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The Effects of Host Plant Species and Plant Quality on Growth and Development in the Meadow Spittlebug (*Philaenus spumarius*) on Kent Island in the Bay of Fundy

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Abstract - *Philaenus spumarius* (Meadow Spittlebug, Homoptera: Cercopoidea) is a cosmopolitan generalist insect that feeds on a wide repertoire of host plants in the field. We studied density and growth of Meadow Spittlebugs on a range of host plants on Kent Island, a boreal island in the Bay of Fundy, NB, Canada. The highest spittlebug densities were on *Cirsium arvense* (Canadian Thistle), although spittlebugs had larger body sizes on *Solidago rugosa* (Rough-stemmed Goldenrod) and *Anaphalis margaritacea* (Pearly Everlasting). We fertilized plots of Rough-stemmed Goldenrod in the field over 3 weeks to examine the effects of plant quality on development of Meadow Spittlebugs. Following fertilization, there were fewer nymphs present in fertilized plots than in unfertilized plots, indicating faster nymph maturation to adulthood on fertilized plants. This study offers an initial report of the host plants used by Meadow Spittlebugs in northeastern boreal habitat, variation in density and performance of the species on a range of host plants, and the effects of plant fertilization on spittlebug life history.

Introduction

Herbivorous insects have long been divided into specialists and generalists (Bernays and Graham 1988). Even generalists, however, may not perform equally on all plant species, as host-plant quality can affect mortality, fecundity, and fitness of generalists (Ali and Agrawal 2012, Awmack and Leather 2002, Bovil et al. 2013, Levins and MacArthur 1969). Additional factors, such as adult lifespan (Wise et al. 2008), plant nutrient content (Mattson 1980), and host-plant densities (Jaenike 1978, Williams 1983) can also influence the host-plant preferences of generalist insects. The preference–performance hypothesis (PPH) suggests that females select oviposition sites in order to optimize offspring fitness (Jaenike 1978). This choice is likely to be especially important for species with immobile or slow-moving nymphal stages, as sessile nymphs have little capacity to switch hosts (Thompson 1988). There are many examples, however, of apparently maladaptive host-plant selection due to other factors such as the availability of optimal hosts (Jaenike 1990), time limitations on decision-making (Mayhew 1997, Prinzing 2003, Wise et al. 2008), and chemical or physical plant defenses against herbivores (Ali and Agrawal 2012).

Philaenus spumarius (L.) (Meadow Spittlebug, hereafter also simply "spittlebug") is a widely distributed polyphagous insect that feeds on the xylem sap of a range of vascular plants (Whittaker 1970). It is one of less than 10% of herbivorous

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insects that feed on more than 3 families of host plants (Bernays and Graham 1988). Meadow Spittlebugs are hemimetabolous and possess an annual life cycle, with female spittlebugs laying 10–50 eggs at the end of the summer season beneath plants in litter or soil, which hatch in the spring (Hamilton 1982). Developing nymphs progress through 5 instars of increasing size, and under laboratory conditions, adults appear 50 days after hatching (Yurtsever 2000). All 5 instars produce a spittle mass, an excretory product resulting from a high ingestion-to-digestion rate of xylem sap and which protects the fleshy nymph at its feeding site from desiccation and insect predation (Weaver and King 1954). Nymphs on the same ramet benefit from feeding in aggregations in the same spittle mass at upper, fleshier parts of the plant (Horsfield 1977), and they will regularly change feeding location on the same plant in their lifetime (Wise et al. 2006).

Nitrogen is a key limiting factor in both plant growth and insect nutrition under natural conditions (Mattson 1980, Séquin 2017). While Meadow Spittlebugs have been found on hundreds of hosts, they exhibit a preference for nitrogen-fixing host plants (Thompson 1994). As xylem tissues contain between 10% and 1% of the amount of nitrogen available in phloem, nitrogen readily available to xylem-feeders like spittlebugs is far less abundant than to phloem-feeding insects (Mattson 1980). Craig and Ohgushi (2002) detected a positive correlation between preference and performance of spittlebugs on 4 species of willow, where high egg densities and offspring survival rates were found on the fastest-growing shoots with higher concentrations of nitrogen. Horsfield (1977) also found higher nymph survival rates with higher concentrations of amino acids. As higher concentrations of amino acids in the xylem are a direct result of fertilization uptake in plants (Malaguti et al. 2001, Selvendran and Selvendran 1973), fertilization has the potential to affect host-plant preference and performance of spittlebugs (Mattson 1980). Agricultural fertilization can therefore increase the vulnerability of crops to pest infestation (Yardım and Edwards 2002, Zhong-xian et al. 2007), due to positive effects on the growth, survival, and fecundity of herbivorous insects (Kytö et al. 1996, Pires et al. 2000, Waring and Cobb 1992). Although Kytö et al. (1996) conclude that fertilization is generally beneficial for sucking insects, fertilization-manipulation studies have had mixed results, and there is some evidence to indicate that plants with high nutrient content may be better equipped to defend themselves against herbivory (Mattson 1980).

This study had 4 components: we (1) created a list of host plants used by Meadow Spittlebugs on Kent Island, a boreal island in the Bay of Fundy, NB, Canada (44°34'54.3"N 66°45'21.3"W; Fig. 1); (2) assessed density and body size of Meadow Spittlebugs on various host plants as proxies for preference and performance; (3) removed spittlebugs from host plants to observe rates of recolonization, as little is known about how much spittlebug nymphs move between host plants; and (4) examined the effects of fertilization of *Solidago rugosa* (Rough-stemmed Goldenrod) on spittlebug development time. In accordance with past studies (Kytö et al. 1996, Thompson 1994, Wise et al. 2006), we expected variation in nymph densities and body sizes of nymphs feeding on different plants and predicted that nymphs in fertilized plots of goldenrod would mature faster when compared to those in unfertilized plots.

