

Impact of Soil Moisture and Mowing Height on the Skewed Distribution of *Ateanius spretulus* (Coleoptera: Scarabaeidae) on Golf Course Fairways and Roughs

ABSTRACT

Ateanius spretulus (Haldeman) grubs are more common in golf course fairways than roughs and the grubs are more likely to damage fairway turf. We evaluated the effects of soil moisture and mowing height on the preference of *A. spretulus* adults for oviposition and colonization. In growth chambers, *A. spretulus* adults were released into turf arenas consisting of two different types of turf cores (cut at fairway height and rough height) placed into soils held at different moisture levels. Seven days after releasing adult beetles, we examined turf cores for eggs and first instars. Seven different experiments were conducted at different time intervals from August 1999 to July 2000. Mowing height did not affect colonization by adult beetles, but they preferred moist soil ($\geq 13\%$ water by volume) to dry soil (8-9%). Adult beetle preference for moist soil may contribute to the skewed distribution of *A. spretulus* grubs towards golf course fairways, which tend to have higher soil moisture than roughs. The univoltine life cycle of *A. spretulus* in Michigan is discussed.

Key words: *Ateanius spretulus*, soil moisture, mowing height, golf courses, colonization, oviposition.

Introduction

Ataenius spretulus (Haldeman) (Coleoptera: Scarabaeidae) is an important pest of golf course turfgrass (Cartwright 1974, Kawanishi et al. 1974, Weaver and Hacker 1978, Wegner and Niemczyk 1979, Wegner and Niemczyk 1981). The distribution of *A. spretulus* grubs on golf courses is skewed toward fairways and results in more frequent damage to fairways compared with adjacent roughs. Natural enemies have been proposed to cause this distribution pattern of *A. spretulus* grubs (Smitley et al. 1998). Mowing practices and chemical use may affect the distribution of *A. spretulus* and its predators on golf course turf (Smitley et al. 1998, Rothwell and Smitley 1999).

When the mowing regime on a golf course was changed, the density of *A. spretulus* grubs remained the same in the first year, but increased in the new fairway and decreased in the new rough in the second year. At the same time, predators became more active in the new rough and less active in the new fairway (Rothwell and Smitley 1999). Similarly, more predacious beetles were found on uncut grassland compared with cut grassland (Morris and Rispin 1987). Among other turf scarab beetles, European chafer, *Rhizotrogus majalis* Razoumowsky, grubs were more common in pastures mowed during the female beetles' oviposition flights than in grass that was not mowed (Gyrisco et al. 1954).

Reduced abundance of predators caused by insecticide application may also cause an increase in the density of some turf pest insects. Insecticide treatment before or during oviposition periods of adult scarab beetles interferes with predation on their eggs and grubs and incurs high populations of white grubs (Terry et al. 1993).

Scarab beetles in turfgrass are affected by soil moisture, texture and pH. May or June beetles, *Phyllophaga crinita* Burmeister, flights and oviposition are closely tied to

rainfall (Gaylor and Frankie 1979). Another scarab turf pest, the southern masked chafer (*Cyclocephala immaculata* Olivier) does not lay eggs in dry soil (Potter 1983). Choice and non-choice tests with Japanese beetle, *Popillia japonica* Newman, and rose chafer, *Macroductylus subspinosus* (F.), show that both scarabs lay more eggs in moist soil, up to field capacity, and that rose chafer has no ovipositional preference for soil textures and Japanese beetle avoids oviposition into pure sand (Allsopp et al. 1992). In the only report of a pH effect on scarabs in turfgrass, the masked chafer (*Cyclocephala* sp.) is adversely affected by low pH (Potter et al. 1996).

Previous observations that *A. spretulus* adults were consistently found to be 2 to 4 times more abundant in the fairway than in the rough may partially explain the higher density of *A. spretulus* grubs in the fairway (Smitley et al. 1998). This may reflect the female's preference of the fairway to rough for an oviposition site. The objectives of this study are to determine how mowing height and soil moisture affect the colonization and ovipositional preference of *A. spretulus* adult beetles.

