Preferential Edge Habitat Colonization by a Specialist Weevil, *Rhinoncomimus latipes* (Coleoptera: Curculionidae)

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ABSTRACT Understanding the behavioral basis of dispersal and colonization is critical in biological control systems, where success of a natural enemy depends in part on its ability to find and move to new host patches. We studied behavior of the specialist weevil *Rhinoncomimus latipes* Korotyaev, a biological control agent of mile-a-minute weed, *Persicaria perfoliata* (L.) H. Gross, by releasing weevils at the forest edge and monitoring their colonization of potted host plants arrayed along the edge, out into the open field, and into the forest. Both distance from the release cage and habitat where plants were located affected colonization, with more than twice as many weevils found on plants at 2 m than at 6 or 14 m; at 14 m, 6–8 times as many weevils colonized plants along the forest edge compared with plants in the open field or within the forest. In a second experiment, weevils that were released in an open field 12 m from the forest edge initially flew in all directions, but again ultimately colonized more plants at the edge than out in the open field. This species may be adapted to seek host plants at the forest edge, because *P. perfoliata* generally is found in riparian corridors in its native range and along forest edges in North America. Results suggest that *R. latipes* will move successfully to new *P. perfoliata* patches along wooded edges, but may not readily locate isolated patches in the open or those embedded in forests.

KEY WORDS dispersal, orientation, biocontrol, *Rhinoncomimus latipes*, *Persicaria perfoliata*

Dispersal of individual herbivores from one habitat patch to another has consequences, not only for individual fitness, but also for population and community dynamics (Grevstad and Herzig 1997, Tilman and Kareiva 1997, Cronin 2003, Bowler and Benton 2005, Dávalos and Blossey 2011). Dispersal behavior can be divided into three phases (Bowler and Benton 2005): the decision to leave the current patch, movement between patches, and the decision to enter and remain on a new patch once one has been found. A greater understanding of the behavioral basis of dispersal within an insect–plant system will improve our ability to predict and possibly influence community dynamics. Such understanding is critical in biological control systems, where success of a natural enemy depends on establishment, impact on the target host before dispersal, and ability to move through a varied landscape and locate and colonize host patches interspersed in the nonhost matrix.

Here we explore the behavior of the specialist weevil, *Rhinoncomimus latipes* Korotyaev (Coleoptera: Curculionidae), which was introduced into North America in 2004 for biological control of the invasive plant, mile-a-minute weed [*Persicaria perfoliata* (L.) H. Gross (Polygonaceae); Colpetzer et al. 2004; Hough-Goldstein et al. 2009, 2012; Lake et al. 2011)]. Previous work on *R. latipes* dispersal and host-finding has shown that these small (≈2 mm long) weevils are able to navigate obstacles in the landscape including streams, tree lines, and hayfields, locating both large mile-a-minute infestations and isolated patches (Lake et al. 2011). Weevils dispersed at an average rate of 1.5–2.9 m/wk after initial release in mostly contiguous patches of mile-a-minute (Lake et al. 2011) and at 4.3 km/yr by 1–3 yr after release in the broader landscape (Hough-Goldstein et al. 2009). Within an experimental array, weevils readily found *P. perfoliata* plants in a matrix of bare ground and nonhost plants (Frye et al. 2010), with 6% of weevils locating *P. perfoliata* plants within 3 h, and 20% by 2 d after release. Although not the focus of the experiment, the study by Frye et al. (2010) also showed that *R. latipes* primarily disperses during daylight hours.

We know that this insect is highly capable of finding its host, but do not know the relative importance of walking versus flight, whether weevils walk or fly in a specific direction (e.g., compass direction, relative to presence of host plants, relative to matrix habitat, up or downwind, or toward or away from the sun); or the importance in host-finding of navigation cues or reluctance of the insect to enter certain habitats. This

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Table 1. Sites where weevils were released and the numbers of weevils observed flying in different directions, 2011

Release site	Coordinates of release site	Direction of open field	Morning sun on cage	Wind direction (from, to)[a]	Number of weevils observed flying toward:				Total
					Left	Open	Right	Forest	
Ecology Woods	39° 39′51″ N 75° 44′35″ W	East	Full sun	Right, left (N-S)	46	59	49	2	156
Webb Farm	39° 40′24″ N 75° 44′10″ W	Northeast	Sun, then shade	Right, forest (N-S)	26	8	4	0	38
Rittenhouse	39° 39′28″ N 75° 45′37″ W	Northwest	Shade, then sun	Left, forest (NE-SW)	4	11	1	1	17
Laird	39° 41′30″ N 75° 45′31″ W	Southeast	Shade	Forest, left (N-S)	0	1	1	0	2
Coverdale	39° 41′42″ N 75° 44′07″ W	Southwest	Shade	Left, right (NW-SE)	0	0	0	0	0
				Total	76	79	55	3	213