Materials and Methods

We collected all data at the Bowdoin Scientific Station on Kent Island, a 93-ha island, during June and July of 2017. To determine the host plants used by Meadow

Figure 1. Study site at Bowdoin Scientific Station at Kent Island in the Bay of Fundy, NB, Canada (44°34'54.3"N 66°45'21.3"W). Dots (bottom image) represent paired fertilizer/control plots of *Solidago rugosa* (Rough-stemmed Goldenrod), for a total of 16 paired plots in fielded areas.

Spittlebugs on Kent Island, we first surveyed all plant species growing there for the presence of spittlebug nymphs. We searched each of the 8 microhabitats on the island (meadow, bog, woods, forest edge, beach margin, salt marsh, fields, gull hills) between 1 June 2017 and 25 July 2017 for signs of spittle, and confirmed presence of Meadow Spittlebugs by brushing aside spittle to reveal the nymph.

To examine preference between different host plants, we surveyed the density of spittlebug nymphs on 4 host plant species—*Oclemena acuminata* (Whorled Wood-aster; *n* = 60), *Anaphalis margaritacea* (Pearly Everlasting; *n* = 60), Rough-stemmed Goldenrod (*n* = 60), and *Cirsium arvense* (Canada Thistle; *n* = 30)—in a 0.24-ha open meadow from 15 June 2017 to 2 July 2017. We chose the 4 species because we found them existing concurrently in both time and space in the same meadow in high numbers (>100 ramets) and observed the presence of nymphs on each at the same time. We measured plant heights and counted the number of nymphs per plant by carefully and temporarily brushing aside spittle to reveal the individuals in each spittle mass. We used a one-way ANOVA and Tukey post-hoc tests to assess variation in plant height. To assess the effect of host plant species on nymph density, we calculated the average number of nymphs per meter of plant height for each species and used a one-way ANOVA to assess the effect of plant species on spittlebug density. We measured the body lengths of 30 nymphs from each of Pearly Everlasting, *Rumex acetosella* (Sheep Sorrel), Rough-stemmed Goldenrod, Canada Thistle, and *Rubus idaeus* (Red Raspberry) plants (*n* = 10–25) found in the same 0.24-ha field between 27 June and 9 July 2017. Nymphs were measured with calipers while still alive, as dead nymphs tended to shrivel. We did not return measured nymphs to the study site. We collected a second round of nymphs 10 days later from the same plant species in the same collection areas and measured again for body length. We also classified nymphs to the nearest instar based on body sizes described in Yurtsever (2000). We used a two-way ANOVA to analyze the effects of host species and sampling period on body size, and one-way ANOVAs and Tukey post-hoc tests to assess differences in body size for each date.

Nymph removal and recolonization

To determine the likelihood of nymphs recolonizing a neighboring area free of spittlebug presence, we cleared all Meadow Spittlebug nymphs by hand from two 0.36-m^2 plots of Rough-stemmed Goldenrod and then monitored the plots for recolonization over a 4-weeks period by counting number of nymphs per plot.

Fertilizer application experiment

To measure the effect of fertilizer on nymph density, we established 16 paired plots in fields dominated by Rough-stemmed Goldenrod on Kent Island (Fig. 1). Plots of goldenrod were 0.36 m^2 and arranged in pairs ~3 m apart. The density of goldenrod plants per plot varied between plots (~35–65 ramets/plot), but all paired plots had comparable goldenrod densities. We measured the height of 30 random goldenrod plants within each plot, which represented 60–90% of the total goldenrod plants. In each paired plot, we hand-checked for nymphs by brushing aside spittle to count individuals on each of the 30 random plants, but nymphs were otherwise undisturbed. After initial density and height measurements, we fertilized 1 of each paired set of plots with 2.2 mL of 30:10:10 N-P_2O_5-K_2O fertilizer dissolved in 10 L water on 11 June 2017 and again on 27 June 2017. Each 0.36-m^2 experimental plot received ~3 L of the fertilizer solution per application, and control plots were left without treatment because rainfall was sufficient to make the water treatment negligible. We again recorded the heights of 30 random goldenrod plants and their spittlebug densities in each plot during 3–6 July 2017. We fertilized experimental plots a third time during 18–21 July 2017 before a final round of censusing, for a total of 3 fertilizer applications and 3 censuses of plant height and nymph density. We assessed the effect of treatment on goldenrod height and proportion of plants with nymphs with separate linear mixed-effect models using the 'lme4' package in R (Bates et al. 2015) for both sampling periods following fertilization, for which we included treatment as a fixed effect and plot as a random effect. After all rounds of fertilization treatment and density censusing, we collected remaining nymphs from all 16 paired plots and measured for body size ($n_{\text{Fertilized}} = 17$, $n_{\text{Control}} = 22$). We assessed the effects of treatment on spittlebug body size with a paired *t*-test and the effects of treatment on instar distribution with a chi-square test.

All statistical analyses were performed in R version 3.4.1 (R Core Team 2018).

