

Variable host phenology does not pose a barrier to invasive weevils in a northern hardwood forest

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- Abstract**
- 1 A suite of invasive weevils has established in hardwood forests of the North American Great Lakes Region. We quantified patterns of host availability and the capacity of adults to succeed in a system with high host variability both within and between seasons in Michigan, U.S.A.
 2. We quantified phenological development of foliage on three host species [sugar maple, *Acer saccharum* Marshall; ironwood, *Ostrya virginiana* (Mill.) K. Koch; and raspberry, *Rubus* spp.]. We estimated adult abundance using emergence traps and sweep net sampling over 3 years, and compared field host associations with laboratory choice assays.
 3. Host plant phenology varied among species, between years, and in their interactions. The four most common weevils, *Phyllobius oblongus* (L.), *Polydrusus sericeus* (Schaller), *Barypeithes pellucidus* (Boheman) and *Sciaphilus asperatus* (Bonsdorff), emerged in early to mid-June, in approximately that order. After emergence, each species showed evidence of host preference based on their abundances on foliage. Overall, *P. oblongus* and *B. pellucidus* were most prevalent on sugar maple, *P. sericeus* was most prevalent on ironwood, and *S. asperatus* was relatively evenly distributed. Laboratory choice tests with *P. oblongus* and *P. sericeus* confirmed these preferences.
 4. These four invasive species comprised over 99% of all 12 845 weevils obtained, suggesting displacement of native species. The optimal sampling methods varied among weevil species.
 5. These invasive weevils contend with the highly variable conditions of their environment, and also potential phenological asynchrony, via relatively late emergence, even at the cost of lower host quality. Annual variation is greater for numbers of adults than larvae, suggesting that mortality of late instars or pupae is particularly important.

Keywords *Barypeithes pellucidus*, belowground herbivory, Coleoptera, Curculionidae, exotic species, *Phyllobius oblongus*, *Polydrusus sericeus*, *Sciaphilus asperatus*.

Introduction

Establishment of an insect herbivore in a new ecosystem often requires an ability to contend with highly variable conditions of

host availability, which is an ability that may relate to feeding breadth (Potter & Held, 2002; Reding, 2008; Haack *et al.*, 2010). Most field studies have examined herbivore diet breadth from a spatial perspective (i.e. evaluating distributions among putative hosts at a fixed time) (Bernays, 1993; Raubenheimer & Bernays, 1993; Singer & Stireman, 2001). However, fewer studies have assessed diet breadth from a temporal perspective (i.e. among putative hosts becoming available or unavailable over time) (Mooney & Tillberg, 2005; Takeuchi *et al.*, 2005). By adopting multiple hosts in phenological succession, herbivores may lengthen their lifespan, potentially increasing fitness (Uechi & Yukawa, 2006).

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A complex of invasive root-feeding weevils (Coleoptera: Curculionidae) has established in North American hardwood forests in the Great Lakes Region (Coyle *et al.*, 2008). *Phyllobius oblongus* (L.) appears to be most common and, together with *Polydrusus sericeus* (Schaller), *Sciaphilus asperatus* (Bonsdorff) and *Barypeithes pellucidus* (Boheman), comprises >96% of all curculionid species captured in recent studies in this area (Pinski *et al.*, 2005a; Coyle, 2011). The adults emerge from the soil in early summer, feed on the foliage of several woody plant species (Witter & Fields, 1977; Pinski *et al.*, 2005b; Coyle *et al.*, 2010b) and can damage or kill seedlings (Simmons & Knight, 1973; Witter & Fields, 1977; Coyle, 2011). Mating and oviposition occur shortly after emergence, and eggs are deposited into the soil. Larvae develop from mid-summer until the next spring, and are speculated to be rhizophagous on several plant species (Witter & Fields, 1977; Coyle, 2011). Larval survival decreases throughout the winter, although larval weight increases, suggesting continual feeding and development (Coyle *et al.*, 2011).

Adult weevils were observed primarily on sugar maple, *Acer saccharum* Marshall early in the 2006 growing season, although more commonly on ironwood, *Ostrya virginiana* (Mill.) K. Koch, and raspberry, *Rubus* spp., later in the season. Sugar maple is the dominant woody species in this northern hardwood ecosystem (Goodburn, 1996). However, sugar maple only flushes once, after which foliage becomes less palatable (Coyle *et al.*, 2010a). By contrast, other hosts such as ironwood and raspberry have indeterminate growth, thereby producing a continuous supply of fresh foliage. Foliage quality in many plants, including sugar maple (Schultz *et al.*, 1982) and other woody plants, declines over the course of a growing season (Feeny, 1970), and several coleopterans have shown negative fitness effects from feeding on older, suboptimal foliage (Bingaman & Hart, 1992; Obermaier & Zwölfer, 1999; Awmack & Leather, 2002).

