Arthropod-Plant Interactions (2015) 9:301–309
DOI 10.1007/s11829-015-9370-3

ORIGINAL PAPER

Predators, host abundance, and host spatial distribution affect the movement of wingless non-colonizing vector *Rhopalosiphum padi* (L.) and PVY prevalence in an oat/potato system

Suzi B. Claflin[1] · Jennifer S. Thaler[1,2] · Alison G. Power[1,2]

Received: 19 November 2014 / Accepted: 3 March 2015 / Published online: 19 March 2015

Abstract In the study of insect-vectored plant viruses, colonizing vector species remain the focus. However, non-colonizing vector species, those that do not settle and reproduce on the viral plant host, are often the most abundant in the field and may be the largest contributors to disease spread. While non-colonists may have a substantial effect on disease prevalence, the factors influencing their movement and transmission on non-host plants have been little studied. Here we evaluated how a common biological control agent (*Hippodamia convergens*), host and non-host plant abundance, and plant spatial distribution impact the movement and density of a wingless non-colonizing vector [*Rhopalosiphum padi* (L.)] and transmission of potato virus Y (PVY) in potatoes in experimental arenas. The results of this work illustrate the importance of plant species function (host or non-host) and distribution to vector behavior and disease spread. Predation, host plant abundance, and plant spatial distribution interactively affected viral prevalence within infected arenas. Increasing the number of vector non-host plants increased the distance and frequency of aphid movement, and the effect was influenced by plant spatial distribution, the arrangement of plant species in the experimental arena. Increasing the number of vector host plants increased the density of aphids. Although the interaction of the plant and predator treatments affected the proportion of potato plants infected in arenas where infection occurred, and host abundance and spatial distribution impacted vector movement and viral prevalence, aphid movement did not appear to mediate the effect of plant and predator treatments on PVY prevalence. This work demonstrates that both wingless non-colonizing vector behavior and transmission are aggregated responses to multiple environmental drivers.

Keywords Pathogen transmission · *Rhopalosiphum padi* (L.) · Potato virus Y · Aphid vectors

Introduction

Insect vectors are an important component of many plant pathosystems; 79 % of plant viruses are vectored by insects (Power and Flecker 2008). Plant viruses are often transmitted by more than one species of insect vector, including many species that do not colonize (settle and reproduce on) the virus's host plant (Gray et al. 2010). Although these non-colonizing vector species do not engage in committed feeding on the viral host and generally have lower transmission efficiencies than colonizing species, they will probe non-host plants and are often the most abundant species in the field (Boquel et al. 2011). Though they may have a significant impact on virus prevalence, non-colonizing species are understudied relative to their potential importance in disease systems. Greater knowledge of the behavior of non-colonizing vectors will improve our understanding of plant virus epidemiology.

Vector behavior, especially movement and probing, is fundamental for both virus acquisition and inoculation (Pirone and Perry 2002) and has a direct impact on virus spread (Fereres and Moreno 2008; Power 1991; Singh et al.

Handling Editor: Robert Glinwood and Heikki Hokkanen.

✉ Suzi B. Claflin
suziclaflin@gmail.com; sbc89@cornell.edu

[1] Department of Entomology, 4124 Comstock Hall, Cornell University, Ithaca, NY 14850, USA

[2] Department of Ecology and Evolutionary Biology, 331 Corson Hall, Cornell University, Ithaca, NY 14850, USA

1988). A number of environmental factors have been demonstrated to affect colonizing vector behavior, including host plant diversity and predation (Bailey et al. 1995; Narayandas and Alyokhin 2006). A recent review shows that host diversity can have varying effects on pathogen transmission; increasing host diversity may amplify, dilute, or leave disease prevalence unchanged (Ostfeld and Keesing 2012). In plant communities, both hosts and non-hosts of the vector, species diversity, and spatial distribution could alter vector behavior through visual, olfactory, or tactile cues; encountering vector non-hosts may encourage increased vector movement and probing until an appropriate host is discovered. For vector species with limited mobility, such as wingless aphids, the fine-scale spatial structure of the plant community, such as the row arrangement of plant species, may also influence movement. If plant species differ in competence as hosts of the virus, the impact of plant diversity on vector movement could have a cascading effect on viral prevalence in the system (e.g., Power 1991; Bottenburg and Irwin 1992).

Predators can affect vector population size and vector behavior (Nelson et al. 2004), but their effect on disease prevalence varies (Finke 2012). In plant pathosystems, predators of vectors have the potential to impact viral prevalence through both consumptive (e.g., reducing vector abundance) and non-consumptive (e.g., modifying vector behavior) effects (Preisser and Bolnick 2008; Finke 2012; Kaplan and Thaler 2012). Predators frequently suppress vector populations and elicit sedentary anti-predator behavioral responses (e.g., hiding), which have the potential to reduce virus prevalence (Moore et al. 2009). However, predators can also elicit active anti-predator behavioral responses (e.g., dropping), which may increase disease prevalence by increasing movement of vectors onto uninfected hosts (Roitberg and Myers 1978). Additionally, the effects of predation, host abundance, and host spatial structure on vector movement and virus prevalence may interact. This short-term greenhouse study assesses the importance of (1) host abundance and spatial distribution, (2) predation, and (3) their interaction for non-colonizing vector movement and virus prevalence.

