

POPULATION ECOLOGY

Patterns of Variation in the Seasonal Dynamics of *Listronotus maculicollis* (Coleoptera: Curculionidae) Populations on Golf Course Turf

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ABSTRACT *Listronotus maculicollis* (Kirby) is a burgeoning pest of *Poa annua* L. in the northeast United States. To develop an understanding of its spatial and temporal association with golf course landscapes, we described the patterns of variation in certain population parameters across site (Fayetteville and Ithaca, NY), year (2004–2006), and management habitat (fairway, intermediate rough, rough). In weekly surveys along fairway transects, we sampled larvae (identified to instar) by soil core extraction and adults (identified to sex and maturation) by hand collection. Five instars were confirmed based on head capsule width measurements; there was no overlap among instars. Sex ratio was significantly male-skewed on the rough versus the fairway. Insect load, a measure of population size based on cumulative insect-days, varied from 3.0- to 18.5-fold across sites and years and averaged 8.7- and 8.0-fold greater on the fairway than rough for larvae and adults, respectively. Visual assessment of stage-specific population fluctuation curves revealed no divergence in adult males and females, i.e., no evidence of protandry. Variation was greater by year than by site in terms of overall shape of the fluctuation curves, relative abundance of overwintered to spring and summer adults, population synchrony, and number of generations (two to three). Evidence of bimodal spring generations showed that early season population synchrony may be linked to the pattern of adults transitioning from overwintering to developmental habitats. The magnitude of variation in population dynamics underscores the relevance of decision-making strategies and has implications for improving both the spatial and temporal targeting of intervention tactics.

RESUMEN *Listronotus maculicollis* (Kirby) es una plaga que va en aumento en *Poa annua* L. en el noreste de los Estados Unidos. Para desarrollar un conocimiento de su asociación temporal y espacial con el ecosistema de canchas de golf, se describieron los patrones de variación en ciertos parámetros poblacionales a través de sitio (Fayetteville e Ithaca, NY), año (2004–2006) y hábitat de manejo (fairway, intermediate rough, rough). En muestreos semanales a lo largo de los transectos del fairway, se muestraron las larvas (identificando el instar) por medio de extracciones de muestras de suelo, y los adultos (identificando el sexo y estado de maduración) por recolección a mano. Se confirmaron cinco instares basados en las medidas del ancho de la cápsula cefálica; no hubo traslape entre instares. La proporción de sexos fue significativamente sesgada hacia los machos en el rough versus fairway. La carga insecto, una medida del tamaño poblacional basado en días-insectos cumulados, varió de 3.0- hasta 18.5-veces más a través de los sitios y años, y fue en promedio 8.7- y 8.0-veces mayor en el fairway versus rough para las larvas y adultos, respectivamente. Una evaluación visual de las curvas de fluctuación poblacional específicas para cada estadio no reveló una divergencia en los adultos machos y hembras, i.e., no hubo evidencia de protandria. Hubo mayor variación al nivel de año que en sitio en términos de la forma de las curvas de fluctuación, abundancia relativa de los adultos hibernados versus los de la primavera y verano, sincronización poblacional y número de generaciones (dos a tres). Evidencia de generaciones bimodales en la primavera demostró que la sincronización poblacional temprana en la estación podría estar asociada al patrón de transición de los adultos desde el hábitat de hibernación hacia el de desarrollo. El magnitud de la variación en la dinámica poblacional subraya la relevancia de las estrategias de toma decisions, y tiene implicaciones para mejorar como se dirigen las tácticas de intervención en espacio tanto como tiempo.

KEY WORDS annual bluegrass weevil, *Poa annua*, population fluctuations, turfgrass

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Listronotus maculicollis (Kirby) is a damaging pest of highly maintained turfgrass in the northeastern United States. Often referred to as the “annual bluegrass weevil” or “Hyperodes weevil,” this insect was first reported causing injury to turfgrass in Connecticut as early as 1931 (Britton 1932). Until the last ≈ 25 yr, damage has been concentrated in southeastern New York. Severe infestations, however, are now being reported from all other states of the northeast, including Delaware, Maine, Massachusetts, New Hampshire, New Jersey, New York, Pennsylvania, Rhode Island, and Vermont (Vittum 1999, 2005, Vittum et al. 1999). The first damaging infestations in Maryland in 2002 (P. Shrewsbury, personal communication) and Ohio in 2007 (Koenig et al. 2008) represent the southern and western fronts, respectively, of the insect’s expanding range of impact in the Mid-Atlantic and north central United States. In Canada, the insect is also widespread in Ontario and Quebec (Simard et al. 2007). It is likely that the geographic area of impact will continue to expand in the near future.

Affected golf courses contend with an annual influx of adult *L. maculicollis* from overwintering sites to the short-mowed areas of the course where damage becomes most prevalent (Vittum and Tashiro 1987). Larvae and adults feed primarily on annual bluegrass, *Poa annua* L. (Vittum et al. 1999, Rothwell 2003). Biology on this host was described by Cameron (1970) and Cameron and Johnson (1971). Females lay eggs between the leaf sheaths. The early instars are stem borers while the later instars are largely crown feeders. A single larva can kill 10–20 stems over the course of development. Feeding injury caused by larvae is expressed as increasing areas of yellow and brown patches, usually first noticed around the collar and perimeter of playing surfaces such as putting greens, tee boxes, and fairways. High populations will cause substantial areas of dead turf that severely impact the visual and functional quality of golf course turf (Vittum and Tashiro 1987).

Poa annua has historically been considered a weed by golf course superintendents because it can easily invade newly seeded stands of creeping bentgrass (*Agrostis palustris* H.) (Miltner et al. 2004). When it becomes the dominant grass species in fairways and putting greens, however, superintendents resort to managing it rather than eliminating it. Currently, control of *L. maculicollis* largely depends on synthetic pyrethroid insecticides, which target overwintered adults in the spring (Vittum 1999, 2005). Timing of applications is recommended based on plant phenological indicators, usually the window between *Forsythia* V. full bloom and dogwood, *Cornus florida* L., full bract. Control of spring generation adults is recommended about the first week of July. Despite these guidelines, infested areas may be treated two to five times per season (McNeill et al. 1999). Although the commonplace reliance on multiple applications could be linked to insecticide resistance or risk-adverse management settings (Cowles et al. 2008), it also supports the idea that target populations are not being accurately predicted in space or time.

Our current understanding of the population ecology of *L. maculicollis* is limited and this probably interferes with best management practices (Peck and Diaz 2005). In terms of spring emergence, overwintered adults transition from hibernation sites and migrate toward the short mowed areas in approximately April. Overwintering occurs in protected areas along tree lines and in leaf litter away from playing surfaces, i.e., not in the developmental habitat on low-mown turf (Diaz and Peck 2007). In terms of voltinism, two generations a year are most commonly reported in the northeast, but it has been shown to vary from one to two in Quebec (Simard et al. 2007) and two to three in southeastern New York, Connecticut, and New Jersey (Vittum and Tashiro 1987, Vittum 1999, McGraw and Koppenhöfer 2007). In general, adults of the first generation emerge by the end of June or early July, whereas adults of the second generation are usually present during mid-August. Adults return to overwintering sites sometime in autumn. To date, the resolution of studies on population fluctuations has not permitted a detailed interpretation of phenology. Such an assessment would profit from studies that track population development over multiple seasons with respect to larval developmental stages.