Results

Host plants, density, and body-size measurements

We observed Meadow Spittlebugs on 32 species and 17 families of plants (Table 1). There are 240 known plants in 54 families on Kent Island (McCain 1975, McIlraith 1986). We compared the number of nymphs per meter of plant on 4 common and co-occurring host-plant species (Fig. 2). There was a significant effect of host species on nymph densities per meter of ramet (one-way ANOVA: $F_{3, 205} = 19.03$, $P < 0.0001$). Tukey post-hoc tests revealed that the density of nymphs per meter of Canada Thistle ramets (8.42 nymphs/meter) was greater than nymphs on Pearly Everlasting (4.61 nymphs/meter; $P = 0.001$), Rough-stemmed Goldenrod (2.72 nymphs/meter; $P < 0.0001$), and Whorled Wood-aster (1.03 nymphs/meter; $P < 0.0001$) (Fig. 3). The average number of nymphs per meter on goldenrod was not significantly different than nymphs per meter on Pearly Everlasting ($P = 0.11$) or Whorled Wood-aster ($P = 0.19$), which had fewer nymphs on average per meter than the rest of species sampled ($P \leq 0.00017$ for all post-hoc comparisons with Whorled Wood-aster, besides goldenrod) (Fig. 3).

We also sampled the body sizes of nymphs found on different plant species (Rough-stemmed Goldenrod, Canada Thistle, Pearly Everlasting, Sheep Sorrel, Red Raspberry) at 2 points in the field season by measuring body lengths. Nymph body size was affected by plant species (two-way ANOVA: $F_{4, 375} = 20.90$, $P < 0.0001$) and sampling period ($F_{1, 375} = 258.28$, $P < 0.0001$), and there was a significant interaction between species and sampling period ($F_{4, 375} = 9.00$, $P < 0.0001$) (Fig. 4). Average size of nymphs was 4.24 mm on 29 June 2017,and 5.39 mm on 8 July 2017, an increase of 25.4% (Fig. 4). According to Yurtsever's descriptions of instar sizes (Yurtsever 2000), spittlebugs were a mix of third and fourth instar nymphs on the first measurement date, and predominantly fourth and fifth instar nymphs at the second measurement. Nymphs on Rough-stemmed Goldenrod were larger than nymphs on all other plants (Tukey post-hoc tests: $P \leq 0.017$) besides Pearly Everlasting earlier in the season ($P = 0.64$), and nymphs on Red Raspberry were smaller than nymphs on all other species for the first body-size measurement (Tukey post-hoc test: $P \leq 0.0004$) but not the second measurement ($P \leq 0.68$). Later in the season, body sizes were similar for nymphs on Rough-stemmed Goldenrod, Pearly Everlasting, and Canada Thistle ($P \geq 0.39$). Between 29 June and 8 July 2017,

Table 1. Host plants of *Philaenus spumarius* (Meadow Spittlebug) on Kent Island in the Bay of Fundy, NB, Canada. Plants were censused from May to July 2017 by checking for spittle masses. Meadow Spittlebugs were found on 32 species and 17 families of plants on Kent Island. * indicate species examined for nymphal density or body size. † indicates species considered invasive in New England (University of Gerogia 2018).

Plant species	Family
Solidago rugosa Mill. (Rough-stemmed Goldenrod)	Asteraceae
Solidago sempervirens L. (Seaside Goldenrod)	Asteraceae
*Oclemena acuminata** (Michx.) Greene (Whorled Wood-Aster)	Asteraceae
*Anaphalis margaritacea** (L.) Benth. (Pearly Everlasting)	Asteraceae
Oclemena nemoralis (Aiton) Greene (Bog Aster)	Asteraceae
Achillea millefolium L. (Yarrow)	Asteraceae
*Cirsium arvense**† (L.) Scop. (Canada Thistle)	Asteraceae
Hieracium aurantiacum L. (Orange Hawkweed)	Asteraceae
Hieracium caespitosum Dumort. (Yellow Hawkweed)	Asteraceae
Impatiens capensis Meerb. (Touch-me-not)	Balsaminaceae
Stellaria graminea L. (Lesser Stitchwort)	Caryophyllaceae
Cornus canadensis L. (Bunchberry)	Cornaceae
Dryopteris spinulosa (VIII.) H.P. Fuchs (Spinulose Wood Fern)	Dryopteridaceae
Vaccinium angustifolium Aiton (Low Bush Blueberry)	Ericaceae
Iris versicolor L. (Larger Blue Flag)	Iridaceae
Oenothera biennis L. (Evening Primrose)	Onagraceae
Epilobium angustifolium L. (Fireweed)	Onagraceae
Abies balsamea (L.) Mill. (Balsam Fir)	Pinaceae
Picea glauca (Moench) Voss (White Spruce)	Pinaceae
*Rumex acetosella**† L. (Sheep Sorrel)	Polygonaceae
Rumex crispus L. (Curly Dock)	Polygonaceae
Ranunculis acris L. (Tall Buttercup)	Ranunculaceae
Sorbus americana Marshall (American Mountain Ash)	Rosaceae
*Rubus idaeus** L. (Red Raspberry)	Rosaceae
Rosa rugosa Thunb. † (Rugosa Rose)	Rosaceae
Rosa nitida Willd. (Shining Rose)	Rosaceae
Rubus hispidus L. (Bristly Dewberry)	Rosaceae
Acer spicatum Lam. (Mountain Maple)	Sapindaceae
Rhinanthus minor L. (Yellow Rattle)	Scrophulariaceae
Solanum dulcamara† (L.) (Bittersweet Nightshade)	Solanaceae
Thelypteris palustris Schott (Marsh Fern)	Thelypteridaceae
Urtica dioica L. (Stinging Nettle)	Urticaceae

nymphs on Sheep Sorrel grew at the slowest rate (0.066 mm/day), and nymphs on Red Raspberry at the fastest rate (0.20 mm/day).

Nymph removal and recolonization

In order to determine how much they move into open resources, we removed spittlebug nymphs from two 0.36-m^2 plots of goldenrod on 14 and 15 June 2017. We found very little recolonization by nymphs over the course of the next month (Fig. 5). Of the 73 and 39 nymphs removed in 2 plots, the recolonization presence peaked at 6 and 3 nymphs, respectively, representing 8.2% and 7.7%, respectively, of original densities.