Hypothesis and predictions

Because of the importance of vector behavior for virus transmission, we hypothesize that the effect of plant abundance and distribution and predation on virus prevalence will be determined by their effect on aphid movement. To test this hypothesis, we assessed the following four predictions: Prediction 1: the presence of predators will increase aphid movement and PVY prevalence, Prediction 2: increasing the vector non-host plant (virus host plant) abundance will increase aphid movement and PVY prevalence, Prediction 3: increasing the distance between vector host plants will increase aphid movement and PVY prevalence, and Prediction 4: vector host plant abundance, spatial structure, and predation will interactively affect aphid movement and PVY prevalence. We investigated these predictions by quantifying wingless adult *R. padi* movement and PVY prevalence in a fully factorial greenhouse experiment, crossing four plant species treatments with two predator treatments (presence or absence of predators). The plant species treatments included an oat monoculture (OM) (virus non-host, vector host), a potato monoculture (PM) (virus host, vector non-host), and two species mixtures (Fig. 1). In the mixtures, the position of the host and non-host plants was manipulated, which allowed for the comparison of the effects of host plant spatial structure on aphid movement.

Materials and methods

Study system

Small increases in PVY prevalence can have a profound effect on commercial potato crops; with every 1 % increase in PVY in the seed stock, yield is reduced by 0.18 t/ha (Scholthof et al. 2011; Nolte et al. 2004). DiFonzo et al. (1997) hypothesized that, because of their abundance, non-colonizing species were the main drivers of potato virus Y (PVY) spread in potato fields. This project evaluated PVY transmission and factors affecting the short distance movement of one of the most abundant non-colonizing aphid species landing in potato fields, the bird cherry oat aphid, *Rhopalosiphum padi* (DiFonzo et al. 1996). Although winged non-colonizing vector adults are most common in agricultural systems, wingless adults were used in this experiment in order to increase aphid–plant interaction, allow for monitoring of interplant movement, and make this study comparable with other work in the area, which generally uses wingless adults of a colonizing species (e.g., Narayandas and Alyokhin 2006). The virus and vector hosts are not congruent in this system; potato is the virus host, oat is the virus non-host, while potato is the vector non-host, and oat is the vector host.

PVY causes an array of symptoms ranging from leaf mottling to necrosis in solanaceous crops, including potatoes, tomatoes, and tobacco. PVY is a stylet-borne virus that does not replicate within its aphid vectors. It is transmitted in less than a minute at different transmission efficiencies by at least 40 species of aphid, the majority of which are non-colonizing species (Gray et al. 2010; Mello et al. 2011). The virus is lost rapidly with vector probing, leaving the vector unable to transmit after feeding on a few plants.

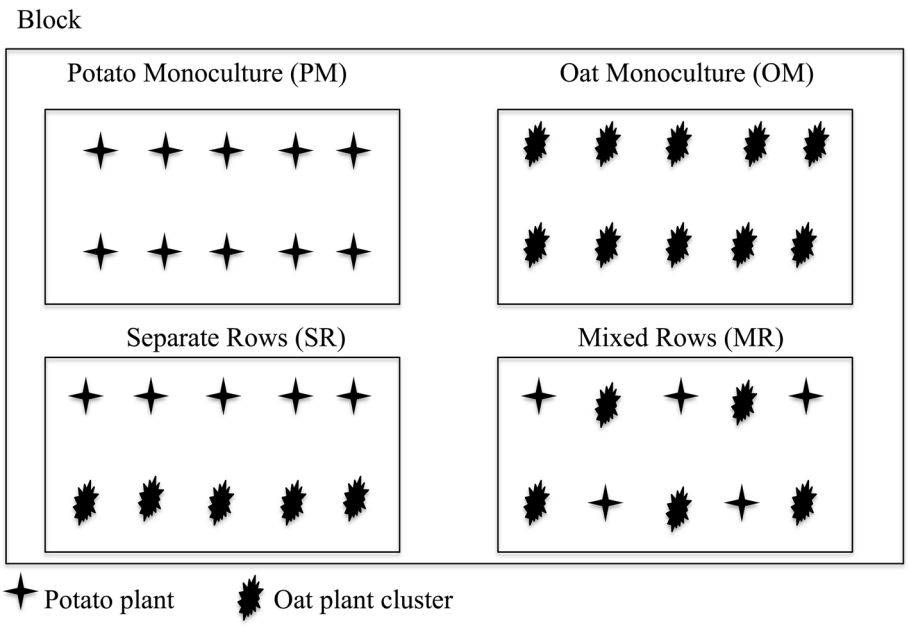

Fig. 1 Schematic of plant treatments: OM, PM, SRs, and MRs. The border signifies the block, which was assigned one of two predator treatment levels (presence or absence of predators)

Additionally, as there is a long history of biological control efforts directed at aphids, the effect of coccinellid predators on aphid behavior is well documented (Obrycki and Kring 2009). In this study, we used a readily available adult coccinellid predator marketed as a biological control agent, *Hippodamia convergens*, and PVY^{NTN}, a necrotic strain of PVY that has increased in incidence in the USA and Canada over the last decade (Gray et al. 2010).

