

Overwintering of annual bluegrass weevils, *Listronotus maculicollis*, in the golf course landscape

Maria Derval C. Diaz & Daniel C. Peck*

Department of Entomology, New York State Agricultural Experiment Station, Cornell University, 630 West North Street, Geneva, NY 14456, USA

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Abstract

Annual bluegrass weevil, *Listronotus maculicollis* (Dietz) (Coleoptera: Curculionidae), adults overwinter in protected areas but their life cycle is completed on highly maintained turfgrass. To better target control tactics on affected golf courses, we need to understand the relationship between overwintering and developmental habitats. Our objectives were to identify factors that influence overwintering site selection and to gather evidence of directional movement. Surveys of natural field populations were conducted in early spring over 2 years to test how abundance of overwintered adults depends on microhabitat (surface composition) and distance from the developmental habitat. The influence of microhabitat on overwintering preference and success was further tested in a multiple-choice and no-choice field experiment by relocating overwintering weevils into experimental arenas where four microhabitats were presented together or singly. The timing and direction of dispersal by walking adults was assessed using paired linear pitfall traps. Results showed that adults could overwinter up to 60 m from the fairway and 10 m into the woods. They were most abundant near the tree line; none were detected within 5 m of the fairway. Microhabitat had a significant effect on abundance in 1 year, being highest in mixed tree litter followed by moss, high-cut grass, and pine litter. Under multiple-choice conditions, high-cut grass was preferred over low-cut grass and leaf litter, followed by pine litter. Pitfall trap captures showed a peak of activity in the spring, and at one site this was directional toward the fairway. There was no directionality or increase in activity in the fall. Based on these results, a new conceptual model of flux between habitats is proposed based on orientation of flying adults to defined tree lines. Defining this behavior will strengthen our ability to target control tactics in space and time against this major turf pest.

Introduction

In golf courses of the northeast and mid-Atlantic, USA, the annual bluegrass weevil, *Listronotus maculicollis* (Dietz) (Coleoptera: Curculionidae), is a growing pest of high maintenance turf (Peck & Diaz, 2005). This native insect is most prevalent in annual bluegrass (*Poa annua* L.) (Poaceae), which is a major component of many golf course playing surfaces in those regions (Miltner et al., 2004). Females insert eggs between the leaf sheaths, early-instars feed within the stem, and later-instars drop down to feed on the crown (Cameron & Johnson, 1971). A single larva can damage up to 20 stems in the course of development (Cameron & Johnson, 1971). Adults feed on

grass blades but cause insignificant damage. Injury due to larvae is expressed as growing areas of yellow and brown patches, usually first noticed around the collar and perimeter of putting greens, tee boxes, and fairways. High populations will cause substantial areas of dead turf that affect the visual and functional quality of golf turf (Vittum et al., 1999).

Listronotus maculicollis is reported to overwinter as adults in protected areas separated from sites where feeding and development occur. Cameron & Johnson (1971) were first to report overwintering in fescue grass (*Festuca* spp.) and among leaves and debris under bushes and trees on or near golf courses. Vittum & Tashiro (1987) reported overwintering in the litter under trees such as oaks (*Quercus* spp.), maples (*Acer* spp.), and spruces (*Picea* spp.), but pointed to the litter of white pine (*Pinus strobus* L.) as

*Correspondence: E-mail: dp25@cornell.edu

a preferred site. Overwintering weevils were mostly recovered from the litter and the top layer (1 cm) of soil (Vittum & Tashiro, 1987).

In early spring, adults begin to move from overwintering sites to short mowed areas on the golf course such as fairways, tees, and greens (Vittum, 1980; Vittum & Tashiro, 1987; Rothwell, 2003). Greens are usually mowed at ≤ 3.5 mm, and tees and fairways at ~ 12 mm, and these playing areas are surrounded by rough at ~ 50 mm, sometimes set off by a border, or intermediate rough at ~ 20 mm. Aside from mowing height, various maintenance regimes based on fertilization, irrigation, and other cultural practices are conducted on these areas. Spring emergence thereby represents a transect of habitats, from overwintering sites in tree litter and other protected areas, through high-mown turf, toward developmental sites in short-mown turf. Field observations suggest that weevil migration is accomplished by walking (Vittum, 1980; Vittum & Tashiro, 1987). The earliest movement typically begins in late March, but many weevils are not active until early or mid-April (Vittum et al., 1999). Adults start to reappear at overwintering sites by late July (Vittum & Tashiro, 1987). In between spring immigration to, and fall emigration from, short-mown turf, *L. maculicollis* completes 1–3 generations (Vittum et al., 1999).

Control of the annual bluegrass weevil is largely based on applications of pyrethroid insecticides that target overwintered adults once they emerge in spring. It is recommended that this application should be timed according to plant phenological indicators, namely, between full bloom of *Forsythia spec.* and full bract of the dogwood *Cornus florida* L. If suppression is unsuccessful, second generation adults can be targeted for control around 4 July (Vittum et al., 1999). Despite these recommendations, applications may be made 2–5 times per season (McNeill et al., 1999). Pesticide resistance may be one reason for increasingly widespread control failures linked to pyrethroids (R Cowles, pers. comm.). As no other control alternatives are available, some golf course superintendents report that they remove pine litter in the fall (or even remove the trees themselves) hoping to reduce overwintering weevil populations (DC Peck, pers. obs.). There is no evidence that this cultural tactic is effective, however.