The main objective of our study was to describe the seasonal fluctuations of *L. maculicollis* developmental stages on golf courses. In particular, we sought to gauge variation in certain population parameters from site to site, year to year, and across management habitats (fairway, intermediate rough, and rough). Results from this study—in terms of population fluctuations, number of generations, population size, and sex ratio—will help us assess if generalizations of population development gleaned elsewhere are broadly applicable to upstate New York and other regions where *L. maculicollis* is becoming a major pest. The results will also enable us to assess how the timing of populations might be better predicted for more efficient application of control tactics.

Materials and Methods

Site Description. Studies were conducted on two golf courses in western New York with a known history of *L. maculicollis* infestations: in Fayetteville at the Onondaga Golf and Country Club (Onondaga Co.; 43.0333° N, 76.0379° W) and in Ithaca at the Robert Trent Jones Golf Course (Tompkins Co.; 42.4570° N, 76.4625° W). General maintenance practices were similar on both courses. Over late spring and summer, rough areas were mowed once per week, whereas fairway and intermediate rough areas were mowed three times per week. In early spring and late autumn (April and November), mowing was done as needed, rough areas one to two times per month; fairways one to two times per week; the intermediate rough was not mown after mid-October. Mowing heights were 57, 32, and 12 mm for the rough, intermediate rough, and fairway, respectively. Among the other relevant maintenance practices, fairways were fertilized in mid- to late-May with 6.1 g N/m², followed every 16 wk with

a slow release fertilizer. Insecticides were not applied to the turf where we conducted this research. The irrigation schedule for the entire golf course was based on computer calculated values of daily evapotranspiration from on-site weather data.

In Fayetteville, we conducted our surveys on the No. 12 fairway in which grass composition (estimated by the superintendent) was annual bluegrass (50%) and creeping bentgrass (50%). The intermediate rough was annual bluegrass (20%), creeping bentgrass (20%), and perennial ryegrass (60%). The rough area was annual bluegrass, Kentucky bluegrass, and perennial ryegrass in similar proportions. In Ithaca, surveys were conducted on the No. 4 fairway that consisted of annual bluegrass (100%). The intermediate rough was annual bluegrass (80%), perennial ryegrass (10%), and Kentucky bluegrass (10%). The rough was annual bluegrass (50%) and fine fescue (50%).

Sample Collection and Processing. Three transects (A, B, and C) were laid out perpendicular to the length of each fairway. The length of the three transects were 45, 60, and 53 m in Fayetteville and 47, 52, and 43 m in Ithaca. The distance between transects A and B and between B and C, respectively, were 66 and 41 m in Fayetteville and 34 and 51 m in Ithaca. Thirteen survey points were demarcated along each transect and temporarily marked with a flag at the beginning of each survey. The first three sampling points were on the rough, \approx 4.0, 2.5, and 0.5 m away from the edge of the intermediate rough. The fourth sampling point fell in the middle of the intermediate rough. Four equivalent sampling points were marked on the opposite end of the transect. The last five sampling points were assigned to the fairway, \approx 0.5 m from the edge of the intermediate rough, in the middle of the fairway, and then two points half way between. Sampling points were designated the same way for each transect, but with the following exceptions. Because the definitive design had not yet been established, the number of sampling points varied from 14 to 16 per transect for the surveys done in Ithaca from 17 to 25 April 2004. In addition, surveys conducted before 9 May 2004 in Ithaca assessed transects on separate days. Therefore, the first complete survey was conducted over 22, 24, and 25 April, the second over 27, 28, and 30 April, and the third over 3, 7, and 8 May. For analyses, the sampling date was represented by the mean of the three sampling dates.

Adult surveys were conducted weekly. In Fayetteville, the survey period was 26 April to 27 September 2004, 11 April to 4 October 2005, and 10 April to 18 September 2006. Surveys were missed on three dates (24 May, 31 August, and 6 September 2004). In Ithaca, the survey period was 17 April to 25 October 2004, 5 April to 5 October 2005, and 28 March to 25 October 2006.

At each sampling point, adults were collected from a 0.25-m^2 area demarcated by a circular template (cut from a sheet of white corrugated plastic) laid on the ground. The template size was based on the area recommended by Vittum et al. (1999) when using soapy disclosing solution for scouting *L. maculicollis*

adults (range, 0.09–0.36 m^2) and matched the area used in populations studied by Simard et al. (2007). We mixed \approx 30 ml (two tablespoons) of lemon-scented liquid dish detergent in 8 liters of water and poured half of this solution over the area within the template. The soap in the mixture functioned as an irritant when it came in contact with the insects. After 2–5 min, the weevils ascended to the top of the foliage, where we collected them with an aspirator. The time spent checking for weevils at each sampling point depended on the density observed during the survey. Overall, it took \approx 30–60 min to conduct the surveys on each transect. Fayetteville surveys were generally conducted between 1000 and 1200 hours on Mondays when the golf course was closed for play. Ithaca surveys were generally conducted on Tuesdays between 0500 and 0700 hours before the golf course was open for play.

All collected weevils were placed in vials with 70% ethyl alcohol. These were transported to the laboratory to determine the sex (male or female) and maturation (callow or mature). Males were smaller than females and definitively distinguished by a median depression on the third abdominal sternite that is absent in the females. In the females, the same region has a slight bulge rather than a depression (Cameron and Johnson 1971, Vittum 1980, Vittum et al. 1999). Callow adults, recently emerged from the pupae, were reddish brown to brown in color, whereas mature adults were generally black.

Larval surveys were also conducted weekly in conjunction with adult surveys. In Fayetteville, the survey period was 17 May to 27 September 2004, 23 May to 4 October 2005, and 1 May to 18 September 2006. Surveys were missed on one date (6 September 2004). In Ithaca, the survey period was 18 May to 23 October 2004, 23 May to 5 October 2005, and 24 April to 25 October 2006. According to Rothwell (2003), larvae should be first expected in the field at 150–200 DD_(13.3°C) (degree day accumulation starting 1 March). We therefore initiated larval surveys the week of 150 DD_(13.3°C). At each sampling point, four 6-cm-diameter samples were removed with a turf-corer (Turf-Tec International, Coral Spring, FL) to a depth of 4 cm. Cores were placed in labeled plastic bags (1-gal size; Ziploc, Racine, WI) and transported to the laboratory. Each core was placed in a 133-ml cup (Fabri-Kal, Kalamazoo, MI) with a screened bottom (glued aluminum screen, 7.6 by 7.6-mm mesh size) and placed inside another cup (163 ml; Fabri-Kal) containing \approx 5 ml of glycerin to capture the larvae. Based on a protocol modified from Goldson (1978), developed to extract *Listronotus bonariensis* K. from ryegrass tillers, cups were placed in a growth chamber for 3–4 d at 30°C, which forced larvae out of the core, through the screen, and down into the glycerin. This method only allowed us to extract larvae and not the immobile pupae. For cores at water field capacity, 65, 77, and 96% of larvae abandon cores within 24, 48, and 76 h, respectively (M.S., unpublished data). Head capsule width of all larvae collected in 2004 and 2005 was measured to determine instar. Measurements were