Plant and insect care

Potato plants (*Solanum tuberosum*, cv. Yukon Gold) were planted in 10.2-cm-diameter pots and grown in the greenhouse in a commercial potting soil (Metro-Mix 360, Sun Gro Horticulture) with fertilizer applied at watering each day. Oats (*Avena sativa*, Sunmark Seeds) were planted in 120-cm^3 cells and grown in similar conditions. Before being used in bioassays, plants were allowed to grow for 2–3 weeks. To produce infected tissue, some potato plants were inoculated with PVY after 2–3 weeks of growth. On each plant, 3–4 new leaves were lightly sprinkled with carborundum and the PVY^{NTN} isolate (source plant: *Nicotiana tabacum*; S. Gray, Cornell University) was manually spread on the leaves using a cotton swab approximately 30 min later. Thirty minutes after exposure to the isolate, the leaves were rinsed with water. The virus was allowed to replicate for at least 14 days before plant material was collected for aphid acquisition of the virus.

Rhopalosiphum padi were maintained in colonies on barley (*Hordeum vulgare*, cv. Romulus) in growth chambers at 20 °C with 24-h light. This colony was founded in the 1960s from a New York State population and has been maintained for use in virus transmission assays. *R. padi* do not colonize (feed or reproduce on) potatoes, but they probe potato plants and other non-hosts, as this behavior is triggered by encountering smooth surfaces such as leaves and is not host-specific (Döring et al. 2004). This superficial probing is sufficient to transmit PVY.

Prior to inclusion in a bioassay, adult coccinellid predators (*H. convergens*, from Rincon-Vitova Insectary) were kept at 4 °C and fed a mixture of honey and water once a week. To prevent flight and encourage on-plant movement, predators had their wings lacquered with clear nail polish before being introduced to the arena.

Experimental procedure

Plants were transplanted into potting soil (Metro-Mix 360, Sun Gro Horticulture) in 50.8 × 25.4 cm black plastic flats in two rows of five plant positions (10 total plant positions/arena). The rows were approximately 15 cm apart, plant positions within rows were approximately 10 cm apart, and all remaining empty space was filled with potting soil. Plants were arranged in one of four treatments: OM, PM, separate rows (SRs) of plant species, or mixed rows (MRs), with alternating plant species within rows (Fig. 1). The plants were placed so that they did not touch between rows, but did touch within rows. In mixture treatments, the pattern of the plants was randomized so that the same species was not always located in the same position in the arena. To approximately equalize the amount of plant material between species, potato pots were thinned to include a single shoot and oat pots were thinned to include six shoots per pot before inclusion in the bioassay. Potato shoots were

approximately 1 cm in diameter and 20–35 cm tall. Oat shoots were approximately 1–2 mm in diameter and approximately 20-cm tall.

The experimental unit was a flat of ten plant positions, which received one of four plant treatments: OM, PM, SRs, or MRs (Fig. 1). A block included one experimental unit of each plant treatment that was conducted at the same time, and each pair of sequential blocks was randomly assigned a level of predator treatment (presence or absence of predators). Twenty blocks, ten with predators and ten without, were conducted over the course of 17 nonconsecutive days.

For each flat, 30 adult wingless aphids were allowed to acquire PVY on infected tissue in a closed petri dish for at least 1 h before beginning the bioassay. This number of aphids was selected in order to limit the risk of all plants in the arenas becoming infected. The aphids were placed between the two rows, 7.6 cm from the first plant in each row. Aphids were introduced on the soil to avoid biasing their behavior by introducing them on either a host or non-host plant. All plants were censused for aphids at 20, 40, 60, 120, and 180 min from the time of release: the highest possible monitoring frequency within the first hour and then hourly until the completion of the assay. The final census included a Euclidean distance (linear distance) measurement of aphid distance from the point of introduction (marked with a toothpick) for all aphids found at the final time point. Because PVY transmission occurs so rapidly, the bioassay was kept brief to capture the initial effect of host plant abundance and distribution on transmission. To allow for observations between censuses and close monitoring of aphid movement with minimal disturbance, cages were not used. In the predator inclusion treatments, two predators were randomly placed in the flat at the same time as the aphid introduction. During the bioassay, they often left the arena by dropping from overhanging plants and, if so, were returned to the arena at a random location during the next census. Predators were unable to access an arena independently. Predators were not observed consuming aphids. Assays were conducted in a windowless room with constant overhead fluorescent lighting, to eliminate variation in light conditions.