The current challenges of annual bluegrass weevil control highlight a need to better understand overwintering behavior and the flux of insects between overwintering and developmental habitats. We therefore sought to determine the factors that influence selection of overwintering sites by testing how well adults survive in different microhabitats, gauging how far from the fairways (developmental sites) they overwinter, and describing directional movement. Among other possibilities, this information may reveal

ways that control tactics might be targeted to ‘intercept’ the insects as they move in from overwintering sites to developmental sites, or as they leave for overwintering sites. Our first hypothesis was that *L. maculicollis* adults have preferences for overwintering habitat based on distance from the fairway (i.e., developmental habitat) and local microsite conditions (i.e., litter composition). Second, we predicted that movement of *L. maculicollis* between overwintering and developmental habitats is directional, occurring during a relatively brief window of time that coincides with warming spring temperatures after snow melt (immigration) and cooling fall temperatures after completion of the last generation (emigration).

Materials and methods

Site description

Studies were conducted on two golf courses in western New York with a known history of *L. maculicollis* infestation: the Onondaga Golf and Country Club (Fayetteville, Onondaga County, NY, USA; 43.0333°N, 76.0379°W) and the Robert Trent Jones golf course (Ithaca, Tompkins County, NY, USA; 42.4570°N, 76.4625°W). Maintenance practices at each course were similar. The rough areas were mowed once per week over late spring and summer. Fairways and intermediate roughs were mowed three times per week. In early spring and late fall (April and November), these areas were mowed as needed, fairways 1–2 times per week, and rough 1–2 times per month; the intermediate rough was not mowed after mid-October. Mowing heights were 12 mm for fairways, 32 mm for intermediate roughs, and 57 mm for roughs. Among the other relevant maintenance practices, fairways were fertilized in mid to late May with 6.1 g N m⁻², followed every 16 weeks with a slow release fertilizer. Insecticides were not applied to the fairways where we conducted this research. The irrigation schedule for the entire golf course was based on computer-calculated values of daily evapotranspiration (ET) from on-site weather station data.

In Fayetteville, we conducted our surveys on the No. 12 fairway that consisted of annual bluegrass (50%) and creeping bentgrass, *Agrostis stolonifera* L. (50%); intermediate roughs were annual bluegrass (20%), creeping bentgrass (20%), and perennial ryegrass, *Lolium perenne* L. (60%); and rough areas were annual bluegrass, Kentucky bluegrass, *Poa pratensis* L., and perennial ryegrass in similar proportions. In Ithaca, surveys were conducted on the No. 4 fairway that consisted of annual bluegrass (100%); intermediate roughs were annual bluegrass (80%), perennial ryegrass (10%), and Kentucky bluegrass (10%); and rough areas were annual bluegrass (50%) and fine fescue, *Festuca* spp. (50%).

Sample collection and extraction

To sample overwintering weevils, soil and associated litter or grass was collected using a 15-cm diameter turf mender (Par Aide®; Lino Lakes, MN, USA) to a depth of 10 cm. Extraction was done in a battery of modified Tullgren funnels located at the New York State Agricultural Experiment Station (NYSAES). Field samples were placed in individual plastic bags for transportation to the laboratory. Samples were placed grass/litter side down in funnels at room temperature. Each funnel (50 cm high, 28 cm top diameter) contained a 0.60-cm mesh screen to suspend the sample 18 cm from the top. A 40-watt bulb was used as a heat source mounted in a cover reflector placed on the top of the funnel. Adults were captured and preserved in plastic cups containing 70% ethyl alcohol. After 3–4 days, depending on moisture in the field samples, each cup was inspected for the number of *L. maculicollis* adults.

Microhabitat survey

In order to determine whether the abundance of overwintering adults varies with respect to microhabitat conditions, we conducted surveys on natural populations in early spring in 2005 and 2006. This was done in Ithaca, because the fairway was surrounded by a rough area that was relatively diverse in terms of surface substrates. Six blocks, separated from one another by >30 m, were demarcated in areas known to harbor overwintering *L. maculicollis* adults, and which included surface microhabitats of pine litter, moss, rough-mown grass, and a combination of pine and deciduous tree leaf litter. Two blocks were an exception in that pine litter was absent. Five samples, as described above, were collected from each of the microhabitat categories in each block. While we did not control for distance from the fairway, samples in each block were separated by ~0.5–3.0 m. Collection dates were 29 March 2005 and 13 March 2006. The specific dates were chosen based on when snow melt and soil thaw permitted sampling, and prior to the mobilization of overwintering adults.