Fertilizer application experiment

Observations of nymph distribution on goldenrod indicated that nymphs predominantly occurred on the top parts of the plant, with 87% of nymphs observed feeding on leaf axils in the upper third of the plants, 11% feeding on the middle third, and 2% on the bottom third. Fertilization treatment had a significant effect on goldenrod height in both sampling periods (linear mixed-effect model: $\chi^2_{1,} = 105.7$, $P < 0.0001$ and $\chi^2_{1,} = 498.4$, $P < 0.0001$; Fig. 6A), with fertilized goldenrod growing 1.8 times faster than unfertilized goldenrod per day over the course of the

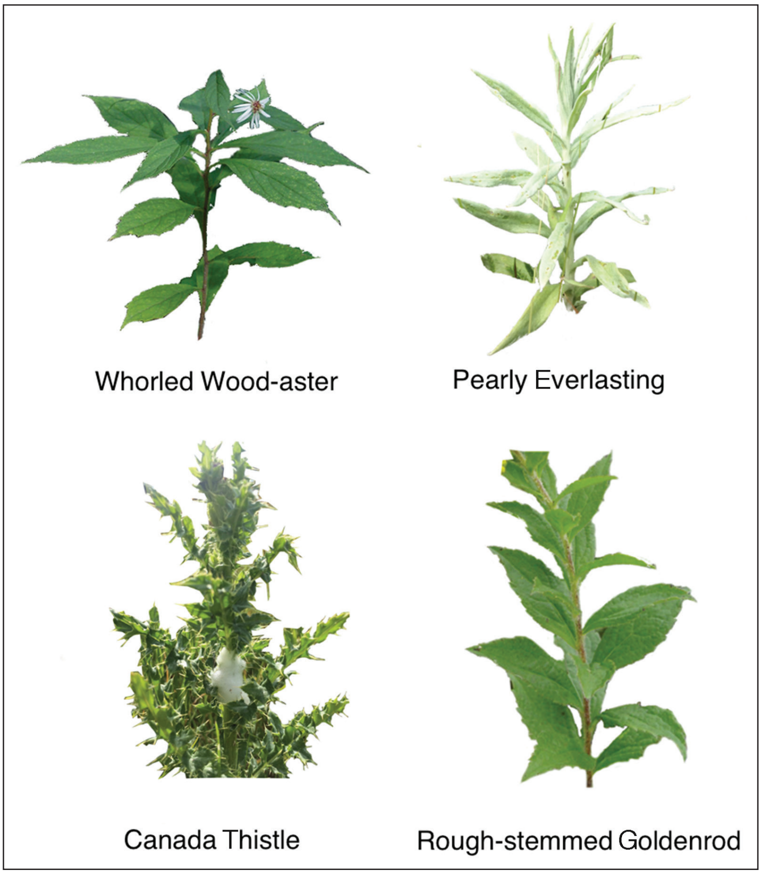


Figure 2.Plants species, to scale, surveyed for nymph density. Whorled Wood-aster and Rough-stemmed Goldenrod images from Donald Cameron [2018]).

measuring period. Treatment had a significant effect on the proportion of plants with nymphs for the second sampling period ($\chi^2_{1,} = 4.67$, $P = 0.031$) but not for the third sampling period ($\chi^2_{1,} = 1.36$, $P = 0.24$). We measured proportion of plants with nymphs for fertilized and unfertilized goldenrod on 8 June 2017 (before treatment),