Materials and Methods

Mowing Height Experiment. Turfgrass modules were established and maintained in a greenhouse (Fig. 1). The average air temperature was 27.8°C in June and 29.4°C in July 1999. Perennial ryegrass (*Lolium perenne* L.) was seeded into 40 plastic pots (15 by 15 cm) filled with loamy sand soil (85.9% sand, 9.9% silt, 4.2% clay, and a pH of 6.5) in March. The grass was irrigated daily and fertilized weekly with 0.8 g/liter of 20:20:20 N:P:K. The grass was clipped by hand twice each wk. Turf maintained as fairway was cut to a height of 1.5 cm while turf maintained as rough was cut to a height of 5.0 cm.

Ten experimental modules were made from 40 square pots filled with turf. Each module consisted of two fairway pots and two rough pots bound tightly together (Fig. 1). The rims of each pot that faced the inside of a module were cut down to the level of the soil surface. Thus *A. spretulus* adults could move around all four grass sections but they could not easily leave the module.

A. spretulus adults were easily found on the surface of golf course greens in Michigan in early June. We collected them at Royal Scot Golf Course, Lansing, MI. Forty beetles were introduced into each module. After beetles were released, each module was covered with a fine-net cage (30 by 30 by 50 cm). The cage was removed briefly each time we watered or clipped grass. These plots were maintained for two months after beetles were released. At the end of the experiment, each section of all modules was torn apart and examined for *A. spretulus* grubs.

Numbers of grubs in the 2 fairway sections were combined and those in the 2 rough sections per module were combined. These numbers of grubs were square root transformed before analysis. Means of grubs found in the fairway were compared to those in the rough using a PROC MIXED statement in SAS software (SAS Institute 1990).

Soil Moisture and Mowing Height Experiment. Seven different experiments were conducted from August to September 1999 and May to July 2000 in a growth chamber. All *A. spretulus* adults were collected at Royal Scot Golf Course, Lansing, MI as previously described. Adult beetles captured in the fall of 1999 were newly emerged, while the beetles collected in the spring and summer of 2000 had already survived the previous winter. The growth chamber was set at 25°C and 60% relative humidity with a photo period of 12:12 (light:dark).

Turf cores (2 cm diameter and 4 cm deep) were taken from annual bluegrass (*Poa annua raptans* L.) fairway and rough at the Hancock Turfgrass Research Center, East Lansing, MI. The fairway was maintained at a mowing height of 1.5 cm with 1.5 cm thatch while the rough was maintained at a mowing height of 5.0 cm with 3.0 cm thatch. No insecticides were applied in 1999 or 2000. The soil of this area was Owosso-Marlette sandy loam with a pH of 7.5.

Turf cores were placed into pots of steam-sterilized loamy sand soil (87.4% sand, 9.3% silt, 3.4% clay, and 7.1 pH). The bulk density of this loamy sand was 1.41 g/cm³ and the saturation point was calculated to be 46% water by volume. The wilting point (-1.5 MPa) was estimated to be approximately 6% water by volume, using the general relationship between soil moisture and soil texture (Brady and Weil 1999).

To achieve the desired soil moisture levels, we added the amount of water determined as a percent by volume into the soil (Fig 2). Soil moisture in the prepared turf arenas was stabilized for 24 h before *A. spretulus* adults were released. Each turf arena was enclosed within a pin-holed transparent plastic bag after beetles were added. In a preliminary experiment, this transparent plastic bag was effective for maintaining soil moisture. After one wk, soil moisture levels were within 2% of the original level.

In the first experiment, two fairway and two rough cores were placed in each of ten round plastic pots (10 cm diameter and 15 cm deep) (Fig. 2A). Soil was maintained at the same moisture level (17% water by volume). Fifteen *A. spretulus* adults were released in each arena on 19 August 1999. One wk later, we pulled out the turf columns and counted adult beetles, eggs and first instars with a dissecting microscope.