Distance survey

In order to determine where *L. maculicollis* adults overwinter with respect to distance from the fairway, we conducted surveys of natural populations in early spring 2005 and 2006. This was done in Fayetteville, because the fairway was surrounded by a long stretch of relatively homogenous rough before a defined tree line. Six transects were laid out perpendicular to the fairway edge in areas where overwintering *L. maculicollis* adults were known to occur. At each designated survey site along the transects, five samples were collected as described above. These sites were located at 1 m into the fairway, center of the

intermediate rough (~1 m from the edge of both fairway and rough), 1 m into the rough, plus every 5 m up to the edge of the tree line. The number of sampling points therefore varied with the length of the transects, which were 42, 50, 52, 52, 57, and 62 m. In 2005, samples were collected on two separate dates (28 March and 4 April), because several sampling sites were still snow covered and frozen on the first date. This survey was repeated the following season on 13 March 2006, but unlike 2005, transects were continued past the tree line so an additional sample could be collected into the woods.

Choice experiment

In order to further establish the microhabitat preferences of overwintering adult *L. maculicollis*, we conducted a multiple-choice experiment. This test was performed twice on a Kentucky bluegrass plot at Cornell University's Bluegrass Lane Research and Turf Center in Ithaca, NY, USA, from 21 to 28 October and from 11 to 15 November 2005. Four different microhabitats were tested, and these were represented by cores collected using a lever action hole cutter (Par Aide®) with 11-cm diameter to a depth of 5 cm. Microhabitat cores were obtained from areas on the Robert Trent Jones golf course with no history of *L. maculicollis*. Cores representing pine litter microhabitat were taken from under a stand of white pine trees on the No. 11 fairway; deciduous tree leaf litter from the edge of a wooded area near the No. 6 tee; and fairway-mown and rough-mown grass from the No. 9 fairway. Litter composition was not measured but it was ~3-cm thick and included largely intact leaves from a mix of hardwoods that included *Acer*, *Carpinus*, and *Quercus*.

One core of each microhabitat type was randomly assigned to one of four locations in a 28-cm diameter and 13-cm tall cylinder arena (cut from a 19-l plastic bucket). Arenas had been pounded into the ground leaving a ~2.5-cm lip exposed. The Kentucky bluegrass inside the arena was stripped off before placing the microhabitat cores. Gaps between the round cores were filled with sand to level off the surface. A total of 10 arenas (replicates) were used.

Fifty adult *L. maculicollis* were released into each arena. These adults were previously extracted from several bags of leaf litter that had been collected from overwintering areas adjacent to the No. 4 fairway. To do that, we soaked a few handfuls at a time in a 7.5-l bucket filled with lukewarm water. When the weevils crawled up to the water surface, we collected them with soft forceps and stored them temporarily in 0.5-l plastic cups covered with screened lids. Adults were released into the experimental arenas within 24 h after collection.

To encourage settling and prevent escape of the adults after their release, each arena was covered with a cylindrical

wire screen cage (two layers of 0.1×0.2 cm mesh) that fit inside the exposed lip of arena. Cages were 10-cm tall and staked into the ground to resist wind. A piece of white tulle cloth (0.1×0.1 cm mesh) covered the cylinder, held in place with a rubber band. After 1 week, each microhabitat core was removed, and the adults were enumerated after extraction in Tullgren funnels.

No-choice experiment

In order to determine the overwintering survival of *L. maculicollis* in different microhabitats, we conducted an in situ no-choice experiment on 21 October 2005 in Ithaca. This time, arenas were cut from 15-cm diameter polyvinyl chloride (PVC) pipe to a height of 5 cm and inserted into the ground leaving a 1-cm lip exposed. Five arenas were set-up in each of the following microhabitats: (i) under white pine trees, (ii) at the edge of a deciduous wooded area, (iii) on fairway-mown grass, and (iv) on rough-mown grass. These sites were located at the same source areas described above in the choice experiment. Thirty *L. maculicollis* adults collected from overwintering areas were released into each arena and covered as previously described. The covers were removed on 30 November 2005 to ensure full exposure to ambient conditions. Each treatment was dug up on 13 March 2006, and the adults were extracted in Tullgren funnels to measure survivorship.

Timing of spring emergence

In order to determine the time of emergence of overwintering *L. maculicollis*, we conducted an experiment in Ithaca on 20 October 2005. Sets of three PVC arenas (as in the no-choice experiment) were installed along the tree line at six separate locations outside of the No. 4 fairway, for a total of 18 arenas. Arenas were separated from each other by 30 cm and sites were separated by ≥ 30 m. Thirty *L. maculicollis* adults were released into each arena and covered as previously described. The covers were removed on 30 November 2005. On 15 March 2006, two data loggers (WatchDog 100 Series Waterproof Button Logger®, East-Plainfield, IL, USA) were placed in the middle arena of each of the six groups. Held in place with a wire flag, one data logger recorded air temperature at the leaf litter surface while the other recorded soil temperature at a depth of 2.5 cm. On 28 March 2006, yellow sticky traps (Stiky Strips™, Medina, OH, USA) were placed around the inside circumference of the arenas to capture adults trying to walk from the overwintering site. The 8×12 cm sticky traps were cut in half and positioned to line the inside of the cylinders, with the sticky side facing into the ring. The sticky traps were replaced as needed and inspected daily to record when the weevils emerged in relation to site-specific air and soil temperatures.