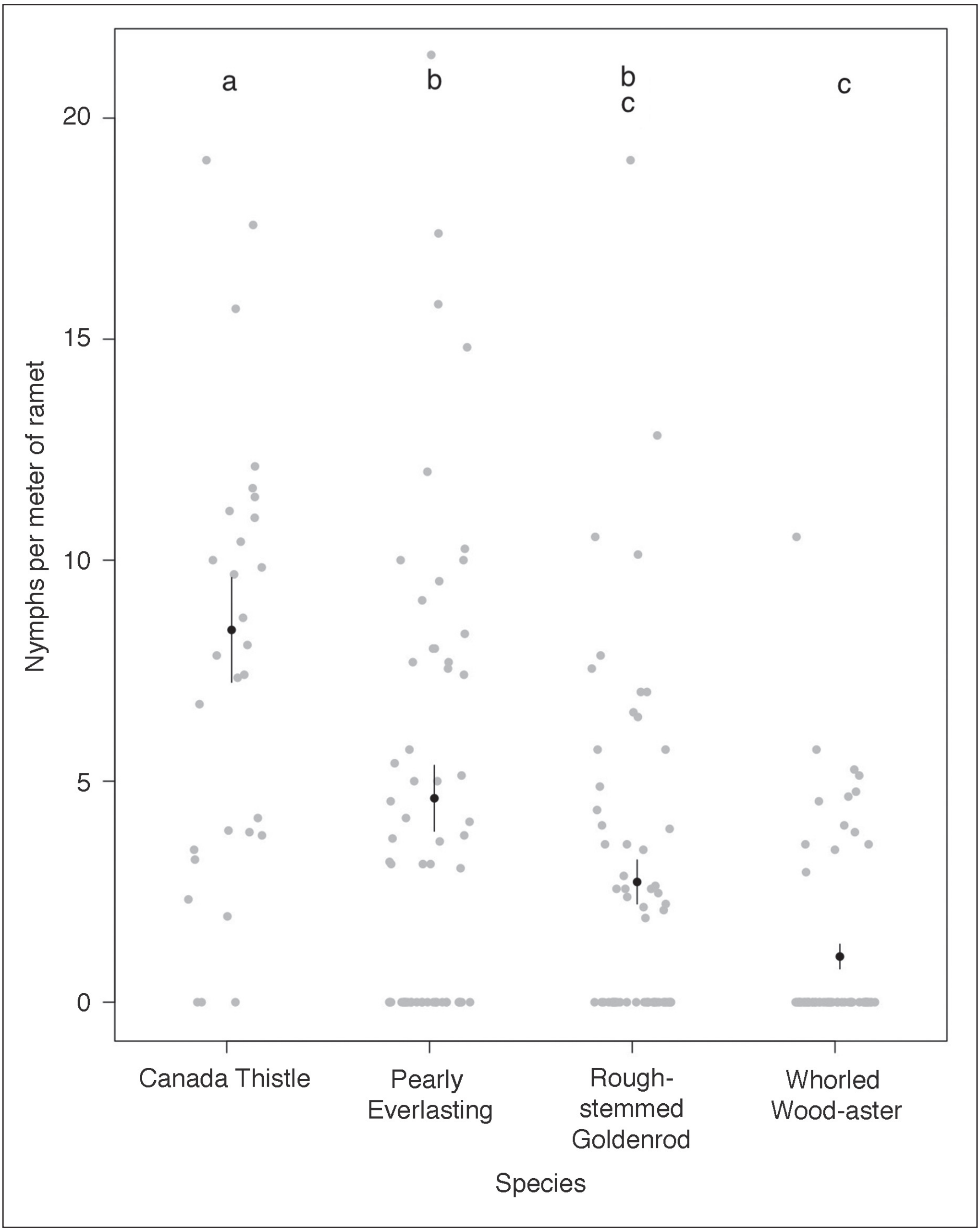


Figure 3. Number of *Philaenus spumarius* (Meadow Spittlebug) nymphs per meter of plant height on 4 different species. Means and standard errors are plotted over the raw data. Plant species that share letters do not significantly differ in Tukey post-hoc comparisons.

3 July 2017 (after the first fertilizer application), and 18 July 2017 (after the second fertilizer application). Before fertilizer treatment, the plots did not significantly differ in the proportion of plants with nymphs (linear mixed-effect model: $\chi^2_1 = 1.82$, $P = 0.178$; Fig. 6B). After the first fertilizer treatment, the fertilized plots had a significantly lower proportion of plants with nymphs ($\chi^2_1 = 4.67$, $P = 0.04$). After the second fertilizer treatment, the proportions of plants with nymphs was low enough for both treatments that there was no significant effect of treatment on proportion of plants with nymphs ($\chi^2_1 = 1.36$, $P = 0.244$). The few remaining nymphs on both fertilized and unfertilized goldenrod were measured for body length at the end of the season, and nymphs on fertilized goldenrod were 3.8% larger, but this was not

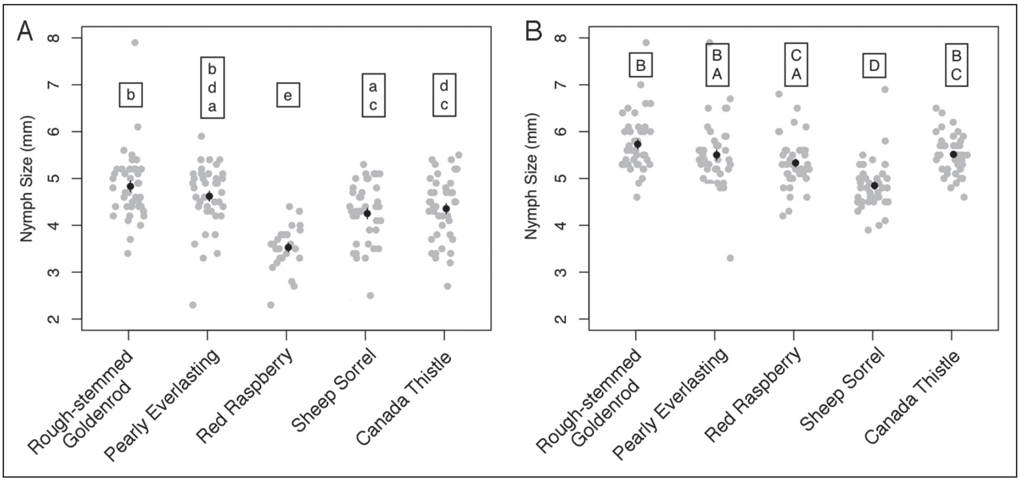
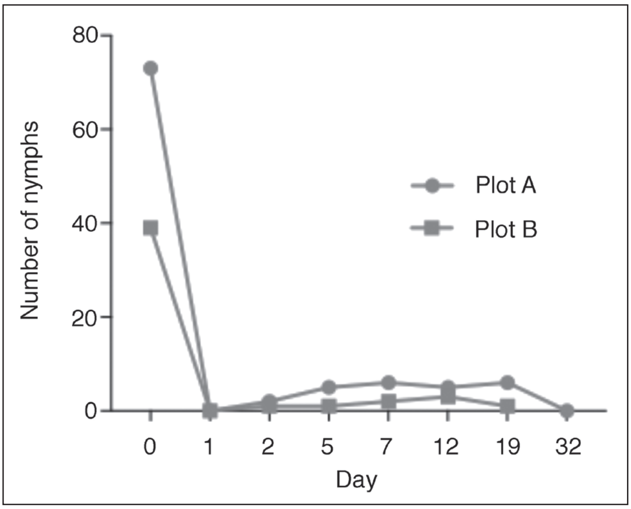


Figure 4. Overall effect of sampling period and plant species on body lengths of *P. spumarius* (Meadow Spittlebug) nymphs (A and B, 29 June 2017 and 8 July 2017, respectively). Means and standard errors were plotted over the raw data. The 2 sampling periods were analyzed separately, and different letters indicate $P < 0.05$ in Tukey post-hoc tests.