In experiments 2 and 3, two different soil moisture levels were created to give *A. spretulus* adults a choice for colonization and oviposition (Fig 2B). Soils containing 9%

and 23% water by volume were prepared. A round plastic pot was divided in the middle by an impermeable plastic sheet. Half of the pot was filled with dry soil (9% water by volume) and the other half with wet soil (23% water by volume). One fairway core and one rough core were implanted into each half of the pot. Fifteen *A. spretulus* adult beetles were released into each of ten arenas on 24 August 1999 (experiment 2). A wk later, we pulled out the turf cores and counted adults, eggs and first instars with a dissecting microscope. Experiment 3 was conducted with the same methods on 4 September 1999.

In experiments 4 to 7, four different soil moisture levels were created to test *A. spretulus* preferences for 8%, 13%, 20% or 26% soil moisture by volume (Fig. 2C). Each arena consisted of four 10 by 10 by 10 cm square plastic pots, tightly pushed together without any gap between pots. The inside rims of the four pots were cut down to the soil surface level to allow beetles free movement. One fairway and one rough core were put in each pot. A total of six plots were set up, including one control that was used for monitoring soil moisture levels. Control pots were weighed each day and water was added to all pots, as needed in the control pots. Twenty *A. spretulus* adults were released in each arena. The arenas were examined one wk later for adults, eggs and first instars. From late May through mid July, four different experiments were sequentially conducted.

If eggs were detected in turf cores, the top 5 cm of soil in each pot was also examined for eggs. Eggs were isolated from soil samples with a semi-automatic elutriator (Byrd et al. 1976) and sugar floatation (Jenkins 1964), which are used to extract nematodes, fungi or insect eggs from soil. The soil samples were filtered through 850 μm coarse and then 75 μm fine steel screens by an elutriator. Eggs and debris mixtures

caught in the fine screen were centrifuged in a 2 mol sugar solution and then in pure water. The eggs floating on the supernatant of the pure water were collected and counted with a dissecting microscope.

Colonization preference of *A. spretulus* adults was determined from the proportion of recovered adults to the total number of adults introduced into each turf arena. These percentage data were arcsine square root transformed before analysis. Each arena was considered as a block. The first experiment was statistically tested as a randomized complete block model by a single factorial analysis of variance (ANOVA) using a SAS PROC MIXED procedure. The remaining experiments were analyzed as a split block model. In this model, the effect of time was nested with the block, and mowing height was considered as the split effect for each moisture level. The effects of time, mowing height and soil moisture were tested by a three-factorial ANOVA. The recovery of adults was compared between the fairway and rough or among different soil moisture levels by a least squares means (LSMEANS) option with PROC MIXED. The numbers of eggs and first instars isolated from turf cores were square root transformed before analysis. The effects of time, soil moisture and mowing height were tested by a three-factorial ANOVA.

Results

Mowing Height Experiment. A mean of 1.8 grubs was found in two fairway sections and a mean of 1.6 grubs was found in two rough sections of each module. Grub occurrence was not different among the fairway and rough sections ($P = 0.92$). We found few survived *A. spretulus* adults at the end of our experiment.

Soil Moisture and Mowing Height Experiment. In experiment 1, mowing

height did not affect colonization by *A. spretulus* adults. Similar numbers of beetles were recovered in the fairway and rough (Table 1).

In experiments 2 and 3, block and mowing height did not impact the colonization behavior of adult beetles. However, more beetles selected turf cores in wet soil than in dry soil, regardless of block and mowing height (Table 2).

In experiments 4 to 7, the recovery of beetles was also not different among blocks or between the fairway and rough. Adult colonization was again significantly different among four different soil moisture levels (Table 2). Adults consistently preferred wet soil to dry soil (Table 2). Multiple comparisons by the least square means test showed that more beetles colonized soils containing $\geq 13\%$ water by volume than 8% ($P \leq 0.001$), while their responses were not different among the three moisture levels $\geq 13\%$ ($P = 0.41$) (Table 1).

Over 50% of the released adult beetles were recovered after one wk in experiments 1 to 3 where each plot was 78.5 cm^2 . Only 28-46% of the beetles were recovered in experiments 4 to 7 where each plot was 400 cm^2 . As the size of the turf arena increases, fewer beetles were recovered. In experiment 7 conducted on 10 July 2000, only 5.7% of the recovered beetles were alive. In the other experiments, over 87% of the recovered beetles survived (Table 3).