Directional movement

In order to determine the timing and directionality of adult *L. maculicollis* movement over the season, we set up and monitored directional pitfall traps in Ithaca and Fayetteville. The traps were permanently established on the ground by 5 April 2005 to capture adults emigrating from overwintering sites to developmental sites on the fairway. The traps were 2 m long sections of 6.4-cm diameter PVC pipe with a longitudinal slit (0.6 cm wide) cut into the up facing side. One end of the pipe was sealed with a plastic cap while the other end led to a trapping device. The trapping device was made of a PVC pipe elbow with a removable fitting. On the bottom of the vertical element was a 0.2-l plastic cup with a screened bottom (0.1×0.1 cm mesh) and aluminium wire handle to contain and remove the captures.

Traps were installed in the field as follows. We dug a trench long enough to fit the entire apparatus and deep enough to position the slit at ground level. One end was dug deeper to fit the elbow with some extra space to handle the trapping device. We then placed the pipe in the trench and positioned it with enough incline to make rainfall run toward the trapping device. Then we filled soil back around it to cover all but the slit. The pitfall traps did not interfere with play, because they were not visible to golfers from a distance. Traps were set up side by side in pairs, parallel to the edge of the fairway. With this arrangement, one trap would largely capture adults walking from the tree line toward the fairway, while the other would largely measure surface movement in the opposite direction. In Ithaca, the distance of the six paired traps from the edge of the fairway and tree line was 6 and 26, 3 and 35, 6 and 21, 5 and 19, 5 and 26, and 7 and 25 m, respectively. Paired traps in Fayetteville were separated by 0.6 m to assuage concerns of the course superintendent. The distance of the paired traps from the edge of the fairway and tree line was 10 and 41, 12 and 10, 9 and 33, 13 and 23, 8 and 27, and 9 and 34 m, respectively. Captured beetles were removed daily throughout the season and the number of adults was assessed. We stopped checking the traps when no more weevils were found (21 September 2005 in Ithaca and 19 September 2005 in Fayetteville).

Statistical analysis

All statistical analyses were carried out using the statistical software package SAS (SAS Institute, 2001). In the microhabitat survey, the different overwintering substrates were analyzed by Poisson regression in PROC GENMOD (distribution = Poisson; link = log; type3; scale = Pearson; $\alpha = 0.05$) after transformation with $\log(x + 1)$. χ^2 analysis was used to test for an effect on the presence of weevils. Differences among the four substrates were then identified

with the least square means (LSMeans) separation test ($P < 0.05$). Because we suspected that variation in winter climate might influence mortality among the treatments in different ways, data were analyzed separately for each year.

In the distance survey, because transect length varied, sample sites were grouped into distance categories as follows: fairway edge (fairway, intermediate rough, and 1 m rough), near rough (5 to 20 m), far rough (>20 m and <tree line), tree line, near woods (≤ 5 m into woods), and far woods (>5 m into woods). A two-way analysis of variance (ANOVA, $P < 0.05$) was used to test for a significant effect of the distance groupings on the abundance of overwintering weevils, followed by LSMeans. Data were transformed with $\log(x+1)$. Due to similarity in patterns between years, data were pooled to simplify expression of the results.

In the choice experiment, the effect of the four overwintering substrates on the number of weevils recovered was analyzed by one-way ANOVA ($P < 0.05$) after transformation with $\log_2(x)$. Due to similarity in results between trials, data were pooled to simplify expression of the results. Differences among treatments were tested with LSMeans. In the no-choice experiment, the effect of microhabitat on the proportion of weevils recovered was analyzed by one-way ANOVA ($P < 0.05$) after transformation with $\log(x+1)$.

In the directional movement study, a paired t-test ($P < 0.05$) was conducted to identify differences in the total number of adults caught over the season approaching traps from the tree line side or the fairway side. A separate t-test was also done on the number of adults caught in each trap per week.

Results

Microhabitat survey

In the 2005 and 2006 microhabitat surveys, a total of 221 and 226 adult weevils were collected, respectively, for overall densities of 11/0.1 m². In 2005, there was no significant effect of microhabitat on the number of overwintering adults recovered ($\chi^2 = 2.04$, d.f. = 3, $P = 0.564$) (Figure 1). In 2006, however, there was a significant effect ($\chi^2 = 11.90$, d.f. = 3, $P < 0.0001$) of microhabitat. Significantly more weevils were recovered in the combined pine and leaf litter (25/0.1 m²) than all other substrates. Moss was second highest (10/0.1 m²), followed by grass and then pine litter. There was no significant difference between grass (6/0.1 m²) and pine litter (1/0.1 m²).