[a] Left and right when facing the forest from the open field.

insect is positively phototactic (Smith and Hough-Goldstein 2012) and generally is found in greater abundance on plants growing in sun than in shade (Hough-Goldstein and LaCoss 2012). Full sun is also the most favorable condition for host plant growth and reproduction (Hough-Goldstein 2008).

In this experiment we conducted replicated releases of large numbers of weevils from the edge of woodlots at five sites, observing the insects' behavior as they initially dispersed by flight, and then tracking their arrival at potted host plants arrayed along the wooded edge, out into the open field, and into the forest. The objectives were, first, to determine if there was directionality to *R. latipes* initial dispersal, with flight rather than walking encouraged by forcing weevils to climb a vertical structure before dispersing; and second, to determine the extent of weevil colonization of host plants located at different distances and within three habitat types: the forest edge, open field, and forest interior. A follow-up study tracked weevil colonization of plants in the forest edge habitat versus the open field when weevils were released in the open field adjacent to a forest edge.

Materials and Methods

Five thousand weevils were sent by overnight courier from the Phillip Alampi Beneficial Insect Laboratory, Trenton, NJ, where *R. latipes* has been reared since 2004 (Palmer et al. 2008), arriving the morning of 3 June 2011. These weevils had been collected from rearing containers between 23 May and 1 June, and held on *P. perfoliata* potted plants before shipping. One thousand weevils were placed in each of five white plastic 19-liter buckets with the center of the top cut out, leaving only the snap-on rim. A cone-shaped piece of netting material (white polyester with a mesh of ≈10 by 8 per cm^2; BioQuip Products, Inc., Gardena, CA) was sewn with a single seam, with a small opening (≈2.5 cm in diameter) left at the top. The bottom of each fabric cone was anchored to the bucket by the snap-on rim. A wooden dowel (1.2 m in length,1.5 cm in diameter) was placed in the center of each bucket, into an empty plastic pot (15 cm in diameter, 14.5 cm in depth), and anchored by two mini elastic cords (25 cm in length) wrapped around the dowel and hooked into small holes drilled in the sides of the bucket. The top of each fabric cone was stapled to the top of the dowel, and secured by a Velcro tie wrapped around the top of the dowel, closing off the opening. White sand was poured around the empty pot, up to the level of the top of the pot. A single potted *P. perfoliata* plant, ≈4 wk old, was placed in the empty pot in each release cage, and the weevils were shaken and brushed onto the plants. The next day, on 4 June, each of these plants was cut at its base, to initiate desiccation so deteriorating host plant quality would encourage dispersal at the time of field release. The cages were kept in the laboratory next to a window until 6 June, when they were taken out to the field for release.

Each cage was taken to a wooded edge of one of five fragmented forest sites in Newark, DE. The five sites varied in the compass orientation of the edge relative to the forest, sun exposure in the morning, and predominant wind direction relative to the edge (Table 1). The distance between release sites ranged from 0.8 to 3.8 km. Vegetation in the open field consisted of mowed grass except for the Ecology Woods, which was bordered by dense tall forbs, and the Rittenhouse site, which had sparse tall grass and forbs. The Laird site open area had mowed grass at 2 and 6 m and tall unmowed grass at 14 m. All five sites were free of *P. perfoliata* in the immediate vicinity of the experiment. To assure that they were isolated from other weevil populations, a sentinel mile-a-minute plant was placed at each release site on 2 June, collected on 3 June, and checked for presence of weevils or feeding damage. All sentinel plants were free of weevil activity except for the plant at the Ecology Woods site, which had one weevil and minimal feeding damage on one terminal. An area encompassing a 0.8-km radius surrounding this site, on the University of Delaware Farm, had been searched intensively for *P. perfoliata* in 2009, and none were found (Frye et al. 2010). Therefore, we believe that the single weevil found here originated from a nearby greenhouse, where other experiments had been conducted, rather than being part of a field population.