In experiments 1 to 4, using adult beetles collected in August, early September and mid May, we did not find any *A. spretulus* eggs or first instars. Meanwhile, we found eggs in experiments 5 and 6 and first instars in experiments 6 and 7. A total of 114 eggs and 172 first instars were isolated in these three experiments. The number of eggs and grubs in experiment 6 initiated on 15 June comprised 82% of the total eggs and first instar grubs found in all 7 experiments.

When eggs and grubs were found, time was a significant factor ($P < 0.01$).

When statistical analysis was run with the numbers of eggs and first instars collected from experiments 5,6 and 7, there was a significant mowing height effect ($P < 0.05$) but no moisture effect ($P = 0.56$) on oviposition.

Egg separation by the elutriator and sugar floatation was effective for isolating *A. spretulus* eggs from soil. In a control run of this process with known numbers of corn rootworm eggs, approximately 70% were recovered. We tested the soil from experiment 6 where the ovipositional activity was the highest, to determine how many eggs were deposited in the surrounding soil instead of in turf cores. Only 8 eggs and 2 first instars were separated from a total of 20 100-ml soil samples.

Discussion

Soil moisture is an important factor for some soil-ovipositing insects like the bean leaf beetle (*Cerotoma trifurcata* (Forster)) (Marrone and Stinner 1983), and the southern corn rootworm (*Diabrotica undecimpunctata howardi* Barber) (Brust and House 1990). In loamy sand soil, moist soil (from -0.1 to -1.0 MPa) is preferred for oviposition by the southern corn rootworm and bean leaf beetle and their ovipositional activity is kept maintaining up to saturated soil moisture. However, the least oviposition by both beetles occurs in the oven dry soil.

In our research, soil moisture was important for *A. spretulus* colonization of turf regardless of whether turfgrass was cut at fairway height or rough height. Adults preferred to inhabit turf cores placed in soil containing $\geq 13\%$ water by volume to soil containing less than 9% water. They, however, did not discriminate among the three levels of soil moisture from 13% to 26%. We expect that the behavior of *A. spretulus*

adults will be affected on golf courses in areas where the irrigation system does not reach. This agrees with the observation of Smitley et al. (1998) where *A. spretulus* adults were scarce in the dry rough where irrigation coverage did not extend.

Only *A. spretulus* adults collected in June and early July oviposited in our growth chamber experiments. In these 3 experiments, eggs and grubs were found in all four soil moisture levels. More eggs and grubs were found in rough turf than in fairway turf cores. However, not enough data were available to determine the ovipositional preference of *A. spretulus* adults because 82% of all eggs and first instars came from a single experiment (experiment 6).

Thatch in perennial ryegrass turf taken from the rough area of the Hancock Turfgrass Research Center is 2-fold thicker than in the fairway turf cores. The soil moisture effect on *A. spretulus* adults may be confounded with mowing height and thatch in our turf arena experiment because organic matter has a greater water holding capacity than any other soil texture. The high water holding capacity of thatch may attract adults and perhaps induce their oviposition in our turf arena.

A. spretulus grub infestation is more common in fairways than roughs of golf courses (Vittum 1995, Smitley et al. 1998). Golf course roughs with high mowing height tend to accumulate more thatch than fairways (Beard et al. 1978, Shearman 1980, Dunn et al. 1981). The spatial distribution of *A. spretulus* grubs in golf courses does not agree with our observations that *A. spretulus* adults homogeneously colonized fairway and rough cores at the same moisture levels in our growth chamber experiments and infestation of grubs was similar in the fairway and rough turf in greenhouse experiments. However, under the field conditions, roughs are likely to be drier than fairways because irrigation is targeted to fairways with some overlap into roughs. Even if the same

amount of water is applied, roughs tend to consume more soil water and become drier than fairways (Madison and Hagan 1962, Shearman 1984, Morhard and Schulz 1998). Therefore, *A. spretulus* females may be attractive to golf course fairways for their oviposition.