Distance survey

In the 2005 and 2006 distance surveys, a total of 35 and 301 adult weevils were collected, respectively, across the six transects. For both years, overwintering adults were absent

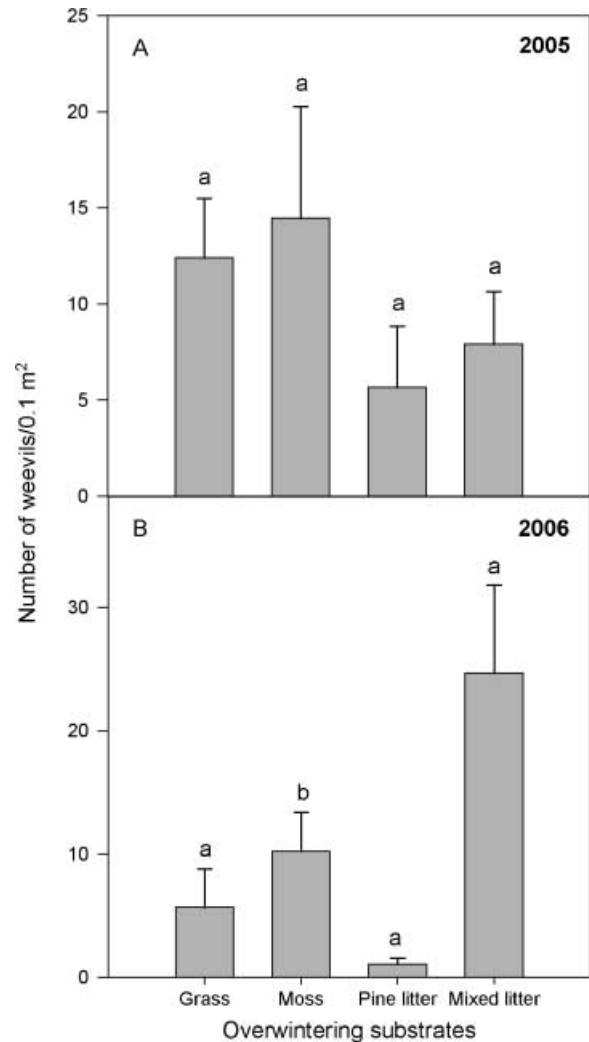


Figure 1 Number of overwintering *Listronotus maculicollis* adults (mean + SE) collected from four microhabitats surveyed in March (A) 2005 and (B) 2006, Ithaca. Columns capped with the same letter are not significantly different ($P > 0.05$). Mixed litter represents combined pine and leaf litter.

in areas sampled on the fairway, intermediate rough, and 1–5 m into the rough (Table 1; Figure 2). Weevils were recovered from 10 to as far as 60 m away from the intermediate rough, and as deep as 10 m past the tree line into the woods. There was a significant difference among distance groupings with respect to the number of overwintering adults collected ($F_{5,66} = 5.397$, $P = 0.0006$). Pairwise comparisons showed that significantly more weevils were recovered from the near woods than the fairway edge or near rough. However, the number of weevils recovered from the far rough, wood edge, and far woods was not significantly different.

Table 1 Percentage of *Listronotus maculicollis* adults captured from overwintering sites along six transects (A–F) at various distances from the fairway in late winter 2005 and 2006, Fayetteville

Distance from edge of fairway (m)	A		B		C		D		E		F	
	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006	2005	2006
–3 ¹	0	0	0	0	0	0	0	0	0	0	0	0
–1 ²	0	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	0	0	0	0	0	0
10	0	0	0	0	100	0	0	6.2	0	0	0	3.5
15	0	0	0	0	0	0	25	6.2	0	0	0	3.5
20	0	0	0	0	0	0.8	0	0	0	0	0	0
25	13.6	4.4	0	7.8	0	0	0	0	0	81.3	0	72.4
30	0	2.9	0	2.0	0	0	25	0	0	6.2	0	17.2
35	13.6	0	0	3.9	0	0	50	62.5	100	6.2	0	3.4
40	9.1	13.0	57.1	11.8	0	66.4	0	18.9	0	0	0	0
45	4.6	4.4	42.9	19.6	0	32.8	–	6.2	–	6.3	0	0
50	54.5	8.7	0	35.3	–	0	–	–	–	–	–	0
55	4.6	47.8	–	19.6	–	–	–	–	–	–	–	–
60	–	18.8	–	–	–	–	–	–	–	–	–	–
n (adults)	22	69	7	51	1	119	4	16	1	16	0	29

¹Fairway.²Intermediate rough.

Choice experiment

Weevil recovery rates were relatively low. In Trial 1, 39% (range 26–60) of the introduced weevils were extracted from the microhabitat cores, with 79, 45, 53, and 19 total individuals from rough-mown, fairway-mown, leaf litter,

