpillars feeding on previously damaged chokecherry plants as measured by either survival or pupal mass. Notably, while none of the plants used in our fitness trials were fed upon by tent caterpillars during the time frame of our experiment, we continued to monitor these plants and

Table 1 Mean host-plant quality values (± 1 SE) of chokecherry leaves with tent caterpillar larvae absent and tent caterpillar larvae present 1 year before leaves were collected. Leaves were tested in the

Treatment	%Water	Toughness	HCN	%C	%N
Tent caterpillar absence	0.028 \pm 0.002	41.34 \pm 1.25	753.57 \pm 30.63	48.18 \pm 0.25	2.51 \pm 0.08
Tent caterpillar presence	0.028 \pm 0.002	47.16 \pm 2.01	769.23 \pm 39.32	48.40 \pm 0.24	2.40 \pm 0.06

spring of 2016 for %water, toughness (g), hydrogen cyanide (HCN ppm), percent carbon (%C), and percent nitrogen (%N). Bold indicates values that differed significantly between treatments

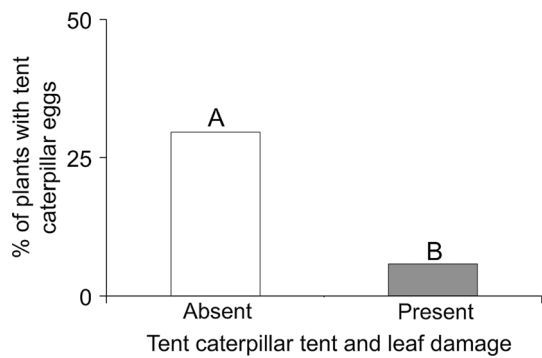


Fig. 3 Percentage of chokecherries surveyed with tent caterpillar eggs on plants with (“present”) or without (“absent”) early season tent caterpillar tents or damage. Significant differences between percentages are indicated with letters

in subsequent years all of the plants in our experiment were eventually used by tent caterpillars, indicating that they all have the potential to be chosen by females as oviposition sites. Thus, it seems unlikely that the negative fitness effects that we found could be caused by inherent differences in host-plant quality unconnected to past tent caterpillar feeding. Furthermore, if plants with tent caterpillars present the previous year were better host plants and were thus selected because of their inherent high quality, we would have expected the opposite result from the one we observed, with tent caterpillars having greater fitness on plants fed upon by tent caterpillars the year before. The significant negative effect of host-plant damage the previous season on female fitness establishes that plant-mediated competition does occur between cohorts of tent caterpillars through bottom-up effects that negatively affect female larval fitness. This finding is particularly interesting given that tent caterpillars are generalist herbivores, which are thought to be less affected by bottom-up effects than specialist herbivores (Vidal and Murphy 2018). We expect this type of negative plant-mediated interaction to be common in consumers that use a food resource that is damaged but not killed during feeding and that survives multiple growing seasons. However, the strength of the interaction likely varies depending on the species involved.

We found that chokecherry leaves were tougher when tent caterpillars had fed on the plants the previous season. Leaf toughness is an important measure of host-plant quality, and increased leaf toughness is known to inhibit larval feeding (Gotoh et al. 2011) and deter oviposition in some insects (Constant et al. 1996). Leaf toughness is also well established as having a strong effect on the ability of early instars of various tent caterpillar species to bite into their host plant, and it has been speculated that toughness plays a key role in larval development (Fitzgerald 1995 and references therein). Our results suggest that

increased toughness may cause female tent caterpillar fitness to decrease when they are reared on previously damaged host plants; we did not find any other significant differences in host-plant quality between damaged and undamaged plants, and it is unclear why toughness did not similarly affect male larvae. We speculate that since males are smaller than females, they may require less leaf material to pupate and may thus more easily compensate for their slow feeding rate on tougher leaves. It would be interesting to test how long plants continue to produce tough leaves after tent caterpillar feeding and whether this effect dissipates after a growing season without damage.

Female tent caterpillar adults appear to use cues of prior tent caterpillar feeding damage, such as the presence of tents or leaf secondary compounds, to avoid low-quality host plants for their offspring, as we found fewer tent caterpillar eggs on chokecherry shrubs with tent caterpillar damage and tents earlier in the season compared to shrubs without tent caterpillars earlier in season. Adult female tent caterpillars may choose to avoid ovipositing on host plants with early season tent caterpillar damage by using a combination of visual and chemical cues from tent caterpillar leaf damage and tent caterpillar tents. It is also possible that adult females do not avoid damaged plants, but are instead attacked before they are able to oviposit on damaged shrubs. We have evidence that tent caterpillar tents increase the density of predators on chokecherry, including predators large enough to attack a tent caterpillar moth (Barnes and Murphy in preparation). Whether adult females are attacked while ovipositing near tent caterpillar tents or their offspring suffer reduced fitness on host plants with prior tent caterpillar damage as we have shown here, both situations would be predicted to select for females that avoid plants that had been previously fed upon by tent caterpillars. Regardless of the mechanism driving avoidance, our oviposition survey demonstrates that time-lagged intraspecific competition alters the behavior of tent caterpillar adults. We speculate that this behavior causes a rough alternation of years of damage on chokecherry with plants having a year of respite after larval feeding; this pattern of alternation of high-damage years could be common in any system where cues from herbivore damage are still present when females are ovipositing.

We show here that plant-mediated competition between cohorts of a generalist herbivore impacts fitness and behavior in non-outbreak conditions. Intraspecific competition between temporally separated cohorts of tent caterpillars negatively affects female larval fitness via decreased plant quality and also affects adult oviposition behavior. Time-lagged intraspecific competition is not commonly studied in non-outbreak conditions, especially for generalists. Our results show that this type of competition can have important fitness and behavioral consequences and thus our work demonstrates the need for further investigation into the role

of between-season intraspecific competition in structuring communities of herbivorous insects.

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Author contribution statement EEB and SMM designed the experiments. EEB performed the experiments, analyzed the data, and wrote the first draft. EEB and SMM wrote and edited the manuscript. Both authors gave final approval on the manuscript.

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