We did not test the survival of *A. spretulus* eggs and grubs in the fairway and rough. However, it is known that the eggs and larvae of some scarab beetles do not survive well under dry soil conditions (Potter 1983). While golf course fairways are not expected to become dry enough to affect the survival of *A. spretulus*, this may be a factor in roughs where irrigation does not reach. The development of Japanese beetle (*Popillia japonica* Newman) and masked chafer (*Cyclocephala* sp.) was delayed and their body weight decreased in tall turf compared with short turf (Potter et al. 1996). Higher activity of natural predators in the rough compared with the fairway may increase the mortality of eggs and grubs in the rough (Smitley et al. 1998, Rothwell and Smitley 1999). Also *A. spretulus* grubs tend to be more highly infected by *Bacillus* sp. in roughs than fairways (Rothwell and Smitley 1999). Eventually, the survival of *A. spretulus* eggs and grubs in golf course roughs may be lower than in the fairway.

Oviposition of *A. spretulus* adults collected between August 1999 and July 2000, adds some key information about their life cycle in MI. Newly emerged adults in August and September did not oviposit. Overwintered adults also did not show ovipositional activity until early June, even though beetles become active on golf courses as early as 1 May. All of the eggs were deposited between 31 May and 10 July. The survival of adults plummeted from 90% in June to 6% in mid July, indicating that few individuals from the overwintered generation survive after mid July. This high mortality in mid July is coincident with reduced flight activity of *A. spretulus* adults at

this time (Johanningsmeier 1999). Their flight activity decreased to almost no detectable level from 26 June to 31 July in 1992 and from 28 June to 9 August in 1993. Flight resumed after mid August, presumably by the new generation. This field data about the flight of *A. spretulus* adults and our laboratory data about their oviposition and mortality support observations that *A. spretulus* is univoltine in MI.

A partial second generation was speculated in MI because of field observations of *A. spretulus* grubs, pupae and callow adults in mid September (Vittum 1995, Smitley et al. 1998). However, in our study, newly emerged adults in late summer did not oviposit but the ovipositional activity of overwintered adults extended to mid July. Second instars of *A. spretulus* were observed in MI from 6 to 26 July 1993 (Johanningsmeier 1999). The oviposition in mid July by the overwintered generation may cause the delayed occurrence of *A. spretulus* grubs in early September. To determine the importance of a partial second generation in MI will require monitoring *A. spretulus* grubs for several years.

Reference Cited

- Allsopp, P. G., M. G. Klein, and E. L. McCoy. 1992.** Effect of soil moisture and soil texture on oviposition by Japanese beetle and rose chafer (Coleoptera: Scarabaeidae). *J. Econ. Entomol.* 85: 2194-2200.
- Beard, J. B., A. Almodares, and R. L. Duble. 1978.** Nitrogen fertilization studies on St. Augustinegrass plus the relationship to thatch and its control. *Texas Turfgrass Research - 1977-78:* 29-33.
- Brady, N. C., and R. R. Weil. 1999.** The nature and properties of soils. Prentice Hall, Upper Saddle River, N.J.
- Brust, G. E., and G. J. House. 1990.** Influence of soil texture, soil moisture, organic cover, and weeds on oviposition preference of southern corn rootworm (Coleoptera: Chrysomelidae). *Environ. Entomol.* 19: 966-971.
- Byrd, D. W., Jr., K. R. Barker, H. Ferris, C. J. Nusbaum, W. E. Griffin, R. H. Small, and C. A. Stone. 1976.** Two semi-automatic elutriators for extracting nematodes and certain fungi from soil. *J. Nematol.* 8: 206-212.
- Cartwright, O. L. 1974.** *Ataenius*, *Aphotaenius*, and *Pseudataenius* of the United States and Canada (Coleoptera: Scarabaeidae: Aphodiinae). *Smithsonian Contrib. Zool.* 154: 1-106.
- Dunn, J. H., K. M. Sheffer, and P. M. Halisky. 1981.** Thatch and quality of Meyer zoysia in relation to management. *Agronomy Journal* 73: 949-952.
- Gaylor, M. J., and G. W. Frankie. 1979.** The relationship of rainfall to adult flight activity; and of soil moisture to oviposition behavior and egg and first instar survival in *Phyllophaga crinita*. *Environ. Entomol.* 8: 591-594.