Figure 5. Re-colonization after nymph removal. Nymphs were removed from all plants in 2 *Solidago rugosa* (Rough-stemmed Goldenrod) plots on Day 0. Plots were monitored for the following 4 weeks for nymph density.



a significant difference (paired *t*-test: df = 30, $t = 1.676$, $P = 0.104$; Fig. 7). There were 11 fourth instar and 6 fifth instar nymphs in the control plot and 4 fourth instar and 12 fifth instar nymphs in the experimental plot. These distributions were also not significantly different (chi-square test: $\chi^2_1 = 3.27$, $P = 0.07$ for fourth instar nymphs; $\chi^2_1 = 2$, $P = 0.16$ for fifth instar nymphs).

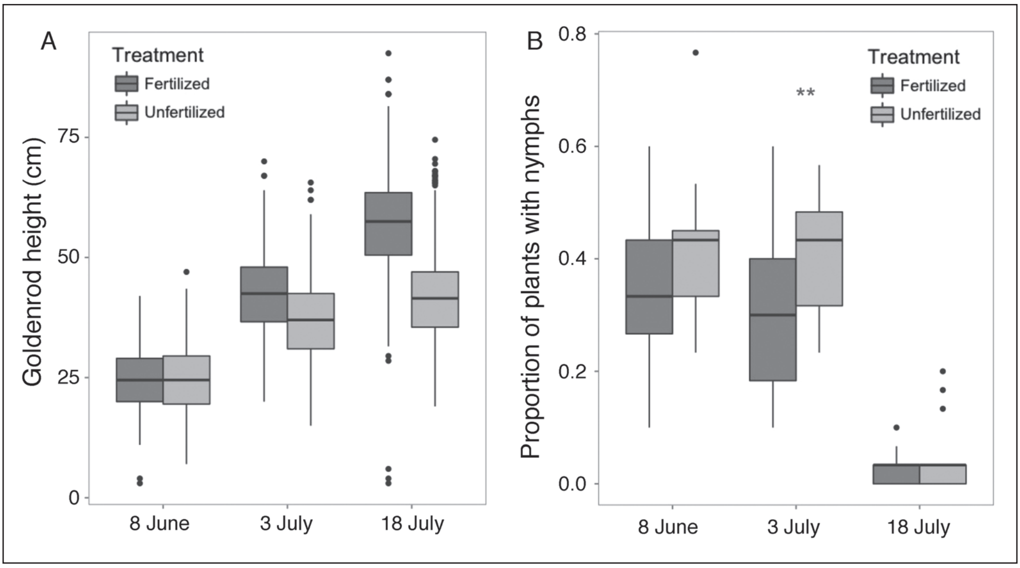
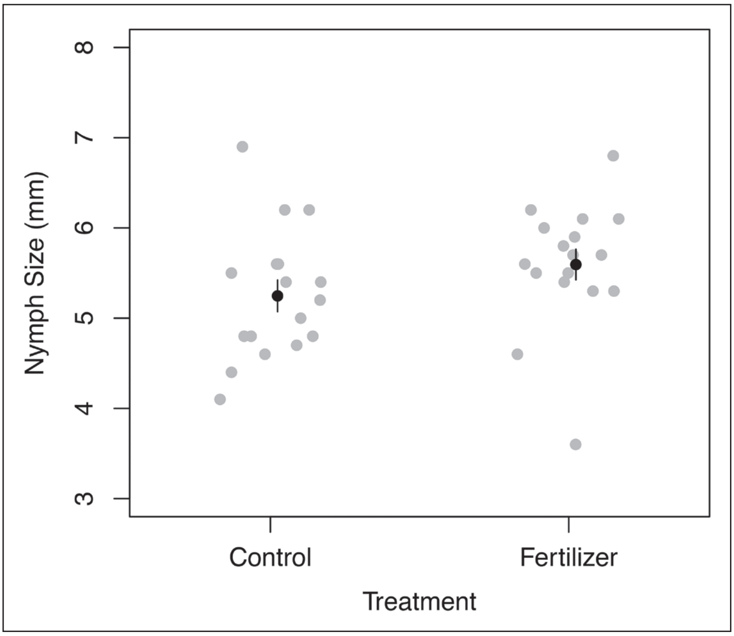


Figure 6. (A) Boxplot of plant height over time for both unfertilized and fertilized *Solidago rugosa* (Rough-stemmed Goldenrod). (B) Boxplot of the proportion of plants with nymphs over time in control and experimental plots. Asterisks indicate significant differences in nymph presence in different treatments.

Figure 7. Mean (± SE) body lengths of nymphs removed from unfertilized and fertilized *Solidago rugosa* (Rough-stemmed Goldenrod) plots at the end of the season. Means and standard errors were plotted over the raw data.



Discussion

We observed Meadow Spittlebugs on 32 species of plants from 17 families, supporting previous research that has demonstrated this insect to be a generalist herbivore on a wide range of host plants (Weaver and King 1954). Although Meadow Spittlebugs are generally thought to prefer herbaceous perennials (Weaver and King 1954), their highly variable diet on Kent Island also included conifers (*Abies balsamea* [Balsam Fir], *Picea glauca* [White Spruce]) and ferns (*Dryopteris carthusiana* [Spirulose Woodfern], *Thelypteris palustris* [Marsh Fern]). We observed nymphs on *Solanum dulcamara* (Bittersweet Nightshade), a plant with known chemical toxicity, and on plants, such as *Urtica dioica* L. (Stinging Nettle) and Canada Thistle, that possess physical defenses, which further indicate the Meadow Spittlebug's capacity to cope with a wide range of host defenses and utilize natural protection from invertebrate predators.