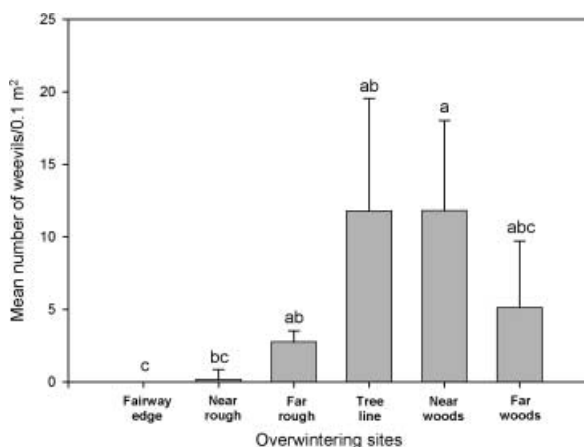


Figure 2 Number of *Listronotus maculicollis* adults (mean + SE) based on location with respect to overwintering habitat for pooled 2005–2006 data, Fayetteville. Location are as follows: fairway edge (fairway, intermediate rough, and 1 m rough), near rough (5–20 m), far rough (>20 m and <tree line), tree line, near woods (≤5 m into woods), and far woods (>5 m into woods). Columns capped with the same letter are not significantly different ($P > 0.05$).

and pine litter, respectively. In Trial 2, 18% (range 6–36) were recovered, with 54, 18, 11, and 5 individuals across the four treatments, respectively. Weevil preferences were significantly affected by overwintering microhabitat ($F_{3,61} = 8.48$, $P < 0.0001$). Pairwise comparisons showed that the number of weevils recovered from the rough-mown grass was significantly greater than the other microhabitats; pine litter was significantly lower than leaf litter but not fairway-mown grass (Figure 3).

No-choice experiment

Very few adults were recovered from the arenas after overwintering. Of the original 30 weevils introduced per arena, only 0–9 individuals were recovered. Percentage of recovery (mean ± SE) from rough-mown grass, fairway-mown grass, leaf litter, and pine litter microhabitats, respectively, was 10.0 ± 4.4 , 9.3 ± 3.8 , 11.3 ± 5.0 , and 10.7 ± 1.6 . There was no effect of substrate on overwintering survival ($F_{3,16} = 0.88$, $P = 0.503$).

Spring emergence experiment

The proportion of overwintering adults that emerged alive and were captured on sticky traps was very low. Only 18 adults, or 3% of the 540 introduced weevils, were recovered. Emergence of those adults occurred over 4 days. From 30 March to 2 April, a total of 4, 11, 2, and 1 weevils, respectively, were caught. No weevils emerged on any other date over the period of observation from 28 March to

7 May. The ambient temperature increased considerably at the week of emergence. The average soil/surface temperatures the week before, during, and after captures were 1.7/0.0, 5.7/9.5, and 4.2/3.2 °C, respectively.

Directional movement

Over the 2005 field season, 707 and 108 adults were collected from the linear pitfall traps in Ithaca and Fayetteville, respectively. In Ithaca, there was an overall significant difference in captures between the paired traps ($t = 5.30$, $P \leq 0.001$), where 44% of adults were caught approaching from the tree line vs. fairway (Figure 4). Most of that is attributed to the differences exhibited early in the sampling period. In week-2, representing the period of 10–16 April, 177 weevils were captured, 151 from the tree line and 26 from the fairway side ($t = 2.08$, $P = 0.051$). In week-3, representing 17–23 April, 178 weevils were captured, 146 from the rough and 32 from the fairway side ($t = 3.26$, $P < 0.0001$). This trend continued for the next 3 weeks but was not significant. After week-6, captures declined steadily and then increased in week-12 (19–25 June), followed by week-14 (3–9 July) and 15 (10–16 July). No weevils were caught from week-18 (31 July–6 August) to 19 (7–13 August). In week-20 (14–20 August) and 22 (28–31 August), weevils were caught from the fairway side alone. The last weevil was caught during week-22.

In Fayetteville, there was also an overall significant difference in captures between paired traps ($t = 2.88$, $P = 0.011$), but more weevils were captured from the fairway side. Week 6 had the highest number of captures, with a few more individuals from the fairway (24) than the tree line side (15) (Figure 4). From week-2 (10–16 April) until

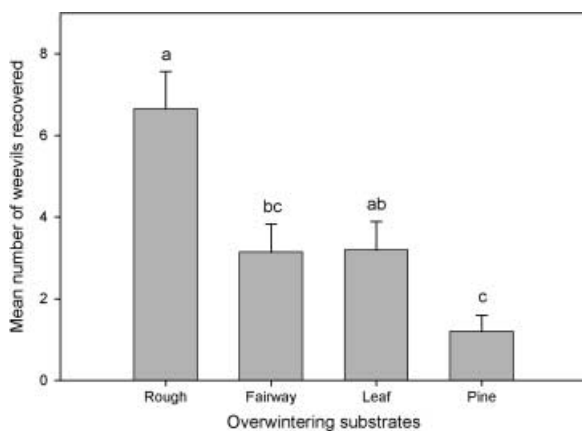


Figure 3 Number of *Listronotus maculicollis* adults (mean + SE) recovered from a multiple choice test for pooled data from two trials in fall 2005, Ithaca. In each trial, 10 arenas were infested with 30 weevils. Columns capped with the same letter are not significantly different ($P > 0.05$).