Measuring aphid density and movement

Aphid density was calculated from the number of aphids found per plant position during the census. By adding up the positive differences between census counts (i.e., times when there were more aphids on a plant at a given time point compared with the previous census count), we estimated the number of unique aphids that were on each plant throughout the census.

The census data were also aggregated into two measures of aphid movement: (1) *linear distance* (cm) travelled by aphids counted on plants at the final census time point from the introduction point and (2) *proportion of aphids leaving plants*. To account for the difference in aphid density between plant species, we calculated the *proportion of aphids leaving plants*, dividing the number leaving (the sum of the negative differences between census time points, when there were fewer aphids on a plant than at the previous time point) by the total number of aphids found on the plant. Each measurement was calculated for an individual plant and averaged across the flat. There was a lot of aphid movement in the plots, but because many aphids were never found on plants, much of that movement occurred on the soil. Therefore, census measurements are a conservative estimate of total aphid movement.

Measuring viral prevalence

After the aphid movement bioassay, all potato plants were removed from the flat and returned to their 10.2-cm pot, bagged in a water and light permeable aphid-proof fabric (Agrifabric Pro-17), and were kept for at least 14 days in a growth chamber (27 °C during the day and 25 °C at night), when foliar samples were taken from each potato plant for enzyme-linked immunosorbent assay (ELISA) analysis (Ellis et al. 1996). To compensate for the fact that treatments differed in the number of potato plants (susceptible hosts), we calculated the viral prevalence as the proportion of potato plants infected per flat, as well as the number of infected plants per flat.

Analysis

In all analyses, plant treatment and predator treatment were included as fixed effects, and block and plant treatment nested within block were included as a random effects. We performed model simplification (Crawley 2007) on the aphid census data, using $\alpha \leq 0.05$ as the threshold of significance. To assess *aphid density* trends throughout the census, the number of aphids per plant was analyzed using a repeated- measures generalized linear mixed effects model with a Poisson distribution, plant and predator treatment as fixed effects, and block as a random effect. *Linear distance* was analyzed with a linear mixed effects model, and the average *proportion of aphids leaving* was analyzed using a mixed effects model. Both models included plant treatment and predator treatment as main effects and their interaction. When differences due to plant treatment or the interaction were found, Tukey's HSD tests were performed. The proportion of aphids on potato plants in the two plant mixture treatments was square-root-transformed and compared with a linear mixed model.

Because of the high number of zero values, a logistic regression was performed on the viral prevalence data. The

proportion of potato plants infected was arcsine square-root-transformed to improve the normality of the data. The logistic regression of the full model, which included predator and plant treatments as factors, indicated that there were no significant differences in PVY prevalence between plant or predator treatments. To explore transmission once inoculation occurs, we analyzed the nonzero values. Flats with infection ($n = 15$; Table 2) were further analyzed using a mixed effects model with plant treatment and predator treatment as main factors and their interaction, in order to assess the effect of the treatment on the proportion of susceptible hosts infected. When differences due to treatment or the interaction were found, Tukey's HSD tests were performed. Analyses were conducted in R (version 2.14.0) and JMP Pro 10.

Results

Prediction 1: The effect of the predator treatment

The predator treatment had no effect on any measurement of aphid behavior. The presence of predators did not affect *aphid density* ($F_{1,18} = 0.33$, $p = 0.57$; Table 2), *linear distance* ($F_{1,14} = 0.26$, $p = 0.62$), the *proportion of aphids leaving* ($F_{1,18} = 0.49$, $p = 0.49$), the *proportion of potato plants infected* ($F_{1,9} = 2.11$, $p = 0.18$), or the average *number of plants infected* ($F_{1,9} = 2.99$, $p = 0.12$).

Prediction 2 and 3: The effect of the plant treatment

After model simplification, time point and plant treatment were the only explanatory factors related to the number of aphids per plant over the course of the census (Table 1). Plant treatment had a strong effect on the *aphid density* ($F_{3,54} = 7.41$, $p < 0.001$; Fig. 2); the number of aphids per plant in the PM was about half the number found in the other plant treatments over the course of the census. On average across plant treatments, oat plants recruited twice as many aphids as potato plants over the course of the bioassay ($F_{1,779} = 20.84$, $p < 0.0001$; Table 2).

Increasing the number of non-host plants significantly increased aphid movement. Aphids moved twice as far in *linear distance* in the PM compared with the other plant treatments ($F_{3,46} = 3.22$, $p = 0.0024$; Fig. 3), and aphids tended to move farther in the MR treatment than in the OM ($p = 0.058$), increasing the average distance by 22 %. The SR treatment and the PM had the most aphids leaving. The average *proportion of aphids leaving plants* was two and a half times lower in the OM than the SR treatment and the PM, with the MR treatment intermediate ($F_{3,54} = 5.124$, $p = 0.0034$; Fig. 4), indicating that plant spatial distribution affected the frequency of aphid movement.