We hypothesized that adult weevils would feed on sugar maple initially but switch host plants to ironwood and raspberry when sugar maple palatability declined. To test this hypothesis, we examined the feeding habits of these invasive weevils and their exploitation of sugar maple, ironwood and raspberry throughout three growing seasons. The first study objective was to characterize the phenology (i.e. budbreak) of sugar maple, ironwood and raspberry. The second study objective was to document weevil distribution patterns throughout their adult activity periods, specifically by quantifying adult emergence and abundance from localized patches of sugar maple, ironwood and raspberry hosts. The third study objective was to determine how sampling method (i.e. sweep netting or emergence trapping) influenced weevil population estimates. Our final objective was to test the extent to which adult field distribution patterns reflected innate feeding preference under controlled conditions.

Materials and methods

Study location

All sampling and foliage collection was conducted in a northern hardwood forest ecosystem near Taylor Lake in the Ottawa

National Forest, Gogebic Co., Michigan, U.S.A. (46°14.4'N, 89°2.9'W). Sugar maple is the dominant tree species, with ironwood, basswood (*Tilia americana* L.) and yellow birch (*Betula alleghaniensis* Britt.) also present (Goodburn, 1996; Pinski *et al.*, 2005a). Raspberry, gooseberry (*Ribes* spp.) and leatherwood (*Dirca palustris* L.) are common understory shrubs. Soils are sandy loam to a depth of 30 cm, below which it becomes more nutrient deficient, clayey and rocky (Coyle, 2011). Air temperatures varied greatly over the course of the present study, although soil temperatures were much more stable (Coyle, 2011).

Budbreak measurements

Seven plots each of predominantly sugar maple, ironwood and raspberry were established (Table 1), each separated by a minimum of 2 m. In no case was a plot of one host species closer than 25 m to another host species. Adult weevils are mobile via walking or flying, so each habitat was physically available to them, regardless of where adults emerged. Seven understory plants (sugar maple or ironwood seedlings or individual raspberry shoots) in each species plot were randomly chosen and flagged to ensure subsequent monitoring of the same plant throughout a season. Budbreak measurements on host plant apical buds were taken approximately weekly in May during 2008 and 2009. Phenological stages were based on Kolb and Teulon (1991): 1 = bud scales swollen from midwinter condition, bud scales not separated; 2 = bud scales start separating, green scale interior visible; 3 = bud scales loose, leaf margins visible; 4 = leaves visible but still folded, less than 2.54 cm long; 5 = leaves beginning to unfold and greater than 2.54 cm long.

Adult emergence in various host plant plots

Thirteen emergence traps were placed on the ground in each of the above-mentioned plots in 2007–2009. Traps consisted of a 2-L clear plastic bottle (Ball Corp., Watertown, Wisconsin) with the top third removed. The inside of the top portion was painted with textured black paint (Rust-Oleum Corp., Vernon Hills, Illinois). The remainder of the bottle was inverted onto the top portion, and secured to the ground by a stake wire flag (Forestry Suppliers, Inc., Jackson, Mississippi) attached to the side of the bottle with duct tape. Emerging adult weevils crawled up the inside of the painted portion, through the opening, and fell into the trap. Traps were checked approximately weekly from

Table 1 Structure of host species plots ($n = 7$ per host) used for budbreak and weevil emergence sampling at the study site

Host	Plot area (m ²)	% Host in plot	Host basal dia. (mm)	Basal area (cm ² m ⁻²) ^a
Sugar maple	19.5 ± 2.7	99.1 ± 0.3	2.77 ± 0.05	1.62 ± 0.24
Ironwood	13.5 ± 1.1	75.8 ± 6.8	7.69 ± 0.51	2.48 ± 0.91
Raspberry	16.7 ± 2.1	96.3 ± 0.7	5.38 ± 0.12	1.50 ± 0.26

^aCalculated using basal diameter.

All measurements are given as the mean ± SE.

4 June to 11 July 2007, 13 May to 29 July 2008 and 30 April to 20 July 2009. Weevils were placed into vials and transported to the laboratory for identification and preservation. Voucher specimens are housed in the Department of Entomology Insect Research Collection at the University of Wisconsin–Madison (Coyle *et al.*, 2010b).

Adult abundance on foliage

Ten additional plots each of predominantly sugar maple, ironwood and raspberry, located at least 50 m from plots used for budbreak and emergence, were randomly sampled approximately once per week. Each sample consisted of 10 sweeps on understory vegetation. Plots had relatively equal amounts of vegetation in the sampling area as determined by a visual inspection. Sweep net sampling was conducted from 8 May to 11 July 2007, 20 May to 21 July 2008 and 6 May to 29 July 2009; these dates were chosen based on previous monitoring of adult populations in the field and observations during the study period. Adult weevils were placed in vials and transported to the laboratory for identification and preservation. Voucher specimens are housed in the Department of Entomology Insect Research Collection at the University of Wisconsin–Madison (Coyle *et al.*, 2010b).

Behavioural choice tests

Adult pairs of *P. oblongus* ($n = 40$) and *P. sericeus* ($n = 25$) were collected on 11 and 20 June 2008, respectively, from sugar maple, ironwood and raspberry. Collections were timed to coincide with the beginning of weevil emergence to ensure they had little previous feeding experience. Although we could not record any previous feeding or mating experience, previous studies have shown that feeding experience prior to capture does not interfere with their ability to make subsequent host choices (Pinski *et al.*, 2005b; Hillstrom *et al.*, 2010; Coyle *et al.*, 2010a, b). Individual pairs were kept in vials, transported to the laboratory and starved for 24 h before each assay.