Twelve potted mile-a-minute plants also were transported to each site on 6 June 2011. The plants were grown from seeds collected locally the previous October, left at room temperature for 3 wk, and then mixed with moist peat moss and placed in a refrigerator at 4°C until they were planted, on 5 or 12 May 2011. Once they had germinated, seedlings were transplanted into 15-cm-diameter plastic pots in MetroMix 510 (Sun Gro Horticulture, Bellevue, WA). All plants selected for use were approximately the same size on 6 June. At each site, plants were placed at intervals of 2, 6, and 14 m from the central release cage along the edge of the woods in either direction from the release site, and at the same intervals perpendicular to the edge, running into the woods and into the open area directly out of the woods.

One observer set up each of the five arrays, and at ≈0930 hours each observer removed the Velcro tie from the top of the release cage so the weevils could emerge from the fabric cone at the top of the dowel. Observers watched the weevils as they emerged and tallied those that flew from the cage, recording the direction that they flew in, either toward the left or right edge (relative to the position of the release cage while facing the forest); toward the open field; or toward the forest. Observers also recorded the predominant wind direction and estimated wind speed (based on visual clues: NOAA 2012), whether the release cage was in sun or shade (and if and when that changed during the observation period), and the direction of the sun in the sky relative to the forest edge. Observers were careful not to block the weevils' view of the sky or sun, and minimized movement around the cages. Weevils were observed for 1 h at Ecology Woods and for 1.5 h at the other four sites. At one of the sites (Webb Farm) weevils were recorded with a digital video camera as they emerged from the release cage and took off.

On the afternoon of the release day and on each of 4 d thereafter between ≈1400 and 1600 hours, all potted plants at each site were examined, the number of weevils present on each plant was counted, and feeding damage was assessed for each plant by using a scale of 0–5 [0, none; 1, low (holes in a few scattered leaves); 2, medium-low (holes in about half the leaves); 3, medium (holes in many leaves); 4, medium-high (holes in most leaves); 5, high (extensive damage on most leaves)]. After weevil counts and damage assessments, each plant was watered thoroughly. Three days after release, all five flight cages were sealed at the top with a Velcro tie and returned to the laboratory, where remaining live and dead weevils were counted.

The release day and subsequent 4 d were sunny, with a brief rain storm in the late afternoon of d 3 only. The temperature at the time of release was 21.5°C (for the Newark, DE Ag Farm Station, 0900–0959 hours), increasing to 26.6°C in the afternoon (1400–1459 hours) when weevils first were counted (DEOS 2012). It was considerably warmer on the subsequent 3 d when plants were revisited, with maximum daily temperatures ranging from 30.4 to 35.3°C.

A follow-up study was conducted in June 2012 using similar methods, except that the release cages were located in the open field 12 m from the forest edge. In total, 10 trap plants were deployed at each site, five along the forest edge, and five parallel to the forest edge but with the center plant 12 m away from the release cage, directly out into the field. Plants in each row were 6 m apart. The same sites were used as in 2011, except the Webb Farm site, which did not have a sufficiently large open field, and was replaced by a site in White Clay Creek State Park (39° 42′37″ N, 75° 46′04″ W), where the open field consisted of an unmowed meadow facing west from the forest. Plants were grown from cuttings (Palmer et al. 2008), and were 7 wk old when placed in the field. Five hundred weevils were released at each site at 1000 hours on 8 June 2012, and the directions of initial flights were tallied for 1.5 h by five different observers, as in 2011. Plants were checked for weevils and feeding damage each afternoon for 9 d, except for the fourth day, when >6 cm of rain fell. The temperature on the release day was 22.8°C at 0900–0959 hours, increasing to 27.2°C by 1400–1459 hours. Maximum daily temperatures during the next 8 d ranged from 22.1 to 33.1°C, with very little rain aside from the fourth day. Release cages were flooded by the heavy rain on day 4, and therefore it was not possible to determine how many live and dead weevils remained in the cages in 2012; however, few weevils remained in the cages by day 3.