Plant treatment had a significant effect on both the *proportion of plants infected* ($F_{1,9} = 5.89$, $p = 0.023$) and the average *number of plants infected* ($F_{2,9} = 5.33$, $p = 0.03$). The *proportion infected* was 56 % greater in the SR treatment than either the PM or the MR treatment, and the *number of plants infected* was half as great in the MR treatment versus the other two treatments.

Prediction 4: The interactive effect of plant and predator treatment

Although the interactive effect of the plant and predator treatments did not influence aphid density or movement, it did significantly impact PVY prevalence. The interaction between treatments did not affect aphid density ($F_{3,54} = 0.88$, $p = 0.46$; Table 2) or movement, in *linear distance* ($F_{3,46} = 0.36$, $p = 0.78$) or the *proportion of aphids leaving* ($F_{3,54} = 0.911$, $p = 0.44$). The *proportion of potato plants infected* was significantly affected by the interaction between plant and predator treatment ($F_{2,9} = 5.67$, $p = 0.026$; Fig. 5), as was the *number of plants infected* ($F_{2,9} = 4.55$, $p = 0.043$; Fig. 6). The presence of the predator doubled the proportion of infection in the PM and the SR treatment, while it reduced the proportion of plants infected in the MR treatment by a third. The *number of plants infected* was half as great in the MR treatment versus the other two treatments.

Hypothesis: Aphid movement and virus transmission.

When analyzed together, none of the metrics of aphid movement or density correlated with the average *proportion of potato plants infected* (*linear distance*, $r = -0.21$, $p = 0.14$; *proportion leaving*, $r = 0.16$, $p = 0.23$; *aphid density*, $r = -0.31$, $p = 0.72$) or the *number of plants infected* (*linear distance*, $r = -0.12$, $p = 0.39$; *aphid density*, $r = -0.14$, 0.60). However, there was a marginal correlation between the proportion of aphids leaving and the number of plants infected ($r = 0.24$, $p = 0.07$).

Discussion

In this highly simplified plant pathosystem, the abundance of vector non-host (virus host) plants significantly affected wingless non-colonizing vector movement and density. In arenas with infection, PVY prevalence was influenced by the interactive effect of the predator and plant treatments. The presence of predators reduced virus prevalence in arenas with a more complex host plant distribution (i.e., the MR treatment) and increased prevalence in arenas with simpler plant distributions (i.e., the SR and PM treatments). Contrary to our hypothesis, this study did not find evidence that vector movement mediated the relationship between

Table 1 Model simplification from the full model of the aphid census data

Model 1	Model 2	Δlog-likelihood	Chi square	*df*	*p* value	Action
Full model	w/o 3-way interaction	2.8	5.7053	3	0.1269	Proceed
w/o 3-way interaction	w/o 3-way interaction or time point: Plant	1.3	2.4769	3	0.4795	Proceed
	w/o 3-way interaction or Pred: plant	2.2	4.3076	3	0.2301	Proceed
	w/o 3-way interaction or Pred: time point	0.1	0.1487	1	0.6997	Remove
w/o 3-way interaction or Pred: time point	w/o 3-way interaction or Pred: time point or Pred: plant	2.2	4.2937	3	0.2314	Proceed
	w/o 3-way interaction or Pred: time point or time point: Plant	1.2	2.3892	3	0.4957	Remove
w/o 3-way interaction or Pred: time point or time point: plant	w/o 2-way interactions	2.2	4.2937	3	0.2314	Remove
w/o 3-way or 2-way interactions	w/o 3-way or 2-way interactions or Plant	61.3	122.44	4	2.20E−16	Proceed
	w/o 3-way or 2-way interactions or Pred	0.7	1.5895	1	0.2074	Remove
	w/o 3-way or 2-way interactions or time point	72.7	145.52	1	2.20E−16	Proceed
w/o 3-way or 2-way interactions or Pred	w/o treat	85	169.87	5	2.20E−16	Keep
	w/o time point	72.8	145.52	2	2.20E−16	Keep

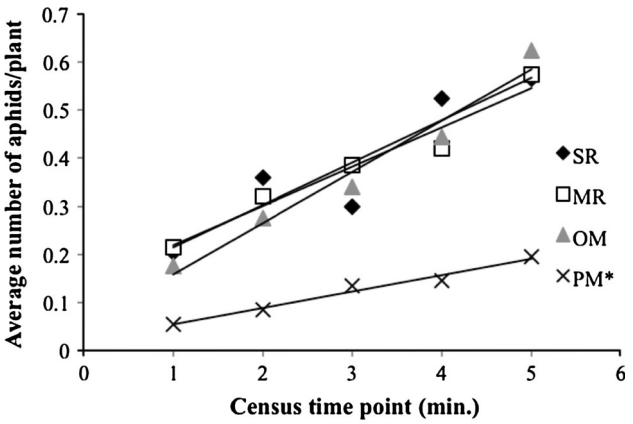

Fig. 2 The average number of aphids on a plant across five census points (20, 40, 60, 120, and 180 min) during the course of 3 h in four plant treatments: OM, PM, SRs, and MRs. Lines are *trendlines*, and *asterisks* indicate a significant difference

predator presence, host plant abundance and spatial structure, and PVY prevalence.