Foliage was collected on the same days as insects. Shoots (at least 30 cm in length) were clipped and transported to the laboratory with the excised ends submerged in water. Shoots were standardized for sun exposure, and only leaves from leaf plastochron index 3–5 (Larson & Isebrands, 1971) and devoid of previous insect or fungal damage based on visual assessment were used in the assays. The leaf plastochron index is a leaf numbering system where the most apical leaf on the stem having a fully-expanded lamina length of ≥ 3 cm is called leaf plastochron index 0, and leaves are numbered sequentially from this point down the branch toward the stem (Larson & Isebrands, 1971).

Three-way choice tests were conducted with *P. oblongus* on 12 June 2008 and *P. sericeus* on 21 June 2008. Two discs (2.8 cm²) were punched from a single leaf from each sugar maple, ironwood and raspberry shoot, and the three pairs of discs were placed together in a plastic Petri dish (tall 2 cm, diameter 15 cm) with moistened Whatman filter paper (Whatman, U.K.) on the bottom, along with a dry Kimwipe (Kimberly-Clark, Dallas, Texas). One apparently healthy pair

of adult weevils was placed in the centre of each dish. Dishes were kept in growth chambers under a LD 16 : 8 h photoperiod and a day : night temperature regime of 24 : 18 °C, and were maintained for 48 h. Leaf disks were digitally scanned (WinFOLIA Pro software, Régent Instruments, Inc., Canada) upon removal to determine leaf area consumed. Remaining plant material from the leaf discs was summed to obtain a final leaf area consumption amount per host plant species per dish.

Statistical analysis

All analysis of variance (ANOVA) tests were conducted using PROC MIXED, Version 9.0 (SAS Institute, Cary, North Carolina), and significant differences among means were examined using Tukey's test with $\alpha = 0.05$ considered significant. Budbreak measurements were analyzed for the effects of host species and time within a year using a two-way repeated measures ANOVA with each year analyzed separately. Data did not require transformation.

We analyzed five adult emergence sample periods each year, which encompassed most of the weevils' activity periods: 4–13 June, 13–19 June, 19–27 June and 27 June to 11 July in 2007; 3–11 June, 11–16 June, 16–23 June and 23 June to 14 July in 2008; and 5–11 June, 11–19 June, 19–26 June and 26 June to 20 July in 2009. These sample periods accounted for 100%, 97% and 94% of total curculionid captures in 2007, 2008 and 2009, respectively. For abundance of adults on foliage, we analyzed seven sample dates each year: 31 May, 5, 11, 19 and 27 June, and 3 and 11 July 2007; 27 May, 3, 9, 16 and 25 June, and 1 and 8 July 2008; 29 May, 5, 11, 21 and 26 June, and 3 and 13 July 2009. Our analysis included 100%, 99% and 99% of all curculionids sampled in 2007, 2008 and 2009, respectively. Emergence and abundance data were log-transformed to achieve normality. Data from each species were analyzed separately using a repeated-measures ANOVA with a spatial power covariance structure based on Julian date with year, host species and sampling date as independent variables.

We tested whether the relative weevil species composition varied depending on the sampling method used by analyzing the ratio of total weevils captured in emergence traps and sweep net samples for all weevil and host species combined using chi-square analyses in PROC FREQ, version 9.0 (SAS Institute). To examine if the relative proportion of a weevil species on the three host species varied with sampling method, we analyzed the ratio of the total number of weevils captured in emergence traps and sweep net samples for each weevil species. To determine whether the sampling methods were equally effective, the ratio of the total number of weevils captured in emergence traps and sweep net samples for each weevil species \times host combination was examined.

Leaf area consumption data from the behavioural choice assay were analyzed using a one-way ANOVA with the three host species nested within each petri dish. Weevil species were analyzed separately, and leaf area consumption rates were square root transformed before analysis to achieve normality. The leaf area of these host species has been shown to be highly correlated with leaf mass, and a viable surrogate for leaf mass

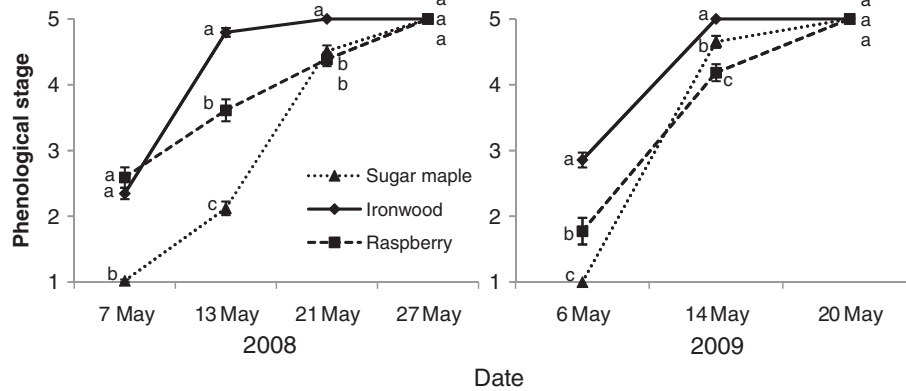


Figure 1 Mean \pm SE budbreak ratings in 2008 and 2009 on three woody plant species at the study site. Different lowercase letters indicate significant differences ($\alpha = 0.05$) between species within a single date.

consumption (Coyle *et al.*, 2010b). Adult size did not differ between weevil species (Coyle *et al.*, 2010b); therefore, we did not adjust foliage consumption for insect size.