Table 1. Total no. of *L. maculicollis* developmental stages collected during population surveys in two sites over 3 yr in New York

Developmental stage	Fayetteville			Ithaca		
	2004	2005	2006	2004	2005	2006
Larvae	301	157	846	823	542	1,169
Instar 1	102	48	343	247	38	302
Instar 2	66	25	166	202	104	264
Instar 3	56	37	141	185	122	290
Instar 4	44	24	107	129	143	219
Instar 5	33	23	89	60	135	94
Callow adults	26	32	5	155	160	78
Males	14	18	3	79	93	52
Females	12	14	2	76	67	26
Mature adults	541	334	170	3,915	1,205	1,955
Males	284	187	71	2,067	640	950
Females	257	147	99	1,848	565	1,005
Adult sex ratio (M:F)	1.11	1.27	0.73	1.12	1.16	0.97
Total individuals	868	523	1,021	4,893	1,907	3,202

done under 50 \times magnification using a binocular microscope fitted with an eyepiece reticle. Each larva was measured with the anterior portion of the head capsule facing upward. The greatest width across the head capsule was recorded.

Data Analysis. To establish the number of instars and identify all field-collected larvae to instar, a histogram was constructed from head capsule width measurements. Each instar was grouped by assigning a boundary at the lowest frequency between adjacent peaks. Mean and SE of width were calculated for each group. According to Dyar (1890), the head capsule width of holometabolous larvae increases geometrically by a ratio that is constant for a particular species. Therefore, the ratio of the mean head capsule width between instars was also calculated to make sure that no instar was overlooked. Five instars were previously described for *L. maculicollis* (Cameron and Johnson 1971). An effect of year and site on head capsule width was also tested with an analysis of variance (ANOVA) for each instar, given that a recent study showed differences in the size of adult *L. maculicollis* with respect to site and year (Simard et al. 2007). These analyses were conducted on all larvae collected in 2004 and 2005. Larvae collected in 2006 were assigned to instar by matching their head capsule width to the calculated ranges.

To describe patterns of variation in population parameters across sites and years, separate fluctuation curves were established for all the developmental stages sampled. For each site by year, weekly abundance was plotted against Julian date using data pooled across the three transects. Seasonal fluctuations were compared among sites and years by making a visual assessment of the overall shape of the fluctuation curves, including the timing and synchrony of population peaks and developmental stages. The total number of generations was interpreted from the superimposed fluctuation curves of the developmental stages. Sex ratio was assessed as the proportion of mature adult males to adult females; differences across years and sites were tested with ANOVA. Population size was assessed using an integrated technique based on cumulative insect-days (Ruppel 1983, Peck 1999).

The number of insect-days accumulated between two consecutive sampling dates was calculated as the product of the number of Julian days since the last survey and the average number of insects captured on the two dates. Unlike total number of captures, this approach is therefore a measure of population size, or insect load, that can be compared between two sites with a different number of sampling events. Finally, to describe patterns of variation with respect to habitat, we compared two parameters—population size and sex ratio—across the rough, intermediate rough, and fairway. All statistical analyses were conducted with SAS (SAS Institute 2001). All means are reported with their SE, range, and sample size.

Results

Material Collected. Over the course of this 3-yr study, the number of *L. maculicollis* developmental stages collected varied greatly between years and sites (Table 1). A total of 12,414 insects were captured and assessed. Among years, the total number of adults assessed varied from 1,539 (2005) to 4,456 (2004), and the larvae from 699 (2005) to 2,125 (2006). Between sites, there were 6.8 times more adults assessed in Ithaca than Fayetteville and 1.9 times more larvae. Early instars were more represented than late instars.

The head capsule width measurements confirmed five instars for *L. maculicollis* (Fig. 1). Differences were detected across years and sites, but these varied with instar. There was a significant effect of site for instar 1 ($F = 14.95$; $df = 3,416$; $P < 0.0001$), instar 3 ($F = 8.99$; $df = 3,392$; $P < 0.0001$), and instar 4 ($F = 8.32$; $df = 3,339$; $P = 0.0016$), but not for instars 2 or 5 ($3,412$; $df = 3,246$; $P > 0.05$). There was a significant effect of year for instar 3 ($F = 11.74$; $df = 3,392$; $P = 0.0007$) and instar 4 ($F = 11.13$; $df = 3,339$; $P = 0.0009$), but not instars 1, 2, or 5 ($df = 3,416$; $3,412$; and $3,246$; $P > 0.05$). Finally, there was a significant site \times year interaction term for instar 1 ($F = 5.45$; $df = 3,416$; $P = 0.020$) and instar 5 ($F = 4.48$; $df = 3,246$; $P = 0.035$), but not instars 2, 3, or 4 ($df = 3,412$; $3,392$; and $3,339$; $P > 0.05$).

Despite those differences and variation, the range of head capsule width measurements from pooled larvae

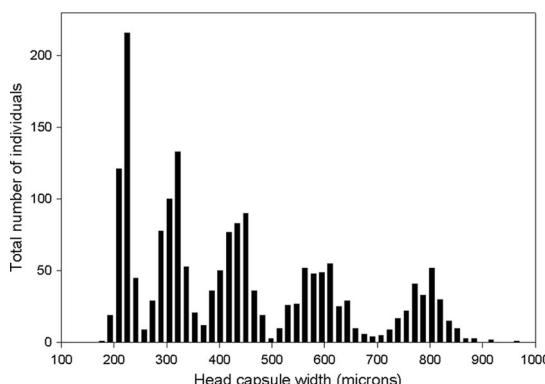


Fig. 1. Frequency distribution of head capsule widths of *L. maculicollis* larvae ($n = 1,823$) collected during population surveys in Ithaca and Fayetteville, NY, over 2004 and 2005.

was nonoverlapping among instars. Means of the head capsule width for instars 1–5 were 222 ± 0.72 (177–257, $n = 420$), 314 ± 1.05 (273–370, $n = 416$), 432 ± 1.33 (386–498, $n = 396$), 589 ± 2.04 (514–691, $n = 343$), and $791 \pm 2.61 \mu\text{m}$ (707–964, $n = 250$), respectively. The mean head capsule width ratio varied across instars 1–5 as 0.707, 0.727, 0.733, and 0.745, indicating that no instar was overlooked based on Dyar's rule of constant ratio between instars.

Sex Ratio. For combined years and sites, the overall sex ratio (male:female) of captured adults was 1.08, or 1.31 and 1.07 for the callow and mature adults, respectively. No effect was detected for site ($F = 0.206$; $\text{df} = 1,2$; $P = 0.69$) or year ($F = 4.498$; $\text{df} = 2,2$; $P = 0.18$). With respect to habitat, sex ratio varied in a consistent pattern across sites and years, whereby it was male-skewed outside the fairway. Precluding intermediate rough because of small sample size, there was a significant difference between fairway and rough habitats ($F = 6.18$; $\text{df} = 1,7$; $P = 0.042$). Mean sex ratio was 0.98 ± 0.03 (0.85–1.05, $n = 6$), 1.55 ± 0.30 (0.60–2.75, $n = 6$), and 1.57 ± 0.27 (0.38–2.33, $n = 6$) for the fairway, intermediate rough, and rough, respectively.