Increasing vector non-host plant abundance had a large effect on aphid density and movement (Prediction 2). The PM had about half the aphid density and more than twice the aphid movement of the OM. This is consistent with the results of other studies (e.g., Srinivasan et al. 2013) that demonstrate that introducing a preferred host of the aphid increased the density of aphids on plants throughout the system. However, while the duration of aphid movement (the *linear distance* traveled) was also primarily driven by vector non-host frequency, the rate of aphid movement (the *proportion of aphids leaving*) was determined by both the frequency and spatial distribution of the non-host plant (Prediction 3). Increasing the frequency of the non-host plant increased movement, and this effect was enhanced by separating the plant species by rows. The increased movement in arenas with more vector non-hosts may be a response to the poor quality of the non-host plants and has been found in other aphid–plant systems (e.g., Sudderth and Sudderth 2014). The effect of host plant spatial distribution, with movement marginally greater in the SR treatment than the MR treatment, indicates that host plant apparency may also play a role.

The predator treatment had no effect on the measures of aphid movement used in this study, consistent with the findings of Narayandas and Alyokhin (2006; Prediction 1). Despite this, the interaction between predator and plant treatments affected the *proportion of plants infected* with PVY in plots where infection occurred (Prediction 4). In accordance with the results of other studies (e.g., Hodge et al. 2011; Roitberg and Myers 1978), the presence of predators increased virus prevalence in arenas with simpler host plant spatial distributions, the PM and SR treatments. However, it had the opposite effect in the MR treatment, where the host plant spatial distribution was more complex. The difference in the effect of predators across plant treatments could reflect the distribution of aphids between the plant species in each mixture, as the proportion of aphids on potato plants was greater in the SR treatment than the MR treatment. A greater density of aphids on potato plants may have resulted in an amplification of transmission. Because the predators were not observed consuming aphid vectors, they may have been influencing the aphids through non-consumptive pathways (Nelson et al. 2004). These non-consumptive effects may include

Table 2 Summary statistics for each predator and plant treatment: SR, MR, PM, and OM; each column lists the cumulative number of aphids found in all ten replicates of each treatment

Treatment	Total number of aphids	Total number of aphids on oat plants	Total number of aphids on potato plants	Total number of infected plants
Predator				
SR	114	71	43	3
MR	70	51	19	3
PM	42	NA	42	9
OM	62	62	NA	NA
No predator				
SR	95	70	25	3
MR	80	58	22	3
PM	42	NA	42	4
OM	93	93	NA	NA

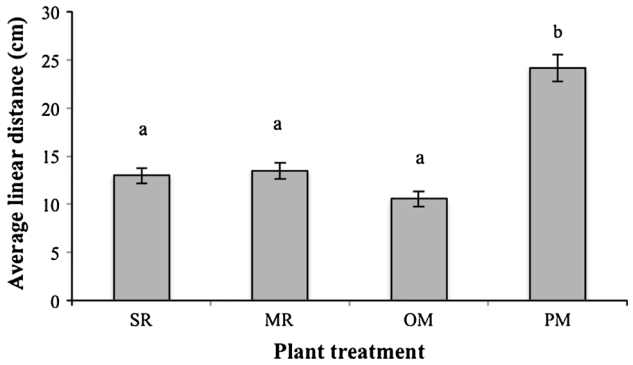

Fig. 3 Average linear distance (cm) travelled by aphids after 3 h in four plant treatments ± SE: OM, PM, SRs, and MRs. *Letters* indicate significant differences

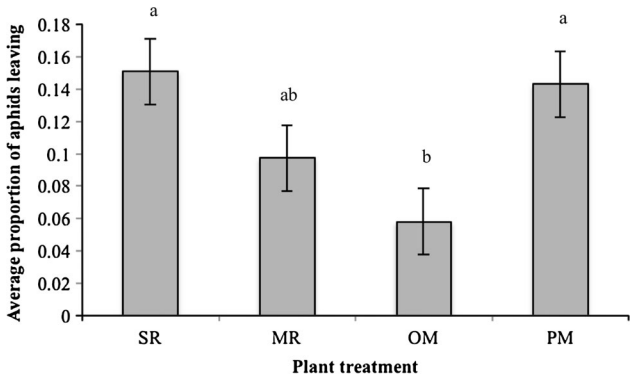

Fig. 4 The average proportion of aphids leaving by plant treatment ± SE: OM, PM, SRs, and MRs. *Letters* indicate significant differences

increased or altered probing behavior by the vectors. It is possible that the presence of predators encourages a 'hit-and-run' approach to probing; superficial probes may allow vectors to maintain greater mobility. If predators elicit