Results

Budbreak differed among host plants

As expected, phenology varied among the host plant species (Fig. 1). In 2008, budbreak was affected by host ($F = 180.33$; d.f. = 2, 528; $P < 0.0001$), date ($F = 763.63$; d.f. = 3, 528; $P < 0.0001$) and the host \times date interaction ($F = 60.78$; d.f. = 6, 528; $P < 0.0001$). Similarly, in 2009, the main effects of host ($F = 54.38$; d.f. = 2, 384; $P < 0.0001$), date ($F = 994.35$; d.f. = 2, 384; $P < 0.0001$) and the host \times date interaction ($F = 32.20$; d.f. = 4, 384; $P < 0.0001$) all significantly affected budbreak. In general, ironwood developed first, followed by raspberry and sugar maple. Differences among hosts were greatest in early or mid-May, although the developmental rate varied between years. All hosts had fully expanded leaves by the end of May, which was before the emergence of adult weevils (Coyle, 2011).

Abundance and patterns of adult emergence varied among host plants

Emergence traps captured 5810 weevils from 2007 to 2009 of which >99% belonged to one of the four investigated species. Weevil emergence was highly variable and affected by the main effects of year, host and sampling date within a season, as well as their interactions (Table 2).

Phyllobius oblongus emergence was greatest in the first week of June 2007, and had no discernable population pattern in 2008 or 2009 (Fig. 2A). The number of adults captured was over 30- and 80-fold greater in 2007 than in 2008 and 2009, respectively. Emergence did not differ among hosts (Table 2).

Polydrusus sericeus began to emerge during the first week of June, peaked during the second week of June, and declined thereafter (Fig. 2B). However, emergence peaked a week later in 2008 than in 2007 or 2009. Emergence did not differ among

hosts, although there was a host \times year interaction (Table 2). In ironwood and raspberry, fewer *P. sericeus* emerged in 2009 than in 2007 or 2008. Emergence in sugar maple was lower in 2007 than 2008 or 2009. Emergence in ironwood and raspberry was significantly greater than in sugar maple in 2007. *Polydrusus sericeus* emergence was 17% greater in 2008 than 2007, and 71% greater in 2008 than 2009.

Sciaphilus asperatus began to emerge in early June each year, and total emergence increased 10-fold from 2007 to 2009 (Fig. 2C). Emergence did not differ among host species, nor was there a host \times year interaction. Peak emergence occurred in June 2009, although emergence was not affected by the host \times date interaction. Emergence patterns were consistent in 2007 and 2008, although more irregular and higher in all three host species in 2009.

Barypeithes pellucidus began to emerge in early June and generally peaked in mid-June, with the exception of 2007 (Fig. 2D). Emergence was over five-fold lower in 2007 than in 2008 or 2009. More than twice as many *B. pellucidus* emerged in ironwood as in sugar maple, and over three times as many emerged in ironwood as in raspberry. During peak emergence, the preferred host was ironwood. Emergence was highest in ironwood in 2008 and 2009, and emergence was low in all host species in 2007.

Otiorhynchus ovatus Germar was captured in emergence traps during 2007 ($n = 2$), 2008 ($n = 7$) and 2009 ($n = 12$). *Hormorus undulatus* (Uhler), the only native species in this complex, was captured in emergence traps in very low numbers in 2008 ($n = 3$) and 2009 ($n = 1$).

Abundance and patterns of adult abundance on foliage varied among host species

We captured 7035 adult weevils in sweep nets from 2007 to 2009. For *P. oblongus*, *P. sericeus*, *S. asperatus* and *B. pellucidus*, we identified significant main effects of year, host and sampling date within a season, as well as their interactions (Table 2).

Phyllobius oblongus abundance on foliage was generally greatest in late May in 2007 and early June in 2008 and 2009

Table 2 Statistical values for the main effects of year, host and date, as well as their interactions, for the emergence and abundance on foliage of four invasive weevil species sampled from 2007 to 2009 at the study site