Statistical Analysis. For 2011, the numbers of weevils and damage scores recorded 3 d after release at different distances (2, 6, and 14 m) and on potted plants within different habitats (in the open field, along the forest edge, and within the forest) were compared using a factorial analysis of variance, with distance and habitat treated as fixed effects and site treated as a random blocking factor (PROC MIXED of the SAS system, version 9.2). Both weevil counts and damage scores were transformed by square root (x + 1) before analysis to improve normality and homogeneity of variances; original means and SEMs are shown in graphs. The LSMEANS statement with the Tukey–Kramer adjustment was used to compare the individual treatments, and the Kenwood–Roger procedure was used to approximate degrees of freedom (Littell et al. 2006, SAS Institute 2008). For 2012, the proportion of weevils at each site that flew during the first 1.5 h in each of four directions with respect to 1) the forest edge, and (2) the direction of the sun in the sky, were compared using PROC MIXED with flight direction as a fixed factor and site as a random factor. Proportions were arcsine-square root transformed before analysis, because some were <0.30 (Snedecor and Cochran 1980). The number of weevils and damage scores [transformed by square-root (x + 1)] on plants at the forest edge versus those out in the open field 8 d after release were compared, again using PROC MIXED with habitat treated as a fixed factor and site as a random factor.

Table 2. Weevils remaining in cages when removed from the field after 3 d, and numbers of weevils that reached any *P. perfoliata* plant over 4 d, 2011

Release site	Number of weevils in cages at 3 d			Number of weevils that reached any plant				
	Live	Dead	Total	5 h	1 d	2 d	3 d	4 d
Ecology Woods	16	18	34	71	159	127	158	151
Webb Farm	30	13	43	31	226	286	289	236
Rittenhouse	12	25	37	55	116	148	179	159
Laird	34	21	55	25	192	263	270	235
Coverdale	31	16	47	15	80	133	143	147
Mean no. (%)[a]	24.6 (2.5)	18.6 (1.9)	43.2 (4.3)	39.4 (4.1)	154.6 (16.2)	191.4 (20.0)	207.8 (21.7)	185.6 (19.4)

[a] For weevils remaining in cages, percentage out of 1,000; for weevils that reached any plant, percentage out of the number that left the cages.

Results

In 2011, the numbers of weevils that flew during the first 1–1.5 h after the tops of the cages were opened varied greatly from site to site (Table 1). The most flights were observed at the Ecology Woods site, which was in full sun throughout the observation period. The Webb Farm site, which was initially in sun but mostly shaded by the end of the observation period, had the second most flights. The Rittenhouse site had few flights at first when it was in shade, but once the cage was in sun weevils started to fly. Very few flights were observed at the Laird or Coverdale sites, which were shaded throughout the observation period (Table 1). Before taking off, many of the weevils that were video-recorded at the Webb Farm site were seen to straighten and extend their front pair of legs while still in contact with the substrate, elevating the head and tip of the rostrum (video available in Supplemental Material, Supp. Video S1). This behavior was observed at the other sites where weevils flew as well.

At the three sites where weevils were observed to fly, they predominantly flew either away from the forest toward the open field (Ecology Woods and Rittenhouse) or toward the direction of the sun in the morning sky (toward the left forest edge [facing the forest] at the Webb Farm site; Table 1). Only three of the 213 weevils that were observed taking off flew in the direction of the forest. The direction of flights was not related to the direction of the prevailing wind, a light to gentle breeze (estimated at 1.8–5.4 m/s), generally moving from north to south at each site, which translated into different directions relative to the right, left, open, and forest direction at the different sites (Table 1).

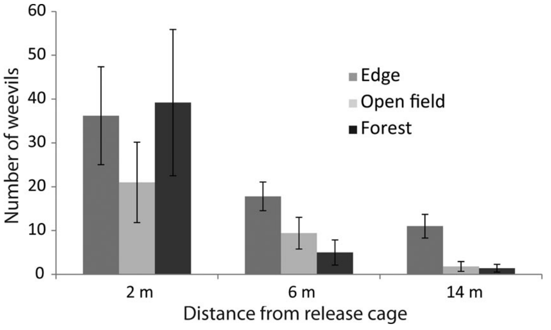

Fig. 1. Mean (±SEM) number of weevils that colonized plants at different distances from the release cage and in different habitat types at five sites, 3 d after release, 2011.

Approximately 4% of the 1,000 weevils at each site failed to exit the release cages during the first 3 d in 2011 (Table 2). Of those that dispersed from the cages, an average of 4% reached *P. perfoliata* plants in the first 5 h, and this increased to 22% by day 3 (Table 2). By day 3 some plants had substantial feeding damage, and the overall number of weevils counted on plants was somewhat lower on day 4 than on day 3 (Table 2).