Population Size. Overall insect load, expressed in cumulative insect-days as a measure of population size, was 1.94- and 6.8-fold higher in Ithaca than Fayetteville for larvae and adults, respectively. Mean variation between sites ($n = 3$) was 2.1-fold for larvae and for adults. In Fayetteville, first-generation larval abundance was 1,817, 307, and 5,763 insect-days from 2004 to 2006. Adult abundance decreased each year from 4,127 to 2,242 to 1,188 insect-days. This translated to an 18.8- and 3.5-fold variation in insect load for larvae and adults, respectively, over the 3 yr of study. In Ithaca, first-generation larval abundance was 4,864, 2,237, and 7,854 insect-days, and adult abundance was 25,692, 8,432, and 13,799 insect-days. This translated to a 3.5- and 3.0-fold variation in insect load for adults and larvae, respectively, over the 3 yr of study.

When we examined insect load with respect to habitat, it varied in a consistent pattern across sites and years whereby it was far higher in the fairway. Pre-

cluding intermediate rough because of small sample size, there was significant difference in insect load between fairway and rough habitats for larvae ($t = 4.518$; $\text{df} = 5$; $P = 0.0063$) and adults ($t = 2.510$; $\text{df} = 5$; $P = 0.0539$). For larvae, overall insect load was 8.3- and 6.4-fold higher on the fairway than on the intermediate rough and the rough, respectively. Mean number of insect days were $3,512 \pm 800$ (946–5,965, $n = 6$), 424 ± 126 (42–928, $n = 6$), and 548 ± 171 (138–1,316, $n = 6$) for the fairway, intermediate rough, and rough, respectively. For adults, insect load was 8.1- and 9.2-fold higher on the fairway than on the intermediate rough and the rough. Mean number of insect days were $7,438 \pm 3002$ (860–19,670, $n = 6$), 914 ± 454.0 (94–3,034, $n = 6$), and 808 ± 415 (136–2857, $n = 6$) for the fairway, intermediate rough, and rough, respectively.

Population Fluctuations. When the population curves of mature adult males and females were assessed separately, they were almost indistinguishable for each site by year (Fig. 2). Protandry, i.e., the earlier appearance of males versus females, was not evident from a visual evaluation of the superimposed fluctuation curves. With respect to abundance, however, there were notable deviations on six specific dates. Despite similar sex ratios overall, female abundance was 1.5- to 2.3-fold greater on three dates of the second population peak in Fayetteville 2006, 1.5-fold greater in the main population peak in Ithaca 2005, and 1.1- and 1.3-fold higher in two of the four main peaks in Ithaca 2006. Given these results, male and female population curves were pooled to simplify the following analyses.

Based on a visual assessment, the superimposed population curves exposed variation across sites and years in terms of the timing and synchrony of abundance peaks and developmental stages, as well as the number of generations achieved. In 2004, both sites experienced a large spring (first) generation of *L. maculicollis*, followed by a small summer (second) generation (Fig. 3; Table 2). Adult weevils were already detected on the first sampling date at both sites, and their appearance in advance of larvae and callow adults showed them to be overwintered adults. Unlike Fayetteville, the curve in Ithaca showed no initial truncation so the surveys may have documented the arrival of the first immigrants. In Fayetteville, overwintered adults peaked on 10 May, and abundance remained relatively high through a second peak, after which it declined and ultimately transitioned from overwintered immigrants to local adults from the spring (first) generation (mature overwintered and local adults could not be physically distinguished). In Ithaca, overwintered adults peaked on 25 May and plateaued through 15 June before a decline. For both sites, instars 1–4 were also detected on the first sampling dates, leading to the truncated population curves that probably did not document their first appearance. Instar 5 was not detected until 1–2 June in both sites, followed by callow adults 20 d later. Both sites experienced a series of successive population peaks

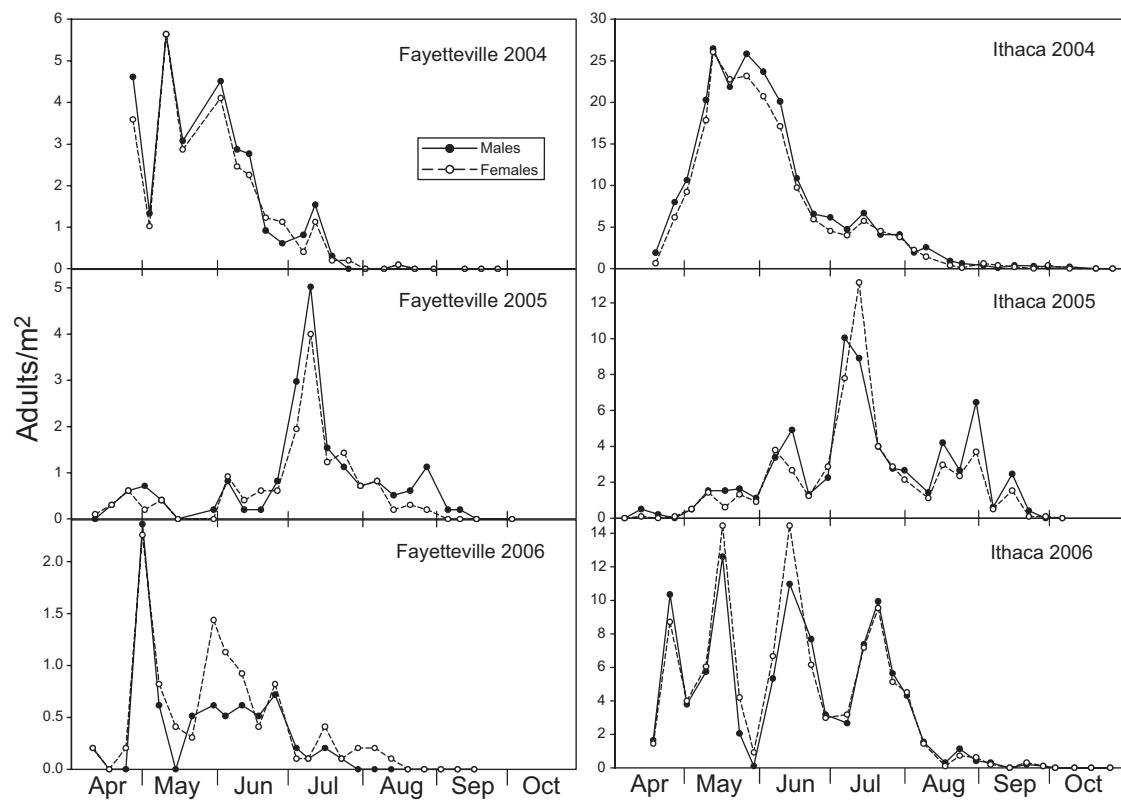


Fig. 2. Population fluctuation curves for male and female adult *L. maculicollis* collected during surveys in Ithaca and Fayetteville, NY, over 2004–2006.

that showed the spring generation. Gauged by the visual progression of developmental stages and the abruptness of population peaks, the development of the spring generation was relatively synchronous. There was a second peak of callow adults at both sites, each preceded by small secondary peaks of instars 1–5. These developmental stages confirmed the presence of a second generation, albeit relatively small compared with the first. No larvae were detected after the last peak of callow adults. In Ithaca, insects were last detected 52 d later than in Fayetteville.