Species	Variable	Emergence			Foliar abundance		
		F	d.f.	P	F	d.f.	P
<i>Phyllobius oblongus</i>	Year	36.23	2,54	<0.001	19.89	2,81	<0.001
	Host	2.45	2,54	0.096	21.68	2,81	<0.001
	Year × Host	1.04	4,54	0.395	3.77	4,81	0.007
	Date	28.84	4,216	<0.001	171.65	6,486	<0.001
	Year × Date	31.39	8,216	<0.001	61.78	12,486	<0.001
	Host × Date	0.70	8,216	0.695	2.14	12,486	0.014
	Year × Host × Date	0.87	16,216	0.608	3.20	24,486	<0.001
<i>Polydrusus sericeus</i>	Year	5.32	2,54	0.008	4.44	2,81	0.015
	Host	1.96	2,54	0.151	16.03	2,81	<0.001
	Year × Host	4.05	4,54	0.006	1.17	4,81	0.329
	Date	33.01	4,216	<0.001	43.60	6,486	<0.001
	Year × Date	17.11	8,216	<0.001	10.52	12,486	<0.001
	Host × Date	1.12	8,216	0.346	4.96	12,486	<0.001
	Year × Host × Date	2.39	16,216	0.003	2.87	24,486	<0.001
<i>Sciaphilus asperatus</i>	Year	96.49	2,54	<0.001	62.43	2,81	<0.001
	Host	0.79	2,54	0.460	9.64	2,81	<0.001
	Year × Host	0.64	4,54	0.639	0.95	4,81	0.437
	Date	7.69	4,216	<0.001	43.41	6,486	<0.001
	Year × Date	9.80	8,216	<0.001	23.14	12,486	<0.001
	Host × Date	1.38	8,216	0.205	0.95	12,486	0.492
	Year × Host × Date	2.61	16,216	<0.001	2.73	24,486	<0.001
<i>Barypeithes pellucidus</i>	Year	61.41	2,54	<0.001	32.71	2,81	<0.001
	Host	19.01	2,54	<0.001	57.01	2,81	<0.001
	Year × Host	3.63	4,54	0.011	28.84	4,81	<0.001
	Date	35.56	4,216	<0.001	44.10	6,486	<0.001
	Year × Date	64.61	8,216	<0.001	29.83	12,486	<0.001
	Host × Date	7.80	8,216	<0.001	8.54	12,486	<0.001
	Year × Host × Date	4.16	16,216	<0.001	12.58	24,486	<0.001

(Fig. 3A). Abundance on foliage was 27% greater in 2008 than 2009, and 52% greater in 2008 than 2007. Adult abundance on sugar maple and raspberry foliage was similar, although 30% fewer were captured on ironwood. More *P. oblongus* were captured on sugar maple (mean ± SE; 10.7 ± 0.9 adults per sweep) than raspberry (9.3 ± 1.2) or ironwood (6.7 ± 0.6). Weevil abundance did not differ among hosts in 2007 but was significantly lower on ironwood in 2008 and 2009 than on sugar maple. There was a great deal of variation in annual foliar density patterns but, in general, *P. oblongus* were initially highest on raspberry, and then shifted to sugar maple.

Polydrusus sericeus abundance on foliage peaked in early July in 2007 and 2009, and in late June in 2008 (Fig. 3B). Abundance on foliage was almost twice as great in 2007 and 2009 as in 2008. Ironwood was the preferred host, with abundance on ironwood foliage (0.70 ± 0.12) being almost twice as high as on raspberry foliage (0.36 ± 0.06), which was almost twice as high as on sugar maple foliage (0.20 ± 0.06).

Sciaphilus asperatus abundance on foliage peaked in early June, with annual variations (Fig. 3C). Abundance was over three-fold greater in 2009 (1.79 ± 0.18) than in 2007 (0.57 ± 0.07) or 2008 (0.50 ± 0.07). Abundance on sugar maple was 39% and 51% higher than on ironwood and raspberry, respectively.

Barypeithes pellucidus abundance on foliage was greatest in early to mid-June; a rain event around 26 June 2009 may

have caused the uncharacteristic mid-activity period decline for that year (Fig. 3D). Abundance on foliage in 2009 was almost four- and five-fold greater than in 2008 and 2007, respectively. Abundance on foliage was much higher on sugar maple (1.80 ± 0.34) than on raspberry (0.44 ± 0.07) or ironwood (0.21 ± 0.06), although abundance on foliage was highest on raspberry in 2007. Abundance on foliage during the sampling periods was more variable on sugar maple than on ironwood or raspberry.

Otiorynchus ovatus were not captured in 2007 or 2008, although six individuals were captured in 2009. We did not capture any *H. undulatus* on foliage.

Sampling method influences relative estimates among weevil species

The relative species composition of the weevil community varied depending on the sampling method used (Table 3; All species/All hosts). Therefore, we cannot make between-species comparisons of abundance. Adult *P. oblongus* were captured in higher numbers via sweep net sampling, whereas all other species were captured in higher numbers in emergence traps. Adult *P. sericeus* were captured more often in emergence traps in sugar maple and raspberry but not in ironwood. Adult *S. asperatus* were consistently captured by both sampling methods; they were obtained in higher numbers in emergence