- Gyrisco, G. G., W. H. Whitcomb, R. H. Burrage, C. Logothetis, and H. H. Schwardt. 1954.** Biology of European chafer *Rhizotrogus majalis* Razoumowsky (Scarabaeidae). Cornell Univ. Agric. Exp. Stn. Mem. 328.
- Jenkins, W. R. 1964.** A rapid centrifugal-flotation technique for separating nematodes from soil. Plant Disease Reporter 48: 692.
- Johanningsmeier, J. S. 1999.** Relationship of *Aphodius granarius* and *Ataenius spretulus* activity to air and soil based degree-day accumulations on Michigan golf courses. M.S. thesis, Michigan State University, East Lansing.
- Kawanishi, C. Y., C. M. Splittstoesser, H. Tahiro, and K. H. Steinkraus. 1974.** *Ataenius spretulus*, a potentially important turf pest, and its associated milky disease bacterium. Environ. Entomol. 3: 177-181.
- Madison, J. H., and R. M. Hagan. 1962.** Extraction of soil moisture by Merion bluegrass (*Poa pratensis* L. 'Merion') turf, as affected by irrigation frequency, mowing height, and other cultural operations. Agron. J. 54: 157-160.
- Marrone, P. G., and R. E. Stinner. 1983.** Effects of soil moisture and texture on oviposition preference of the bean leaf beetle, *Cerotoma trifurcata* (Forster) (Coleoptera: Coccinellidae). Environ. Entomol. 12: 426-427.
- Morhard, J., and H. Schulz. 1998.** Einfluß von Artenzusammensetzung, Schnitthöhe und Bewässerungsart auf den Wasserverbrauch von Intensivrasen. Rasen. Turf. Gazon. 29: 103-109.
- Morris, M. G., and W. E. Rispin. 1987.** Abundance and diversity of the coleopterous fauna of a calcareous grassland under different cutting regimes. J. Appl. Ecol. 24: 451-465.
- Potter, D. A. 1983.** Effect of soil moisture on oviposition, water absorption, and survival

of southern masked chafer (Coleoptera: Scarabaeidae) eggs *Cyclocephala immaculata*.

Environ. Entomol. 12: 1223-1227.

Potter, D. A., A. J. Powell, P. G. Spicer, and D. W. Williams. 1996. Cultural practices affect root-feeding white grubs (Coleoptera: Scarabaeidae) in turfgrass. J. Econ. Entomol. 89: 156-164.

Rothwell, N. L., and D. R. Smitley. 1999. Impact of golf course mowing practices on *Ataenius spretulus* (Coleoptera: Scarabaeidae) and its natural enemies. Environ. Entomol. 28: 358-366.

SAS Institute. 1990. SAS/STAT user's guide: version 6. 4th ed. SAS Institute, Cary, NC.

Shearman, R. C. 1980. Thatch accumulation in Kentucky bluegrass as influenced by cultivar, mowing, and nitrogen. HortScience 15: 312-313.

Shearman, R. C. 1984. Cultural practice effects on turfgrass water use. Agronomy Abstracts: 154.

Smitley, D. R., T. W. Davis, and N. L. Rothwell. 1998. Spatial distribution of *Ataenius spretulus*, *Aphodius granarius* (Coleoptera: Scarabaeidae), and predaceous insects across golf course fairways and roughs. Environ. Entomol. 27: 1336-1349.

Terry, L. A., D. A. Potter, and P. G. Spicer. 1993. Insecticides affect predatory arthropods and predation on Japanese beetle (Coleoptera: Scarabaeidae) eggs and fall armyworm (Lepidoptera: Noctuidae) pupae in turfgrass. J. Econ. Entomol. 86: 871-878.

Vittum, P. J. 1995. Black turfgrass ataenius, pp. 35-37. In R. L. Brandenburg and M. G. Villani [eds.], Handbook of turfgrass insect pests. Entomological Society of America, Lanham, MD.