In 2005, both sites experienced both a large spring and summer generation, followed by a smaller autumn (third) generation (Fig. 4; Table 2). Adult surveys began 1–2 wk earlier than 2004, but adults were already detected on the first sampling date in both sites. Larvae were also detected on the first sampling date in both sites. In contrast to 2004, the size of the overwintered adult population was far smaller relative to the size of local adult populations from the spring and summer generations. The major population peaks were attributed to adults of the spring generation and occurred in the middle of the season, not the beginning. In Fayetteville, the major peak of overwintered adults was 25 April, but this was followed by a secondary peak 42 d later. These gave rise to a series of successive peaks representing

instars 1–5 of the spring generation. In Ithaca, the spring generation initiated in a bimodal fashion coincident with an early and late group of immigrants that peaked 35 d apart. These cohorts produced an early- and late-arising spring generation that was apparent through instars 1–3 but could not be distinguished in instar 4 or instar 5. Callow adults of the spring generation peaked in the two sites on 5–6 July. After the first generation, each site experienced successive peaks that showed how the spring generation gave rise to larvae and callow adults of a summer generation, followed by a smaller autumn generation. Callow adults of the summer generation peaked 15–16 August. No callow adults were detected from the autumn generation. In Fayetteville, adults were last detected nearly a month later than 2004. In Ithaca, last detection was 16 d later than in Fayetteville.

In 2006, like 2004, both sites experienced a large spring generation followed by a small summer generation (Fig. 5; Table 2). A major difference, however, is that the spring generation was clearly bimodal. In Fayetteville, overwintered weevils were detected on the first sampling date, and these were aligned with a subsequent series of small peaks representing instars 1–3 and probably culminating in the first detection of callow adults on 31 May. The major peak of overwintered adults was aligned with defined peaks of another

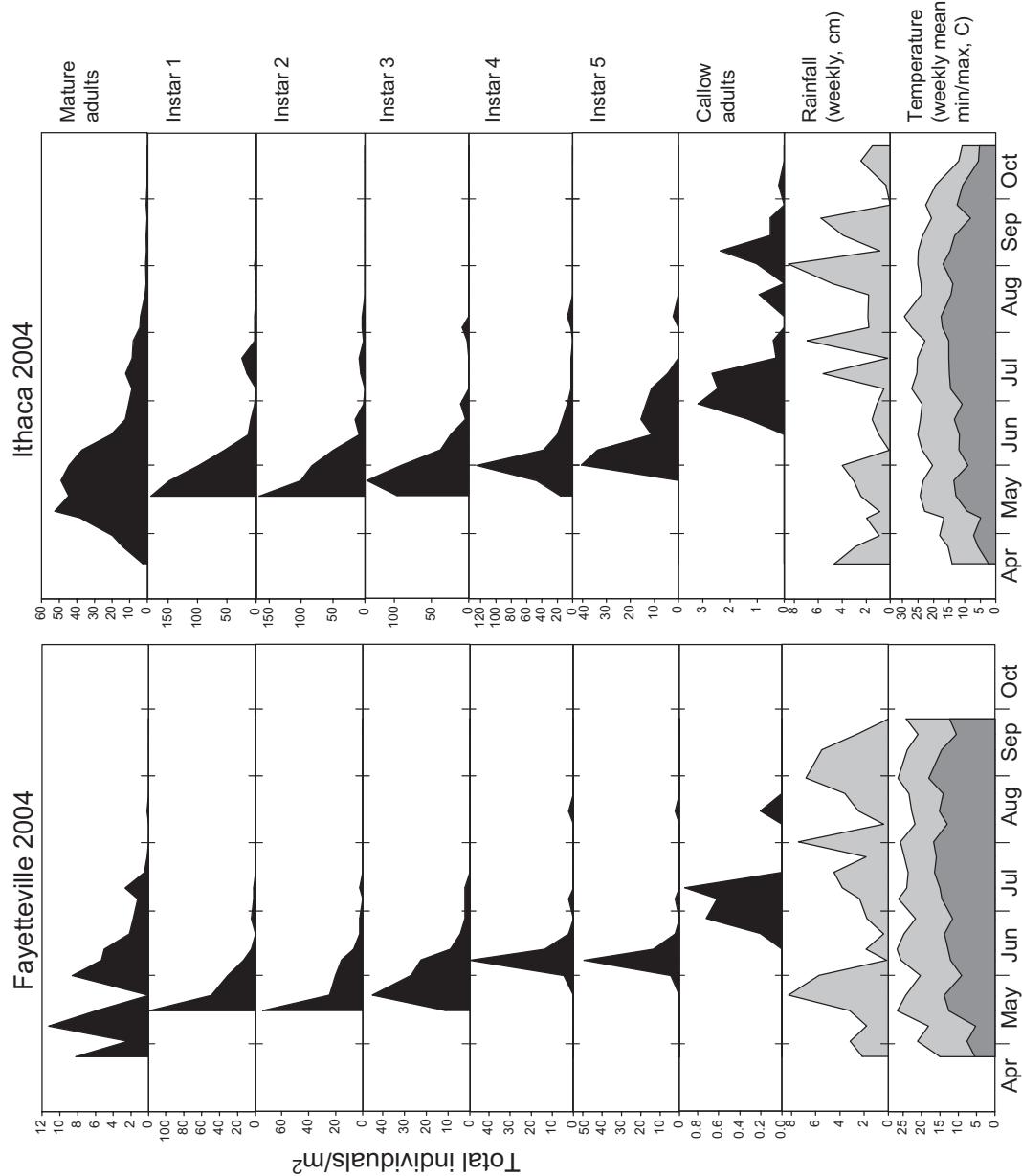


Fig. 3. Population fluctuation curves of total *L. maculicollis* (adults, instars 1–5, and callow adults) collected during population surveys in Ithaca and Fayetteville, NY, in 2004.