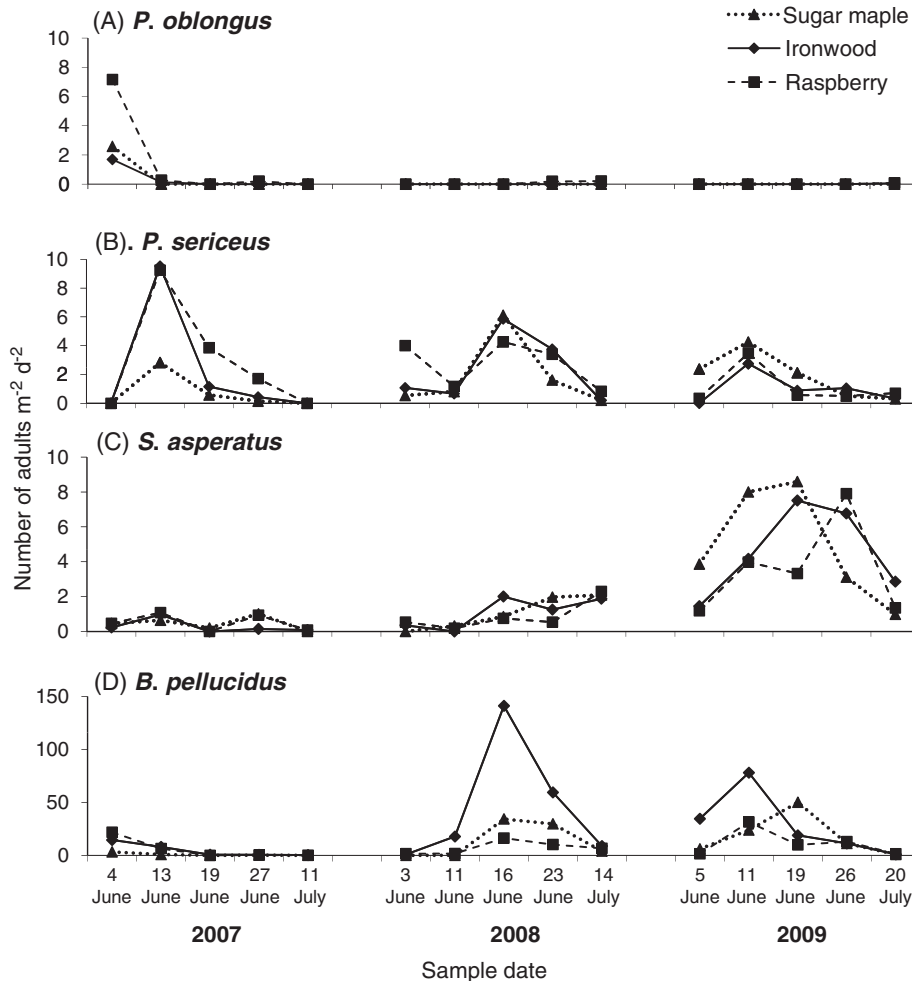


Figure 2 Adult weevil emergence (adults/m²/day) in sugar maple, ironwood and raspberry plots for (A) *Phyllobius oblongus*, (B) *Polydrusus sericeus*, (C) *Sciaphilus asperatus* and (D) *Barypeithes pellucidus* during 2007–2009 at the study site.

traps in ironwood and raspberry but not in sugar maple. Adult *B. pellucidus* were captured in much greater numbers via emergence traps, and sweep net sampling did not appear to accurately represent adult populations compared with emergence trap capture rates.

Phyllobius oblongus and *P. sericeus* feeding preferences under controlled conditions

Phyllobius oblongus consumed 23% and 46% more sugar maple foliage than ironwood and raspberry, respectively ($F = 7.99$; d.f. = 2, 38; $P = 0.0013$) (Fig. 4). *Polydrusus sericeus* consumed over twice as much ironwood foliage than raspberry, and over four times more ironwood foliage than sugar maple ($F = 292.18$; d.f. = 2, 24; $P < 0.0001$).

Discussion

We hypothesized a sequence, based on our first year of sampling, in which foraging plasticity allowed these herbivores to

progress from one host species to another, as the foliage of early developing plants became less palatable and the foliage of subsequent host species began to develop. Extending our observations over 3 years did not, however, support this hypothesis. Instead, these weevils typically delayed emergence until all three of their primary hosts were likely to have produced foliage, even though some foliage was likely to be suboptimal. This relatively cautious strategy may have facilitated establishment in a variable ecosystem such as the northern hardwood forest, where winter severity, snow presence on the ground and the timing of host budbreak can vary greatly from year to year. The ability to utilize a broad range of host plants is a common characteristic of many invasive invertebrates (Walter *et al.*, 2010; Zhang *et al.*, 2010). Dietary flexibility can provide a competitive advantage over conspecifics (Nylin & Gotthard, 1998) and be directly advantageous for the growth and development of eggs (Sasakawa, 2009), larvae (Unsicker *et al.*, 2008; Morales Ramos *et al.*, 2010; Trudeau *et al.*, 2010) or adults (Marteleto *et al.*, 2009).

Weevil emergence was not phenologically synchronous with budbreak in any host, in contrast with several lepidopteran