Weaver, J. E., and J. D. Hacker. 1978. Bionomical observations and control of *Ataenius spretulus* in West Virginia. W. V. Univ. Agric. For. Exp. Stn. Curr. Rep. 72.

Wegner, G. S., and H. D. Niemczyk. 1979. The *Ataenius* of Ohio. Ohio J. Sci. 79: 249-255.

Wegner, G. S., and H. D. Niemczyk. 1981. Bionomics and phenology of *Ataenius spretulus*. Ann. Entomol. Soc. Am. 74: 374-384.

Figure Captions

Fig.1. Module consisting of two fairway pots and two rough pots in our greenhouse experiment.

Fig.2. Turf arenas consisting of fairway turf cores and rough turf cores placed into soils having different moisture levels: one moisture level (A), two moisture levels (B) and four moisture levels (C).

Table 1. Percentage of *A. spretulus* adult beetles recovered from the total number of released beetles.

Experimental series	Mowing height	Soil moisture (% by volume)			
		8-9	13-14	17-20	23-26
1	Fairway	—	—	26.7 ± 5.1	—
	Rough	—	—	30.7 ± 2.8	—
2-3	Fairway	14.9 ± 2.2a	—	—	21.3 ± 2.7b
	Rough	9.7 ± 2.1a	—	—	27.2 ± 3.6b
4-7	Fairway	2.1 ± 0.8a	5.3 ± 1.2b	4.6 ± 0.8b	4.3 ± 1.0b
	Rough	3.3 ± 0.6a	4.3 ± 0.9b	4.6 ± 1.0b	6.1 ± 1.1b

Means ± SE within a row followed by the same letter are not significantly different ($P = 0.05$; LSMEANS statement in SAS MIXED).

Table 2. Factorial ANOVA for testing the effects of time, block, soil moisture, and mowing height on the colonization of *A. spretulus* adults.

Exp	Source of variation	F	df	P
1	Block	0.39	9, 9	0.91
	Mowing height	0.46	1, 9	0.51
2-3	Time	0.37	1, 18	0.55
	Block	0.61	9, 18	0.77
	Moisture	18.36	1, 18	0.0004**
	Mowing height	0.10	1, 18	0.75
	Time (Block) ^a	0.10	9, 18	0.10
	Time X Moisture	0.31	1, 18	0.02*
	Time X Mowing height	0.39	1, 18	0.02*
	Moisture X Mowing height	3.34	1, 18	0.009**
	Time X Moisture X Mowing height	10.33	1, 18	0.005**
	4-7	Time	0.69	3, 16
Block		2.01	4, 16	0.14
Moisture		4.33	3, 48	0.009**
Mowing height		2.18	1, 16	0.16
Time (Block)		1.87	12, 16	0.12
Time X Moisture		1.35	9, 48	0.24
Time X Mowing height		5.32	3, 16	0.01**
Moisture X Mowing height		1.18	3, 48	0.33
Time X Moisture X Mowing height		2.00	9, 48	0.06

P-values followed by one or two asterisks are significant at the 5% or 1% confidence level, respectively.

^aBlock effect was nested with time effect.

Table 3. Recovery of *A. spretulus* eggs, first instars and adults from turf arenas introduced with *A. spretulus* adults collected from a golf course in Lanisng, MI .

Life stage	Exp 1 22 Aug 99	Exp 2 31 Aug 99	Exp 3 11 Sep 99	Exp 4 27 May 00	Exp 5 6 June 00	Exp 6 22 June 00	Exp 7 17 July 00
Eggs ^a	0	0	0	0	1.2 ± 0.6	4.6 ± 1.9	0
First instars ^a	0	0	0	0	0	7.2 ± 1.8	1.5 ± 1.0
Adults ^b	86	116	103	56	92	58	70
Adults (recovered, %) ^c	57.3	77.3	68.8	28.0	46.0	29.0	35.0
Adults (survived, %) ^d	87.2	93.6	95.2	94.5	91.3	89.7	5.7

^a Mean ± SE per turf arena.

^b Total recovered in each experiment.

^c Percentage of recovered *A. spretulus* adults in the total released beetles.

^d Percentage of live *A. spretulus* adults in the total recovered beetles.