Solidago spp. (goldenrods) are fast invaders of disturbed habitats and dominate old-field communities in the northeastern United States (Uriarte 2000). We witnessed large numbers of Meadow Spittlebug nymphs on Rough-stemmed Goldenrod, a perennial with a central stem densely covered in hairs and the most common host plant on Kent Island. We observed the overwhelming majority (87%) of spittlebug nymphs feeding on the upper, fleshier leaf axils of goldenrod, which aligns with Horsfield's (1977) observations that Meadow Spittlebug nymphs fed on young, upper leaves with xylem relatively high in amino acids. Younger instars are less capable than larger instars of penetrating the stylet lower on the plant (Hoffman and McEvoy 1986). A combination of both insect and plant traits therefore contribute to the location of nymphal feeding on the ramet.

In addition to the presence of spittlebug nymphs on a wide range of host plants, the density of nymphs also varied on different plants. Several factors may impact rates of colonization in plant communities, including natural variation in plant nutrient content, predator–prey interactions, physical plant characteristics, and rhizobial or mycorrhizal associations (Koricheva et al. 2009, Mauricio et al. 1997, Thompson 1994, Yurtsever 2000). We found significantly more nymphs per meter of stem on Canada Thistle than on Rough-stemmed Goldenrod, Pearly Everlasting, and Whorled Wood-aster (Fig. 4). Canada Thistle is an introduced European species with no known microbial or fungal associations that increase nutrient absorption (Magee and Ahles 1999). It is highly capable of invading disturbed areas and can decrease plant diversity in surrounding areas (Stachon and Zimdahl 1980). Thistle may also offer physical protection from predators; the curled, prickly leaves effectively disguise spittle masses and perhaps deter insect or avian predators. However, research on plants with trichomes has shown that other types of physical defense may restrict spittlebug feeding (Hoffman and McEvoy 1986).

We found variation in spittlebug body size on different host species (Fig. 4). If females preferentially oviposit next to plants where nymphs will have the highest performance (in accordance with the preference–performance hypothesis (PPH); Jaenike 1978), body sizes should be largest on plants with the highest densities of nymphs. Spittlebugs grew on all 5 species of perennial herbs surveyed over the course of the season, and were most densely aggregated on Canada Thistle, followed by Rough-stemmed Goldenrod and Pearly Everlasting. Even though nymphs were most dense on thistle plants, they were largest on Rough-stemmed Goldenrod throughout the season. The slowest nymph growth rate and smallest average body length late in the season was seen on Sheep Sorrel, which is an invasive perennial found across North America that thrives in acidic, infertile soils and disturbed areas (Brooks et al. 1986, Fitzsimmons and Burrill 1993). It could be, therefore, that the areas on Kent Island where we observed Sheep Sorrel had poor soil quality that had downstream effects on nymphal feeding and nutrient acquisition rate. We anecdotally observed lower densities of nymphs per plant on Sheep Sorrel than other plants. It is possible, therefore, that the preference–performance hypothesis may hold for low quality Sheep Sorrel as well as high quality Pearly Everlasting, which had nymphs with the largest body sizes and high densities. High densities and small nymph body sizes suggest that the PPH does not hold on Canada Thistle, however, which may indicate maladaptive behavior, or potentially that thistle has other qualities that make it an adaptive host choice such as defense from predators. Choice tests to directly measure female preference, and experiments to measure predation rates on these different host plants would help further inform the extent to which nymphal densities are indicators of adaptive preferences in spittlebugs.

Plants with lower C:N ratios may offer a higher and more constant supply of nitrogen to their hosts, which could speed development. This does not appear to be the case, however, with nymphs on Rough-stemmed Goldenrod and Pearly Everlasting. While Pearly Everlasting has a low C:N ratio and medium protein potential, Rough-stemmed Goldenrod has a high C:N ratio and low protein potential (USDA, NRCS 2018), and nymphs were marginally larger on goldenrod than on Pearly Everlasting. C:N ratios of angiosperms, however, are subject to change during floral transition (Corbesier et al. 2002), and differences in flowering phenology may cause non-parallel shifts in plant nutrition. Therefore, while we attribute differences in body size to host-plant quality, we cannot rule out local changes in plant chemistry, microhabitat variation, or hatch-date variation.

While the preference–performance hypothesis predicts female oviposition behavior in hemimetabolous insects (Jaenike 1990), spittlebug host-plant selection may occur in both the nymphal and adult stages. Initial nymphal choice for a feeding site upon spring emergence is limited to surrounding plants within crawling range, which are generally the same plants, or descendants of plants from the previous season (Wise et al. 2008). Previous research has shown that though hopping adults are far more mobile, their preferred host species remain relatively constant between nymph and adult stages (Wiegert 1964). In nymphs, vertical movement up and down the stem is more common than extra-ramet moving (switching hosts), as nymphs regularly change feeding locations (Wise et al. 2006). Once established on a ramet, individual nymphs seemed to be unlikely to switch hosts. In order to assess the frequency with which the Meadow Spittlebug moves around between plants, we removed all of the nymphs from plots of goldenrod and tracked recolonization. Nymphs failed to reestablish the original densities (Fig. 5), which supports observations by Halkka et al. (1967). While crawling nymphs have limited mobility, hopping adults are far more capable of covering large distances, and do so more readily (Weaver and King 1954). Our observations of low-mobility nymphs on a wide range of host plants on Kent Island support the idea that while individual spittlebugs can feed on many hosts, movement between plants is uncommon.