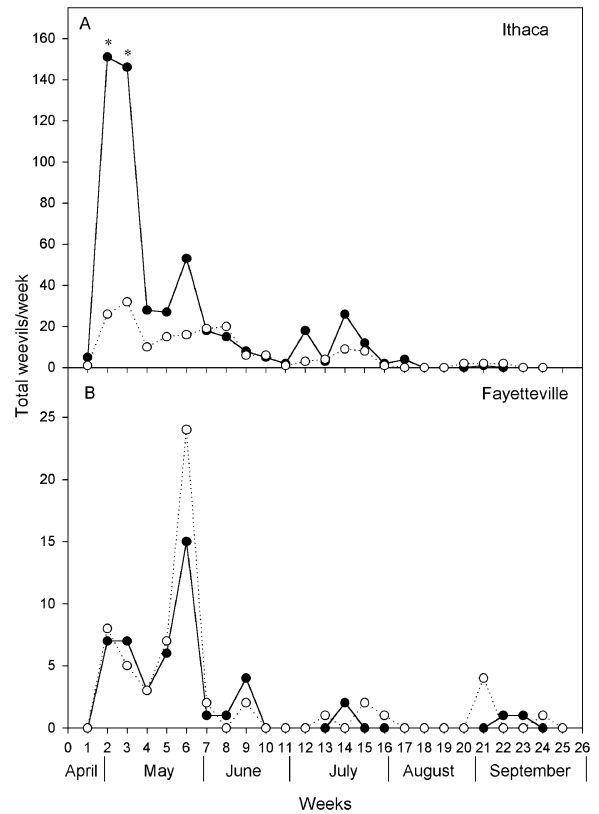


Figure 4 Total adult weevils collected weekly from linear pitfall traps from 5 April to 31 August 2005 in (A) Ithaca and (B) Fayetteville. Filled circles represent captures from the tree line side and open circles from the fairway side. Asterisks indicate significant differences in captures between paired traps according to week ($P \leq 0.05$).

week-9 (29 May 29–4 June), the number of captures was almost equal for both traps. There were no captures from week-10 to 12 (5–25 June) or week-17 to 19 (24 July–20 August). In week-21 (21–27 August), four weevils were caught from the fairway side alone. The last capture was week-24 (11–17 September) from the fairway side.

Discussion

Our 2-year distance survey showed that *L. maculicollis* seeks out overwintering sites near the tree line, at least in turf environments where woods form a visually distinct habitat feature. Some adults were found to overwinter as far as 60 m from the fairway, and up to 10 m past the tree line into the woods, indicating the magnitude of potential displacement. Nevertheless, this must be tempered by the possibility of adults arriving from closer areas. While *L. maculicollis* is considered to be most prevalent in short-mown turf, we do not know enough about its

developmental habitat requirements to gauge how rough-mown habitats contribute to population development.

Examples of similar patterns of displacement between habitats by overwintering adults are common among weevils. For instance, adults of the plum curculio (*Conotrachelus nenuphar* Herbst) tend to overwinter close to the edge of wooded areas adjacent to orchards (Lafleur et al., 1987), and the boll weevil (*Anthonomus grandis* Boheman) will overwinter along the tree line adjacent to cotton fields (Fye et al., 1959). Among other turfgrass insect pests, overwintering adults of the bluegrass billbug (*Sphenophorus parvulus* Gyllenhal) seek shelter in thatch, soil crevices, bark mulch, and leaf litter in September and October (Potter, 1998). Adults of the black turfgrass ataenius (*Ataenius spretulus* Haldeman) overwinter along the edges of wooded roughs or in woodlots adjacent to the golf course (Wegner & Niemczyk, 1981). In the case of the hairy chinch bug (*Blissus leucopterus hirtus* Montandon), adults seek protection in dense thatch, leaf litter, or similarly sheltered sites (Maxwell & McLeod, 1936).

With respect to microhabitat conditions, our results did not support the idea that pine litter is a preferred substrate. The supposition that white pine litter harbors and even attracts *L. maculicollis* populations is so prevalent among turfgrass managers that some practice pine litter removal in an attempt to suppress weevil damage (DC Peck, pers. obs.). In the extreme, tree removal has even been justified based on its potential to solve problems in areas of the course with consistent infestations. While early work has shown that weevil populations can be quite high under white pine trees, up to 1700/m² (Vittum & Tashiro, 1987), weevil abundance in other potential microhabitats was not thoroughly investigated for an explicit comparison. Results of our no-choice experiment revealed that adults were capable of overwintering under all microhabitat conditions we tested, but our choice experiments showed pine litter to be the least preferred microhabitat. Weevils preferred to settle in rough-mown grass, followed by a combination of pine and leaf litter and fairway-mown grass to overwinter. To understand their annual bluegrass weevil problems, golf course superintendents may do best to focus on defined tree lines, not white pine needle litter per se (Vittum et al., 1999), unless those pines comprise the tree line.

Our late winter surveys showed overwintering adults to be absent from the fairway, the intermediate rough, and up to 5 m into the rough. While this appeared to demonstrate that adults dispersed completely away from the main developmental sites to overwinter, this may not have been the case. The lack of adults in those areas could have been due to overwintering mortality. Although our no-choice studies were meant to reveal differential mortality across

microhabitat conditions, the data were inconclusive. The low recovery rates may have been caused by escape if adults became active once the cage was removed. This may have indeed been the case, given that the winter was comparatively warm, with 26 days in January, for instance, with temperature highs above -1.1 °C. Vittum (1980) is the only other research to date that bears on this issue, and those findings show most of the overwintering adults were recovered from semiprotected areas in the fall and only larval and pupal stages were found in the turfgrass in late fall.