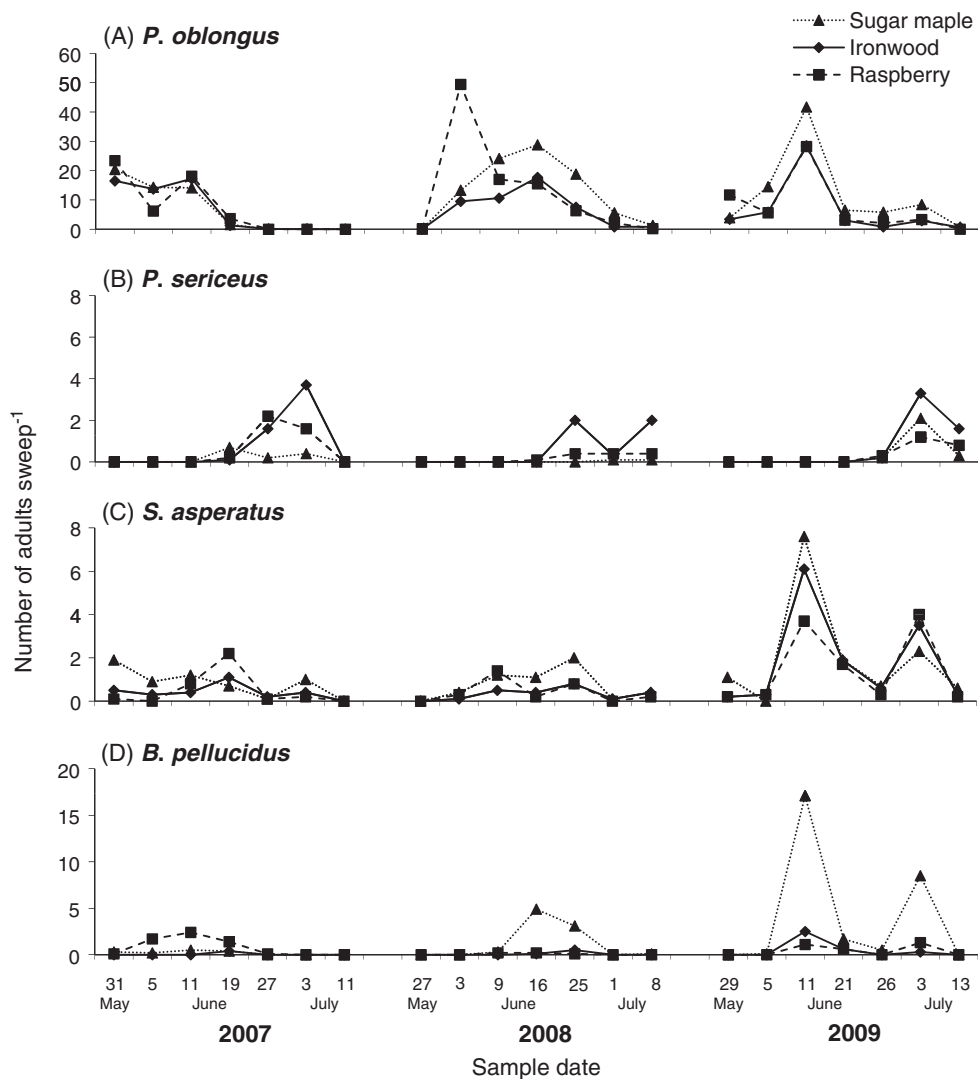


Figure 3 Abundance of adult (A) *Phyllobius oblongus*, (B) *Polydrusus sericeus*, (C) *Sciaphilus asperatus* and (D) *Barypeithes pellucidus* on sugar maple, ironwood, and raspberry foliage during 2007–2009 at the study site.

species for which larval hatching concurrently with host budbreak is well established (Feeny, 1970; Hunter, 1992; van Asch & Visser, 2007; Butt *et al.*, 2010; Singer & Parmesan, 2010). The fitness consequences of poor synchrony can be starvation when an herbivore emerges before suitable foliage is available or, conversely, reduced growth if palatability of foliage has already declined (Mattson, 1980; Scriber & Slansky, 1981). To avoid the risk of emerging too early in the growing season, these invasive weevils appear to reduce that risk by consuming older foliage if necessary, thereby minimizing the potential cost of relatively delayed emergence because foliage palatability does decline with time (Coyle *et al.*, 2010a).

Phyllobius oblongus lived longer on raspberry foliage but consumed ironwood at a greater rate than sugar maple (Coyle *et al.* 2010b). When foliage age was considered, however, *P. oblongus* adults preferred and performed better on newly-formed sugar maple foliage (Coyle *et al.*, 2010a). Therefore, the finding that *P. oblongus* were more often captured on

sugar maple in the present study is in agreement with the study by Coyle *et al.* (2010a) in that newly-formed sugar maple foliage (i.e. the dominant foliage type available when *P. oblongus* adults emerge) would be more attractive to these weevils. Additionally, the field abundance of *P. sericeus* corroborated our laboratory findings in that ironwood and raspberry were preferred hosts (Coyle *et al.*, 2010b). Our metric for preference and performance was leaf area consumption. Foliage palatability may have differed among host species, however, although we did not test foliar nutrition content of the host leaves. Overall, it appears that the numerically dominant weevil *P. oblongus* prefers and performs well on the dominant host available during early summer (i.e. sugar maple) and this probably contributes to the population size for *P. oblongus* in this system.