Weevils were not evenly distributed on the potted plants. On day 3, when most sites had accumulated the maximum number of weevils, both distance from the release cage and habitat where plants were located had a significant effect on weevil numbers and feeding damage, with no significant interaction (Figs. 1 and 2; Table 3). Overall, more than twice as many weevils were found on plants 2 m from the release cages as on plants at 6 m (differences of LSMEANS from PROC MIXED: $t = 3.81$, approximate df = 51, $P = 0.0011$) and more than five times as many were at 2 m compared with plants at 14 m ($t = 5.64$, df = 51, $P < 0.0001$). The overall number of weevils at 6 m was not significantly different than at 14 m ($t = 1.82$, df = 51, $P = 0.1719$;

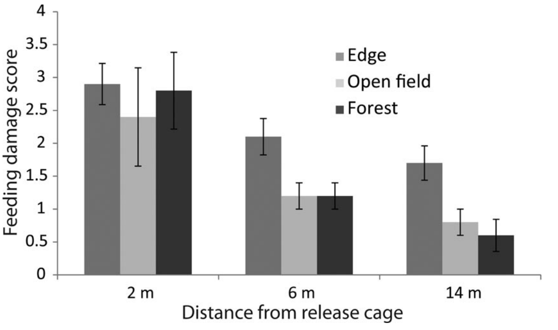

Fig. 2. Mean (±SEM) feeding damage scores (0, none; 1, low [holes in a few scattered leaves]; 2, medium-low [holes in about half the leaves]; 3, medium [holes in many leaves]; 4, medium-high [holes in most leaves]; 5, high [extensive damage on most leaves]) for plants at different distances from the release cage at five sites and in different habitat types, 3 d after release, 2011.

Table 3. Results of analysis of variance (PROC MIXED) for effects of distance and habitat on 1) number of weevils colonizing and 2) feeding damage recorded on plants at different distances and located in different habitats 3 d following release, 2011

Effect	DF	*F*	*P*
1) Number of weevils			
Distance	2, 51	16.56	**<0.0001**
Habitat	2, 51	4.41	**0.0170**
Distance*habitat	4, 51	1.07	0.3830
2) Feeding damage			
Distance	2, 47	22.12	**<0.0001**
Habitat	2, 47	7.87	**0.0011**
Distance*habitat	4, 47	1.01	0.4116

Tests conducted on square root $(x + 1)$ transformed weevil counts and damage scores.

Fig. 1). Similar results were found for feeding damage scores, with more damage at 2 m compared with 6 or 14 m ($t = 4.36$, df = 47, $P = 0.0002$, and $t = 6.53$, df = 47, $P < 0.0001$, respectively) and marginally greater at 6 m than at 14 m ($t = 2.17$, df = 47, $P = 0.0878$; Fig. 2).

Overall there were marginally or significantly more weevils and more feeding damage on plants located in the edge habitat compared with those located either within the forest ($t = 2.16$, df = 51, $P = 0.0883$ for weevils; $t = 3.13$, df = 47, $P = 0.0082$ for damage) or in the open field ($t = 2.64$, df = 51, $P = 0.0287$ for weevils; $t = 3.34$, df = 47, $P = 0.0046$ for damage). There was no difference in the number of weevils or feeding damage for plants in the open field compared with those in the forest interior ($t = 0.42$, df = 51, $P = 0.9070$ for weevils; $t = 0.18$, df = 47, $P = 0.9828$ for damage). On average, at the 14 m distance, six times as many weevils colonized the mile-a-minute plants along the edge than those placed in the open field and eight times as many weevils were found on the plants at the edge compared with plants placed within the forest (Fig. 1).

In 2012, an average of 143.2 ± 13.1 (mean ± SEM), or 28.6% of the 500 weevils in each release cage, flew at the five sites during the initial 1.5-h observation period. The weevils flew equally in all directions from the release point, with respect to both the direction of the forest edge ($F_{3,13} = 1.19$, $P = 0.3509$) and the direction of the sun in the sky ($F_{3,13} = 1.32$, $P = 0.3088$). Maximum colonization of the plants occurred 8 d after release, when 17% of released weevils had reached any plant (Table 4). On average, 1.6 times as many weevils colonized the plants in the edge habitat compared with the open field ($t = 3.04$, df = 42.1, $P = 0.0040$; Fig. 3). Feeding damage scores averaged 1.21 ± 0.22 overall, with no difference between plants at the forest edge and those in the open field ($F_{1,42} = 0.93$, $P = 0.3397$).