Trap captures were highest in the spring, coinciding with the period when we anticipated mobilization of adults from overwintering sites to developmental sites. Some evidence was gathered in support of a window of directional *L. maculicollis* adult movement in the spring toward the fairway, but there was no evidence of a fall window of movement going back to overwintering sites. In the site where directional movement was documented (Ithaca), the week with the highest trap captures coincided with the first collections of adult weevils on the fairways as part of parallel population studies (Diaz, 2006). In the first week of trap captures (5–9 April), five adults were collected from pitfall traps, but none were detected on the fairway in the population surveys. But the following week, trap captures increased to an abrupt peak of 177 adults (10–16 April) and the first adults were detected on the fairway (12 April). Pitfall trap captures showed a relatively narrow window of weevil activity, suggesting some degree of synchrony in spring emergence. In contrast, Rothwell's (2003) pitfall trapping detected no such trend, probably owing to the fact that very few weevils were captured. The location of our pitfall traps was probably close to suitable habitat, as we collected such a high population of weevils early in the season.

While traps in both sites showed an early spring window of adult activity, directionality based on those captures was documented in Ithaca but not in Fayetteville. Besides overall size of the population, the other major difference between sites was that paired traps in Fayetteville were separated by ~0.6 m; those in Ithaca were side by side. We propose one scenario under which separated traps might not register directional movement. If weevils make short-distance flights away from overwintering areas, and then followed these by making explorative non-directional walks of <0.6 m, followed again by flight, we would not expect differential capture rates between traps. If an adult were to land in the gap between the two traps, then either trap would be as likely to capture them. This idea merits further investigation.

There are two explanations for why we did not detect weevils returning to overwintering sites. First, so few weevils were caught in the traps from late summer through

fall that this may have led to the absence of any detectable pattern indicative of directional movement. A second explanation is that adults might fly, rather than walk, to return to the overwintering sites. Cameron & Johnson (1971) and Vittum (1980) both reported that *L. maculicollis* is capable of flight. Cameron & Johnson (1971) reported two seasonal peaks in the proportion of adults with well-developed flight muscles. In early April, ~30% had developed vs. undeveloped flight muscles, coinciding with the period when weevils are moving into the developmental habitats. A similar incidence was observed during late June to early August when the new generation of adults had fully developed. Less than 10% of the population had fully developed wing muscles over the rest of the period from March to October. On the other hand, Vittum (1980) found 25% of the weevils with well-developed flight muscles in early June and mid August while wing muscle development was low (<5%) over the rest of the period of March to December. The high incidence in August coincides with the time when the weevils were observed to begin returning to overwintering sites. From late August to late September, the abundance of weevils in surveyed overwintering sites increased. The timing of muscle development in field populations supports the idea that weevils could fly back to overwintering sites beginning in late summer.

Based on our results, we propose the following conceptual model. In the late summer and fall, adults emigrate from developmental habitats and immigrate to overwintering habitats largely by flight. To accomplish this, they orient to defined tree lines as a broad visual cue. Once they reach the edge of the navigable horizon, they drop from the air column and settle into preferred microhabitats according to secondary cues related to composition of the substrate. A 'snow-fence effect' hypothesis was proposed by Fye et al. (1959) to explain similar behavior in the boll weevil (*Anthonomus grandis* Boheman). They showed that 90% of adults overwintered <55 m into the woods. Because weevils were recovered closest to the edge where tree and bush cover was greatest, they proposed that when adults fly into the woods they fall out on the far side of an intercepting tree or bush and remain there to overwinter. For *L. maculicollis*, this hypothesis would explain the prevalence of overwintering adults along the tree line as well as the lack of a window of directional movement on the ground. Dispersal by walking may be more prevalent in the spring among weevils that move from overwintering to developmental habitats.

There is a clear need to strengthen our results on the overwintering behavior of *L. maculicollis* in the golf course landscape. Studies of other factors that influence overwintering preferences should be conducted, including an emphasis on how the quality of different overwintering habitats affects survival. Temperature and soil moisture

influence the time of emergence of overwintering weevils and other beetles (Dixon et al., 1979; Parajulee et al., 1996; Raworth & Choi, 2001; Jo & Smitley, 2006) and might also be involved in overwintering site selection and survival. A more accurate prediction of when weevils emerge from overwintering habitats will be helpful in optimizing spring and early summer weevil control programs. Further investigation is also needed on potential approaches for suppressing *L. maculicollis* in its overwintering habitat before it reinvades susceptible turf. Cultural practices such as raking or removing litter along the edges of the woods might have a role in managing overwintering populations (Fye et al., 1959). Non-chemical alternatives such as fungal entomopathogens could also be evaluated for their potential (Parajulee et al., 1996).

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