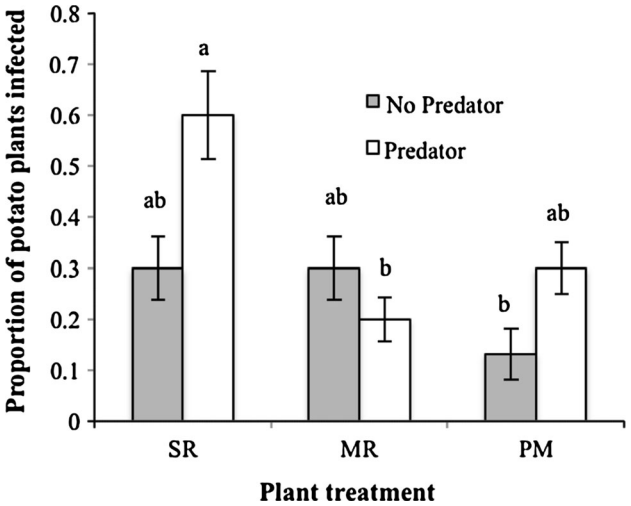

Fig. 5 The proportion of potato plants infected in two predator treatment levels (presence and absence of predators) by plant treatment, excluding the OM (where no infection is possible) and uninfected plots ± SE: PM, SRs, and MRs. *Letters* indicate significant differences

increased briefer, epidermal probing, which is required for PVY transmission (Boquel et al. 2011), this could explain the corresponding jump in viral prevalence.

The *number of potato plants infected* followed a similar pattern to the *proportion of plants infected*. However, while the *proportion of infected plants* was slightly different in the PM and SR treatments, the *number of plants infected* was the same. With no continuous virus source, vectors rapidly lose their ability to transmit the virus after probing one plant (Nault 1997), and it may be that the maximum amount of transmission occurred in both the PM and the SR treatment, resulting in the same number of plants infected and the twofold difference in proportion of plants infected.

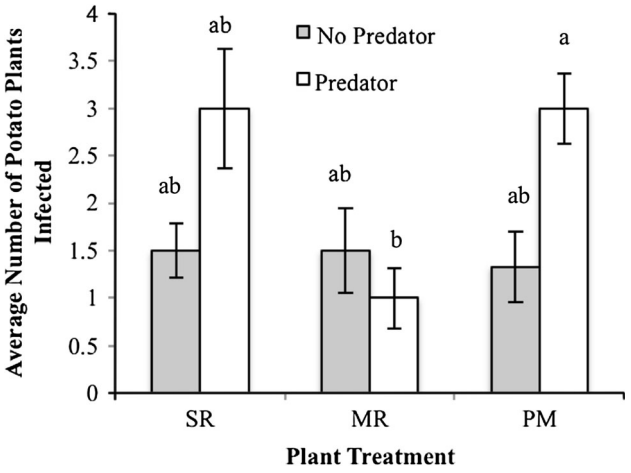

Fig. 6 The number of potato plants infected by plant treatment, excluding the OM (where no infection is possible) and uninfected plots ± SE: PM, SRs, and MRs. *Letters* indicate significant differences

While our findings have implications for future work, the simplified design and the use of wingless adult aphids in this study distance the results from agricultural application. This work should be replicated with winged adults and in a field setting before conclusions can be drawn for the management and mitigation practices. Although aphid movement and density had no clear relationship with PVY prevalence, counter to our initial hypothesis, the effects of predators and host plant abundance may be mediated by other vector behaviors, such as probing (Boquel et al. 2011), and may be dependent on intraplant movement. The results of this study demonstrate that wingless non-colonizing vector behavior and transmission of PVY are aggregated responses to multiple environmental drivers and emphasize the behavioral complexity of viral inoculation. Disentangling the relative importance of these factors, particularly in winged non-colonizing vector species, warrants further investigation.

Acknowledgments The authors are grateful to Katja Poveda and Chris Stieha for assistance with statistical analysis, and to the members of the Power and Thaler labs for their intellectual input and support. Support for this project was provided in part by NSF DEB-1015903 and USDA Hatch NYC-183449 awarded to A. G. Power and USDA Hatch NYC-1397406 awarded to J. S. Thaler.

Conflict of interest The authors declare no conflicts of interest.