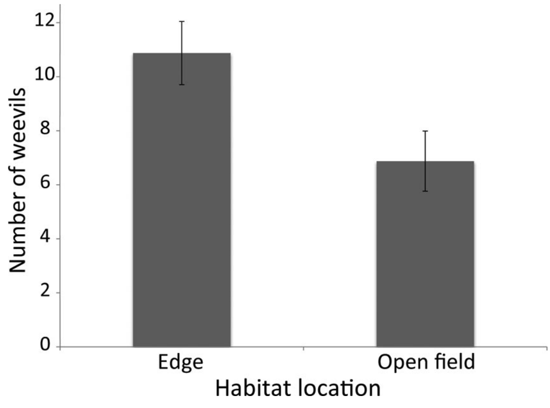

Fig. 3. Mean (±SEM) number of weevils that colonized plants in the open field and at forest edge at five sites, 8 d after release, 2012.

Discussion

In 2011, weevils initially took flight only at sites that were in full sun, or when sunlight first struck the release cage at the site that was initially in the shade. This pattern was probably primarily a temperature effect rather than an effect of sunlight per se, because in 2012 between one quarter and one third of the weevils flew during the 1.5-h observation period at all five sites. In 2011, the temperature at the time of release (21.5°C) was probably close to the minimum required for flight, but once sunlight contacted the small dark-colored weevils, their body temperature would have quickly risen high enough for flight to occur. In 2012, the temperature just before release was ≈22.8°C, suggesting that the minimum temperature for flight in this species is ≈22°C. Flight initiation has been shown to occur only above some minimum temperature for other insect species (Meyer 1982, Kjær-Pedersen 1992, Duan et al. 1998, Prokopy et al. 1999, Tansey et al. 2010), which is not surprising considering the intense metabolic requirements for flight in small poikilothermic organisms.

Table 4. Numbers of weevils that reached any *P. perfoliata* plant over 9 d, 2012

Release site	Number of weevils that reached any plant								
	5 h	1 d	2 d	3 d	5 d	6 d	7 d	8 d	9 d
Ecology Woods	12	51	68	100	110	117	143	141	127
Rittenhouse	40	74	90	100	78	104	101	106	99
Laird	4	18	27	25	26	32	29	44	44
Coverdale	8	17	15	21	32	36	35	46	50
White Clay Creek	29	44	83	89	90	83	100	93	98
Mean no. (%)[a]	18.6 (3.7)	40.8 (8.2)	56.6 (11.3)	67.0 (13.4)	67.2 (13.4)	74.4 (14.9)	81.6 (16.3)	86.0 (17.2)	83.6 (16.7)

[a] Percentage out of 500.

The direction of initial flight at the three sites where it was observed in 2011 was generally away from the forest edge or toward the sun, rather than either toward or away from the predominant wind direction or in some constant compass direction. In 2012, when weevils were released in the open field 12 m from the forest edge, initial flight direction was random with respect to either direction of the forest edge or direction of the sun in the sky. In the greenhouse, Smith and Hough-Goldstein (2012) found that in the absence of a host plant, *R. latipes* was strongly positively phototactic, moving from a central tube toward a cage in the sun rather than toward a shaded cage, even when the shaded cage contained a plant and the cage in the sun did not. Here, however, although weevils in 2011 flew away from the dark, shaded woods, in 2012 there was no definite orientation toward the sun. Because weevils were observed from 1000 hours until 1130 hours in 2012, it could be that the sun was close enough to apogee that no distinct direction was apparent to weevils taking flight. Prokopy and Owens (1983) noted that at early stages of host or habitat selection, insects perceive an overall difference in light intensity between the earth and sky, and may use the horizon line for orientation. In addition, polarized light patterns in the sky can provide stable orientation signals for flying (Prokopy and Owens 1983). Thus, *R. latipes* released without a host plant may simply opt for undirected, but straight-line movement by using light-compass orientation, as is common in insect dispersal flights (Johnson 1963, Atkins 1980, Jermy et al. 1988).