Table 2. Julian (calendar date) chronology of selected events in the seasonal fluctuations of *L. maculicollis* on golf course fairways across years and sites in New York

Chronology of select events	2004		2005		2006	
	Fayetteville	Ithaca	Fayetteville	Ithaca	Fayetteville	Ithaca
Start sampling						
Adults	117 (26 April)	108 (17 April)	101 (11 April)	95 (5 April)	100 (10 April)	87 (28 Mar.)
Larvae	138 (17 May)	139 (18 May)	143 (23 May)	143 (23 May)	121 (1 May)	114 (24 April)
First detection						
Overwintered adults	117 (26 April)	108 (17 April)	101 (11 April)	102 (12 April)	100 (10 April)	107 (17 April)
Instars 1–4	138 (17 May)	139 (18 May)	151 (31 May)	143 (23 May)	121 (1 May)	114 (24 April)
Instar 5	154 (2 June)	153 (1 June)	164 (13 June)	143 (23 May)	151 (31 May)	114 (24 April)
Larvae	138 (17 May)	139 (18 May)	151 (31 May)	143 (23 May)	121 (1 May)	114 (24 April)
Callow adults	173 (21 June)	174 (22 June)	178 (27 June)	180 (29 June)	151 (31 May)	157 (6 June)
Overwintered adult abundance peaks						
Early peak/cohort	131 (10 May)	146 (25 May)	115 (25 April)	130 (10 May)	100 (10 April)	114 (24 April)
Late peak/cohort	154 (2 June)	167 (15 June)	157 (6 June)	165 (14 June)	121 (1 May)	136 (16 May)
Spring generation abundance peaks						
Instar 1	138 (17 May) ^a	139 (18 May) ^a	151 (31 May)	150 (30 May) ^a	142 (22 May) ^c	114 (24 Apr) ^b
				172 (21 June) ^c		143 (23 May) ^c
Instar 2	138 (17 May) ^a	139 (18 May) ^a	164 (13 June)	150 (30 May) ^a	156 (5 June) ^c	114 (24 Apr) ^b
				172 (21 June) ^c		149 (29 May) ^c
Instar 3	145 (24 May)	146 (25 May)	164 (13 June)	158 (7 June) ^a	156 (5 June) ^c	114 (24 Apr) ^b
				172 (21 June) ^c		157 (6 June) ^c
Instar 4	145 (24 May)	153 (1 June)	164 (13 June)	158 (7 June)	156 (5 June) ^c	129 (9 May) ^b
						157 (6 June) ^c
Instar 5	161 (9 June)	153 (1 June)	171 (20 June)	172 (21 June)	163 (12 June) ^c	129 (9 May) ^b
						179 (28 June) ^c
Callow adults	180 (28 June)	181 (29 June)	186 (5 July)	187 (6 July)	186 (5 July) ^c	188 (7 July) ^b
						201 (20 July) ^c
Summer generation abundance peaks						
Callow adults	229 (16 Aug.)	251 (7 Sept.)	227 (15 Aug.)	228 (16 Aug.)	233 (21 Aug.)	248 (5 Sept.)
Last detection						
Larvae	229 (16 Aug.)	245 (1 Sept.)	241 (29 Aug.)	264 (21 Sept.)	233 (21 Aug.)	256 (13 Sept.)
Callow adults	229 (16 Aug.)	281 (7 Oct.)	241 (29 Aug.)	257 (14 Sept.)	186 (5 July)	283 (10 Oct.)
Mature adults	229 (16 Aug.)	281 (7 Oct.)	255 (12 Sept.)	271 (28 Sept.)	226 (14 Aug.)	270 (27 Sept.)
End sampling						
Adults	271 (27 Sept.)	299 (25 Oct.)	277 (4 Oct.)	278 (5 Oct.)	261 (18 Sept.)	298 (25 Oct.)
Larvae	271 (27 Sept.)	299 (25 Oct.)	277 (4 Oct.)	278 (5 Oct.)	261 (18 Sept.)	298 (25 Oct.)

^a Peak likely occurred before the start of sampling.

^b Early cohort.

^c Late cohort.

series of progressive life stages that led to the peak of instar 5. A small summer generation was revealed by the detection of instars 1–4 after the last detection of callow adults. In Ithaca, overwintered adults were first detected 17 April followed by peaks 7 and 29 d later. As in Fayetteville, each of these cohorts was aligned with a subsequent series of peaks for each instar. In contrast, the bimodality was retained through callow adults. The main peaks for each instar were associated with the later cohort that led to the main peak of callow adults on 20 July. The subsequent detection of instars 1–5 revealed a small summer generation, but the low population synchrony obscured an assessment of timing. As in 2004, the size of the overwintered adult population at each site was relatively large compared with the subsequent local populations. In Ithaca, insects were last detected 50 d later than in Fayetteville.

Discussion

Results gathered over 3 yr from two geographical locations showed the magnitude of variation as ex-

pressed by population synchrony, insect load, voltinism, and sex ratio. In general, those parameters varied more among years than between sites. The results also showed that two population parameters—sex ratio and insect load—were highly influenced at the landscape scale by management habitat.

Population Fluctuations. A major source of variation in population fluctuation curves was synchrony of the spring generation. Early season population synchrony seems to be strongly linked to the pattern of spring immigration by adults transitioning from overwintering habitats to developmental habitats. At both sites in 2006 and one site (Ithaca) in 2005, fluctuation curves of the spring generation showed overlapping cohorts of early and late appearing larvae. In each case the bimodality lost its expression by the arrival of callow adults. These cohorts were initially aligned with bimodal peaks of immigration by overwintered adults. Immigration over a relatively brief window of time would likely have led to a more synchronous period of oviposition and subsequent population development, as in 2004. In contrast, gradual immigration over an extended window