References

Bailey SM, Irwin ME, Kampmeier GE, Eastman CE, Hewings AD (1995) Physical and biological perturbations: their effect on the movement of apterous *Rhopalosiphum padi* (Homoptera: Aphididae) and localized spread of Barley Yellow Dwarf Virus. Popul Ecol 24:24–33

Boquel S, Ameline A, Giordanengo P (2011) Assessing aphids potato virus y transmission efficiency: a new approach. J Virol Methods 178:63–67

Bottenburg H, Irwin ME (1992) Using mixed cropping to limit seed mottling induced by Soybean Mosiac Virus. Plant Dis 76(3):304–306

Crawley MJ (2007) The R book, 1st edn. Wiley, West Sussex

DiFonzo CD, Ragsdale DW, Radcliffe EB, Gudmestad NC, Secor GA (1996) Crop borders reduce potato virus y incidence in seed potato. Ann Appl Biol 129:289–302

DiFonzo CD, Ragsdale DW, Radcliffe EB, Gudmestad NC, Secor GA (1997) Seasonal abundance of aphid vectors of potato virus y in the Red River Valley of Minnesota and North Dakota. J Econ Entomol 90:824–831

Döring TF, Kirchner SM, Kühne S, Saucke H (2004) Response of alate aphids to green targets on coloured backgrounds. Entomol Exp Appl 113:53–61

Ellis P, Stace-Smith R, Bowler G, Mackenzie DJ (1996) Production of monoclonal antibodies for detection and identification of strains of potato virus y. Can J Plant Pathol 18:64–70

Fereres A, Moreno A (2008) Behavioural aspects influencing plant virus transmission by homopteran insects. Virus Res 141:158–168

Finke D (2012) Contrasting the consumptive and non-consumptive cascading effects of natural enemies on vector-borne pathogens. Entomol Exp Appl 144:1–11

Gray S, De Boer S, Lorenzen J, Karasev A, Whitworth J, Nolte P, Singh R, Boucher A, Xu H (2010) Potato virus y: an evolving concern for potato crops in the United States and Canada. Plant Dis 94:1384–1397

Hodge S, Hardie J, Powell G (2011) Parasitoids aid dispersal of a nonpersistently transmitted plant virus by disturbing the aphid vector. Agric For Entomol 13:83–88

Kaplan I, Thaler JS (2012) Phytohormone-mediated plant resistance and predation risk act independently on the population growth and wing formation of potato aphids, *Macrosiphum euphorbiae*. Arthropod Plant Interact 6:181–186

Mello AFS, Olarte RA, Gray SM, Perry KL (2011) Transmission efficiency of potato virus y strains PVY^{O} and $PVY^{N\text{-}Wi}$ by five aphid species. Plant Dis 95:1279–1283

Moore SM, Borer ET, Hosseini PR (2009) Predators indirectly control vector borne disease: linking predator–prey and host–pathogen models. J R Soc Interface 7:161–176

Narayandas GK, Alyokhin AV (2006) Interplant movement of potato aphid (Homoptera: Aphididae) in response to environmental stimuli. Environ Entomol 35:733–739

Nault LR (1997) Arthropod transmission of plant viruses: a new synthesis. Ann Entomol Soc Am 90:521–541

Nelson EH, Matthews CE, Rosenheim JA (2004) Predators reduce prey population by inducing changes in prey behavior. Ecology 85:1853–1858

Nolte P, Whitworth JL, Thornton MK, McIntosh CS (2004) Effect of seed-borne potato virus y on performance of Russet Burbank, Russet Norkotah, and Shepody potato. Plant Dis 88:248–252

Obrycki JJ, Kring TJ (2009) Aphidophagy by coccinellidae: application of biological control in agroecosystems. Biol Control 51:244–254

Ostfeld RS, Keesing F (2012) Effects of host diversity on infectious disease. Annu Rev Ecol Evol Syst 43:157–182

Pirone TP, Perry KL (2002) Aphids: non-persistent transmission. Adv Bot Res 36:1–19

Power AG (1991) Virus spread and vector dynamics in genetically diverse plant populations. Ecology 72:232–241

Power AG, Flecker AS (2008) The role of vector diversity in disease dynamics. In: Ostfeld RS et al (eds) Infectious disease ecology: the effects of ecosystems on disease and of disease on ecosystems. Princeton University Press, Princeton, pp 30–47

Preisser EL, Bolnick DI (2008) The many faces of fear: comparing the pathways and impacts of nonconsumptive predator effects on prey populations. PLoS One 3:e2465

Roitberg BD, Myers JH (1978) Effect of adult coccinellidae on the spread of a plant virus by an aphid. J Appl Ecol 15:75–779

Scholthof KG, Adkins S, Czosnek H, Palukaitis P, Jacquot E, Hohn T, Hohn B, Saunders K, Candresse T, Ahlquist P, Hemenway C, Foster GD (2011) Top 10 plant viruses in molecular plant pathology. Mol Plant Pathol 12:938–954

Singh MN, Khurana SMP, Nagaich BB, Agrawal HO (1988) Environmental factors influencing aphid transmission of potato virus y and potato leafroll virus. Potato Res 31:501–509

Srinivasan R, Alvarez JM, Cervantes F (2013) The effect of an alternate weed host, hairy nightshade, Solanum sarrachoides (Sendtner) on green peach aphid distribution and Potato leaf roll virus incidence in potato fields of the Pacific Northwest. Crop Prot 46:52–56

Sudderth EA, Sudderth EB (2014) Quantifying aphid behavioral responses to environmental change. Entomol Exp Appl 150:7–18