The fully extended, head-up stance observed before take-off may have indicated that weevils were assessing volatile host-plant cues. A similar behavior has been described for hard ticks, which climb a blade of grass or similar structure and wait for a passing host with their front legs outstretched. For ticks, such behavior is triggered by a variety of cues, and has been interpreted as host-seeking or questing behavior (Sonenshine 1993). Under equal light conditions, Smith and Hough-Goldstein (2012) found that *R. latipes* responded to host-plant cues, although their study did not clearly distinguish possible visual from chemical cues.

In 2011, more weevils were found on plants at 2 m than on plants at 6 or 14 m from the release site. Studies with other host-specific herbivores also have noted that host plants close to a release site are more likely to be found than plants farther away from the release (Kareiva 1985, Grevstad and Herzig 1997, De Clerck-Floate et al. 2005). In our study, an average of 4% of the weevils reached any plant 5 h after release, but this increased to 16% after 1 d and to a maximum of 22% by 3 d after release. In 2012, the weevils took longer to find any host plant, probably due in part to the cooler temperatures that year and in part to the greater distance of the plants from the release site, but by 8 d after release >17% had found a host plant. These percentages are comparable to those found in similar studies. For example, Kareiva (1985) found that ≈16–20% of *Phyllotreta* flea beetles released 2 m from a host plant patch found the plants within 1 d, but this percentage was reduced greatly when beetles were released further away or when the plants were surrounded by nonhost vegetation rather than bare ground. Grevstad and Herzig (1997) found that ≈17% of *Galerucella* leaf beetles found purple loosestrife host plants within 7 d when they were released 15 m from the host, but the percentage dropped and the time required to find a host plant increased at longer distances. With release distances of 25 m or more from host plants, percent recovery of host-specific herbivorous insects can be <5% (Jonsen et al. 2001, Dávalos and Blossey 2011).

The direction of initial flights observed in both 2011 and 2012 was not reflected in the numbers of weevils that ultimately colonized host plants placed in different habitats. In 2011, few *R. latipes* colonized plants placed within the forest at distances >2 m from the release cage. This is consistent with the weevils' known propensity to avoid host plants in the shade (Hough-Goldstein and LaCoss 2011, Smith and Hough-Goldstein 2012). In addition, the presence of understory shrubs and trees may have reduced the weevils' ability to move through the forest habitat, or masked host cues from plants deep in the forest. Similar reduced host-finding by specialist insects within complex or dense matrix (nonhost) habitat has been found for other species (Kareiva 1985, Jonsen et al. 2001, Dávalos and Blossey 2011).

A surprising result in our study was that more weevils colonized the plants placed at the edge of the woods compared with plants placed in the open field, in both 2011 and 2012. Based on our observations of initial dispersal flights in 2011, and the known positive response of weevils to sunlight, we expected more weevils to be found on the plants in the open field than in any other habitat. However, host-finding in both of these experiments occurred over several days' time, and probably resulted from a series of short flights plus walking after the initial flight from the release cage, with different cues used early and later in the host-finding process.

It is possible that orientation after the initial flight was in fact toward the edge habitat. *Persicaria perfoliata* occurs primarily in riparian areas in its native range (Hyatt and Araki 2006) and along the edges of forests in eastern North America (Lake et al. 2011). Therefore, *R. latipes* may have evolved a host-plant search strategy concentrated on edge habitats. Animals living on shorelines have been shown to orient parallel or perpendicular to the waterline, sometimes called y-axis orientation, to remain in the appropriate habitat (Warrant and Dacke 2010). Further research is needed to determine whether *R. latipes* orients in this way. It is also possible that in these experiments the potted plants in the open field were less desirable because they were more subject to drying (despite daily watering) and excessive heat, whereas those partially shaded by the forest edge may have provided a better habitat for the weevils.

Implications for Biological Control. *Persicaria perfoliata* in its North American range provides a very different environment for its host-specific herbivores than in Asia, where it is used heavily by a variety of herbivores (including human use in traditional medicine), and rarely has been reported as a noxious weed either in agriculture or in the environment (Ding et al. 2004). Dispersal and host-finding behavior by *R. latipes* probably evolved with relatively small and rare patches of *P. perfoliata,* whereas in eastern North America the plant currently exists in much larger areas of near-monocultures. Even in North America, however, the distribution of the plant is patchy, and the ability of *R. latipes* to move through the landscape and find new patches will be one key to its success in controlling its host. The current study suggests the weevil will move successfully to new patches along wooded edges, but may be less likely to locate isolated patches in the open or those embedded in forests. Alternate management strategies or human-assisted colonization may be necessary at such sites.

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