All four weevil species exhibited high annual variation in their numbers of emerging adults. By contrast, the larval densities of these species have been relatively consistent

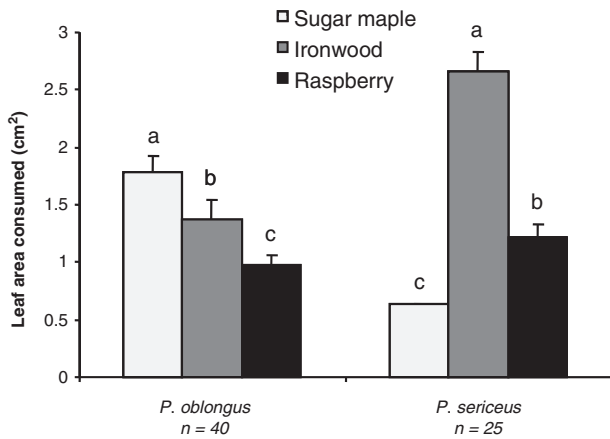


Figure 4 Feeding preferences of *Phyllobius oblongus* and *Polydrusus sericeus* in laboratory three-way choice tests. Bars represent leaf area consumption per weevil over a 48 h feeding period. Within a host species, means sharing the same lowercase letter are not significantly different at $\alpha = 0.05$.

from 2005 to 2008 (778 ± 53 larvae/m²/year) (Coyle *et al.*, 2008), although the abundance of individual species was not determined. The cause of this highly variable adult emergence compared with relatively consistent larval density is not readily apparent because soil temperatures during the present study stayed above the critical level at which high mortality occurs: $-3\text{ }^{\circ}\text{C}$ (Coyle *et al.*, 2011). Similarly, there were no flooding events or obvious signs of extensive predation, parasitism or disease.

Estimating the relative abundances of various members of this invasive complex is confounded by differences in optimal sampling methods for each species (Table 3). For example, *P. oblongus* can be effectively sampled by sweep net sampling but not emergence traps, as also observed by Pinski

et al. (2005a). By contrast, *B. pellucidus* can be effectively sampled by both emergence and pitfall traps (Werner & Raffa, 2000; Bouchard *et al.*, 2005). We captured comparatively low numbers of *P. sericeus* and *S. asperatus*, possibly because *P. sericeus* prefers birch (Pinski *et al.*, 2005b; Hillstrom *et al.*, 2010), an uncommon host species in our study area (Goodburn, 1996). We did not sample in the upper canopy, although *P. sericeus* is known to occur at canopy heights up to 6 m (Pinski, 2004), whereas *P. oblongus* is found at heights up to 5.5 m in the canopy (Simmons, 1972). The nocturnal lifestyle of *S. asperatus* (Witter & Fields, 1977) may have contributed to its relatively low numbers captured in sweep net samples. Other studies also suggest that *P. sericeus* and *S. asperatus* are, in general, less abundant than *P. oblongus* or *B. pellucidus* in this weevil complex (Bouchard *et al.*, 2005; Pinski *et al.*, 2005a; Coyle *et al.*, 2011).

The complete dominance of this complex of invasive weevils suggests that they may have displaced native root-feeding weevils. Although this cannot be proven without equivalent sampling having been carried out before the arrival of this invasive weevil complex, this appears to be more likely than the alternative (i.e. that no root feeding arthropods were ever abundant) given the dominance of Curculionidae, the largest family of all organisms in terrestrial ecosystems. *Sciaphilus asperatus* was the first of these species documented in North America in 1884, followed by *B. pellucidus* in the early 1900s, *P. oblongus* in 1923 and *P. sericeus* in 1934 (Coyle *et al.*, 2008). Anecdotal evidence suggests that, by the 1950s, this complex of invasive weevils had firmly established in the northern hardwood forests of Michigan’s Upper Peninsula (W. J. Mattson, personal communication). The ability to rapidly exploit resources is recognized as a major mechanism contributing to invasive species’ displacement of native species (Holway, 1999). The combination of a risk-avoiding emergence strategy and polyphagy appears to have contributed at least in part to this suite of invasive weevils’ current status as the

Table 3 Numbers of four invasive weevil species captured in emergence traps and sweep net samples on three host species from 2007 to 2009 at the study site

Weevil species	Host	Emergence	Sweep net	Ratio	χ^2	P
All	All	5785	7029	0.8	120.8	<0.001
<i>Phyllobius oblongus</i>	Total	60	5607	0.011	5249.5	<0.001
	Sugar maple	11	2241	0.005	2208.2	<0.001
	Ironwood	11	1407	0.008	1374.3	<0.001
	Raspberry	38	1959	0.019	1847.9	<0.001
<i>Polydrusus sericeus</i>	Total	586	278	2.1	109.8	<0.001
	Sugar maple	160	42	3.8	68.9	<0.001
	Ironwood	183	151	1.2	3.1	0.080
	Raspberry	243	85	2.9	76.1	<0.001
<i>Sciaphilus asperatus</i>	Total	796	631	1.3	19.1	<0.001
	Sugar maple	296	261	1.1	2.2	0.138
	Ironwood	269	193	1.4	12.5	<0.001
	Raspberry	231	177	1.3	7.1	0.008
<i>Barypeithes pellucidus</i>	Total	4343	513	8.5	3020.8	<0.001
	Sugar maple	1267	377	3.4	481.8	<0.001
	Ironwood	2264	44	51.5	2135.4	<0.001
	Raspberry	812	92	8.8	573.5	<0.001

Ratios were calculated as emergence:sweep net for all weevil species. All chi-square analyses were conducted with 1 degree of freedom.

dominant rhizophagous insect fauna in this northern hardwood forest ecosystem.

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