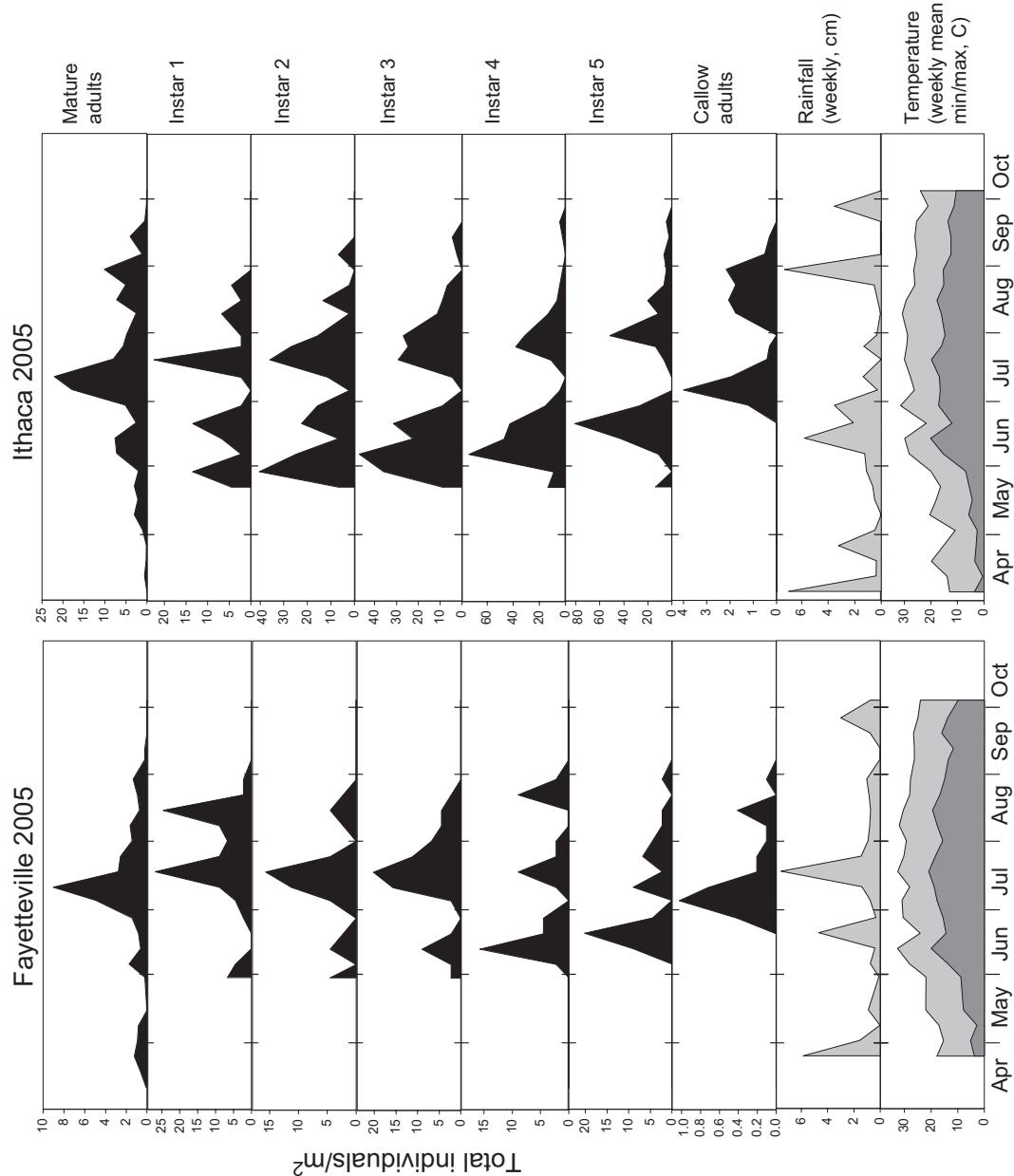


Fig. 4. Population fluctuation curves of total *L. maculicollis* (adults, instars 1–5, and callow adults) collected during population surveys in Ithaca and Fayetteville, NY, in 2005.

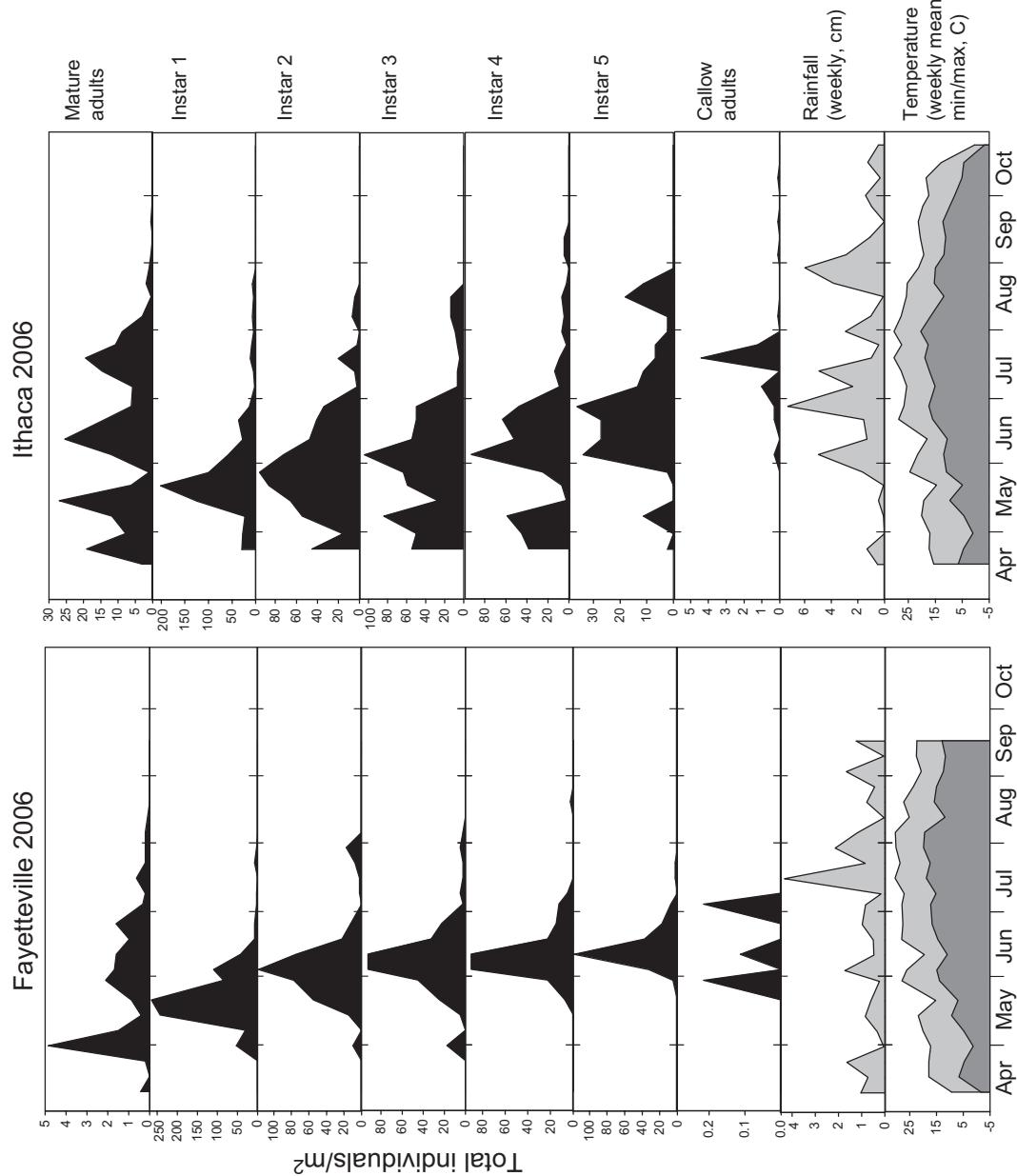


Fig. 5. Population fluctuation curves of total *L. maculicollis* (adults, instars 1–5, and callow adults) collected during population surveys in Ithaca and Fayetteville, NY, in 2006.

of time would likely have led to a less synchronous population development, as in 2005 and 2006. The influence of early season weather conditions on the emergence of *L. maculicollis* adults from overwintering sites has not been studied. Given that these adults are the primary target of early season preventive controls, management would profit from studies designed to predict the arrival of these immigrants (Peck and Diaz 2005).

Vittum and Tashiro (1987) studied field populations on several golf courses in downstate New York and Connecticut. Their surveys, conducted from May to September 1976–1978, did not gather data on the pattern of immigration by overwintered adults to the fairway. Results over the spring and summer generations showed that some developmental stages were present on all sampling dates, a consequence of overlapping generations and an indication of low population synchrony. Population peaks were also poorly defined and gave little evidence of population synchrony. One limitation of that study was that immature life stages were pooled into two groups: instars 1–4 and instar 5 with prepupae. Grouping of the life stages reduced resolution and limited interpretations from those data.