As we have shown that movement in the Meadow Spittlebug is limited during nymphal stages, we can compare the developmental effects (performance) of feeding on different host species or treatments. We attempted to boost nymph performance by artificially manipulating C:N ratios of Rough-stemmed Goldenrod through the introduction of fertilizer. As expected, fertilized goldenrod grew faster and taller than unfertilized plants (Fig. 6A). Nitrogen levels frequently limit plant growth (Mattson 1980, Séquin 2017), and xylem sap-sucking insects may benefit directly from plants with high nitrogen levels or plants grown in soil with plentiful levels of inorganic nitrogen (Kytö et al. 1996). Hartley and Gardner (1995) measured distribution and abundance of Meadow Spittlebug adults on fertilized *Calluna vulgaris* (L.) Hull (Scotch Heather), and witnessed a significant increase in abundance of adults on nitrogen-fertilized plants. As our research was conducted early in the season, we examined numbers of nymphs on plants, which declined over the experimental period as nymphs reached adulthood (Fig. 6B). There was a smaller proportion of fertilized goldenrod with nymphs after the first round of fertilizer application, suggesting that nymphs on fertilized goldenrod developed to adulthood faster. Duration of development is an important indicator of host-plant quality, with longer periods of development indicating poor host quality (Silva et al. 2017). Accelerated adulthood may have consequences for fitness or population structure (Johnson et al. 2016, Ju et al. 2011, Van Dongen et al. 1997). For example, earlier opportunities to mate may present polyandrous females with more time to breed before low temperatures limit their survival and reproductive activity (Yurtsever 2000). Additionally, if mobile adults are able to better escape predation, then faster development also would decrease the length of time spent as a vulnerable juvenile (De Lestang and Miller 2009, Pastorok 1981). Finally, development on fertilized plots with lower C:N ratios may also increase body sizes, lengthen the adult life stage and increase fecundity due to increased access to amino acids necessary for survival and egg production (Awmack and Leather 2002, Waring and Cobb 1992). As we did not measure adults, we cannot confirm that larger nymphs resulted in larger adults along with reaching adulthood faster. However, there is evidence of multiple mating in both in-laboratory and natural settings (Yurtsever 2000), and because long-lived adults can survive until fall's first frosts (Weaver and King 1954), feeding on host species that allow them to emerge earlier may provide adults with increased opportunities to mate. At the very least, having adults of equal size and fecundity emerge from different hosts at staggered points in the season and mate would likely have implications for population structure.

While disappearing nymphs most likely indicate faster development times, an alternative explanation is an increase in predation in fertilized plots. If fertilizer had a non-exclusive effect on spittlebugs, it may have caused an overall increase in insect abundance, attracting a higher number of predators and therefore increasing the likelihood of spittlebug predation by spiders, *Formica* spp. ants, or wasps (Hoffman and McEvoy 1986, Weaver and King 1954). The foamy spittle, however, serves as an effective viscous barrier against most invertebrate attacks (Karban 1986, Whittaker 1970). Birds are also known predators of the Meadow Spittlebug, and on Kent Island, *Passerculus sandwichensis* (J.F. Gmelin) (Savannah Sparrow) forages in the same fields as the Meadow Spittlebug during the breeding season (Whittaker 1970; Z.M. Wood, pers. observ.). However, observations of avian predation on Meadow Spittlebugs remain few and isolated (Whittaker 1970), and it is not clear why predation by birds would be higher in fertilized plots than in unfertilized plots.

Another explanation for different rates of disappearance involves the possibility that fertilized plants were better equipped to defend against herbivores. The fitness costs of herbivore-induced defense are high, and Cipollini and Bergelson (2001) found that reduced nutrient availability may constrain the ability of *Brassica napus* (L.) (Turnip) to generate chemical defense, which could increase herbivore damage in the field. However, other studies report depressed levels of phenolic chemical defense in experimentally fertilized plants (Bernays and Chapman 1994, Tuomi et al. 1984) or heightened investment in defense in nutrient-limited or damaged conditions (Agrawal et al. 2002, Sampedro et al. 2011). Therefore, it is possible that nutrient enhancement of Rough-stemmed Goldenrod reduced chemical defense, allowing for higher rates of spittlebug herbivory on fertilized plants. It is worth investigating the interactions between reduced chemical defense and overall herbivory to determine the potential combined effects on spittlebug presence.

At the end of the season, we measured the remaining 39 nymphs in our experimental and control plots, accounting for just 6% of the original 642 nymphs. Nymphs on fertilized goldenrod were slightly (3.8%) larger than nymphs on unfertilized goldenrod and the distribution was slightly more skewed towards fifth instar nymphs on fertilized goldenrod at the end of the season, but neither of these trends represent significant differences (Fig. 7). Whether small sample size is responsible for the lack of significant difference in body sizes and instar distributions, or the small number of nymphs still remaining were different from the rest of the nymphs in other ways, the short and long-term effects of fertilizer on preference, performance, and population dynamics of Meadow Spittlebugs need further examination.

This study offers an initial account of the natural variation in preference and performance of the Meadow Spittlebug on several host plants in a boreal habitat. We observed natural variation in preference and performance on a range of host plants, contributing to the understanding of Meadow Spittlebug as a polyphage with preferences. We also show that nymphs appear to mature to adulthood faster in fertilized plots. As agriculture continues to employ the widespread use of nitrogen fertilizers, careful work to chart the long-term, downstream effects of fertilizer on spittlebug behavior, phenology, and performance is necessary to develop management strategies that consider the life histories of insect herbivores.

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