A second major source of variation was relative size of the overwintered adult population compared with the subsequent generations. For both sites in 2004 and 2006, the size of the overwintered adult population far surpassed that of the spring and summer generations. In contrast, across both sites in 2005 the overwintered adult population was far smaller than the spring and summer generations. The similarity across geographical sites supports the idea that populations may have been influenced by the same set of broad density-independent factors such as climate. Survival of overwintering populations could be favored by a milder winter climate, whereas success of spring populations could be enhanced by other environmental variables. Success of adults making the transition from developmental sites to overwintering sites might also play a role.

Number of Generations. Another expression of variation among years in our study was in the number of generations completed. Both sites experienced one complete generation and a partial second generation in 2004 and 2006 and two complete generations and a partial third in 2005. Climate is a likely factor for the differences in voltinism. Temperature conditions in 2005 may have been more favorable for population development than 2004 and 2006, either accelerating the rate of development or extending the effective growing season. Fayetteville experienced 2,850 growing degree days (base 10°C; 1 May to 30 September) in 2005, which was 15.4% higher than 2004 and 12.9% higher than 2006. Ithaca experienced 2,482 GDD in 2005, which was 10.4% higher than 2004 and 9.5% higher than 2006. Whatever the cause, the factors were broad enough to affect both sites in a similar way. Similarities between the two sites could be attributed to their relative proximity. Fayetteville is located ≈62 mi northeast of Ithaca.

Across the range of distribution of *L. maculicollis*, voltinism is usually documented as two or three generations per year. In Quebec, two generations per year were completed in most of the 19 golf courses studies over 2001–2003 (Simard et al. 2007). Two to three generations have been reported in southeastern New York (Westchester Co.), Connecticut (Fairfield Co.) (Vittum and Tashiro 1987), and northern and central New Jersey (McGraw and Koppenhöfer 2007). Further research may ultimately show voltinism to be linked to latitude. In any one region, however, it may be that variation in climate from year to year is the main factor that influences the number of generations produced by *L. maculicollis*, and less so the landscape level parameters such as physical and topographical differences between golf courses.

As for *L. maculicollis*, the number of generations achieved by two other species of *Listronotus* depends on temperature and habitat. The Argentine stem weevil, *L. bonariensis* H., is a serious pest of pasture grasses in New Zealand. This species typically completes two generations a year but may achieve a third in the warmer regions (May 1961, Goldson 1981, Barker et al. 1989). The carrot weevil, *Listronotus oregonensis* L., can also complete one to three generations per year depending on location (Boivin 1999). In some circumstances, warm summer conditions and the presence of host plants early in the spring may lead to a complete or partial third generation of this pest (Boivin 1999).

The relatively small size of the ultimate generation of *L. maculicollis* may be the result of mortality and/or earlier transition to overwintering sites. For all years and sites, the population density of adults and larvae declined by the end of the season suggesting the time when adult populations start returning to overwintering areas to seek shelter (Diaz and Peck 2007). Vittum and Tashiro (1987) also reported that *L. maculicollis* populations decreased from mid-August into early autumn over all 3 yr of study. Environmental cues linked to transition are unknown; nevertheless it is reasonable to suggest that a proportion of adults might move to overwintering sites while another proportion remains at developmental sites to initiate another generation.

Effect of Management Habitat. The two population parameters examined—*insect load* and *adult sex ratio*—were both strongly affected by management habitat. Adults and larvae of *L. maculicollis* were much more prevalent (6.4- to 9.2-fold) on the fairway than the intermediate rough and the rough. This fits the idea that their impact is traditionally expressed on short-mown turf, but until now, no data had been gathered to ascertain whether this is because of increased host plant susceptibility or increased abundance. On the fairway itself, damage is traditionally observed on the periphery, but as our data were assessed, they do not contribute to a better understanding of that general observation. Rothwell (2003) described the distribution of *L. maculicollis* across a fairway in Connecticut from 2000 to 2001 and found adult and larval populations to be uniformly distributed. In 2001, significantly more second generation

larvae were found at the center of the fairway compared with the fairway edges.

The predominance of *L. maculicollis* on the fairway could be explained by differential mortality caused by natural enemies. When studying the habitat selection of *Ataenius spretulus* H., *Aphodius granarius* L., and the presence of natural enemies on golf courses, Smitley et al. (1998) found that rough mown areas had significantly more potential predators, such as rove beetles (Staphylinidae) and ants (Formicidae), compared with fairway mown grass. In a subsequent study (Rothwell and Smitley 1999), rove beetles were found to be three times more abundant in rough versus fairway habitats, and twice as many larvae were infested by the pathogen *Paenibacillus* sp. (causal agent of milky spore disease). In addition, predation of *A. spretulus* eggs and larvae by rove beetles and ground beetles (Carabidae) was higher in the rough than fairway (Jo and Smitley 2003). The role of natural enemies on the density of *L. maculicollis* across fairway and rough management habitats therefore merits further study.

Another factor could be habitat preferences. In *A. spretulus* larvae, a preference for short mowed turfgrass was observed (Smitley et al. 1998). That study reported 3- to 10-fold higher abundance in golf course fairways than roughs. However, a follow up study conducted in the greenhouse and growth chamber (Jo and Smitley 2006) showed that, based on oviposition behavior, adults did not choose turf habitat with respect to mowing height. Given a choice between fairway and rough turf plugs with different soil moisture levels, *A. spretulus* adults preferred turf plugs with 13–26% volumetric moisture content over turf plugs in soil at 8–9% moisture. These reports may be of importance to our finding of significant numbers of *L. maculicollis* larvae on fairways during the summer months and warrants further study to determine whether mowing height or other factors may influence preference of adult *L. maculicollis* for oviposition.

With respect to the other parameter examined, male:female sex ratio was ≈1:1 on the fairway, but it was highly male-skewed on the intermediate rough (1.55) and the rough (1.57). Given the low abundance of *L. maculicollis* in rough habitats, it is unlikely that this phenomenon has any meaningful relevance to pest status or management. Whether this could be attributed to factors such as diverging reproductive status or habitat preferences remains to be assessed.

Implications for Pest Management. Because of the wide variation in population density and phenology of *L. maculicollis* life stages across years and sites, our results underline the importance of scouting and assessing thresholds before a decision is made to intervene. With studies to better elucidate the role of natural enemies, habitat preferences, and host plant susceptibility, we will be better positioned to ascertain how habitat manipulations could be incorporated into control programs to reduce abundance and injury. Local and landscape level determinants of *L. maculicollis* incidence might include geographic isolation,

soil texture, host plant composition, cultural practices, and insecticide applications against other turf insect pests (Simard et al. 2007).

In addition, the proper timing of chemical applications to target immigrating overwintered adults is crucial if pest management practitioners are to suppress the development of one, two, or three subsequent generations. Therefore, predicting the timing of the different life stages of *L. maculicollis* over the season using phenological models might be a useful tool (Diaz 2006), especially when applied in accordance to our most recent understanding of overwintering preferences and the flux between overwintering sites and developmental sites (Diaz and Peck 2007). This approach might open up opportunities to “intercept” adults as they transition between overwintering and developmental habitats, especially if those phenological events can be predicted in space in time.

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