Harmonic Radar: Assessing the Impact of Tag Weight on Walking Activity of Colorado Potato Beetle, Plum Curculio, and Western Corn Rootworm

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ABSTRACT The impact of electronic dipole tags on the walking activity of three insects was determined using video tracking software. Results varied within and between the three species studied. The heaviest tag mounted on the pronotum of the Colorado potato beetle, *Leptinotarsa decemlineata* (Say), reduced its mean horizontal speed slightly but significantly. The mean horizontal speed of plum curculio, *Conotrachelus nenuphar* (Herbst), was significantly reduced by a light tag but not by heavier tags. The mean horizontal speed of the western corn rootworm, *Diabrotica virgifera virgifera* (LeConte), increased slightly when a tag was attached. A tag mounted to the dorsum of the Colorado potato beetle and the plum curculio slightly changed their climbing speed. Changes in the walking speed were variable but remained well within the range of values recorded in the literature. The impact of the additional tag weight was within the range of constraints to movement (e.g., slopes, barriers, etc.) normally experienced by insects in their environment. The results confirm that tags presently available will have minimal impact on the walking behavior of Colorado potato beetle, provide an estimate of the optimal tag weight for the plum curculio and show that a lighter tag and a better attachment method are required for the western corn rootworm. Because of the ability of insects to adapt to a wide range of landscapes and to their own body weight changes, the additional tag weight had a limited impact compared with the value of the ecological information gathered using this technology.

KEY WORDS dispersal, tracking, movement, path

Electronic tags are an integral part of harmonic radar tracking systems developed to study the walking movement of insects (Mascanzoni and Wallin 1986, Wallin and Ekbom 1988, Wallin 1991, Lövei et al. 1997, Boiteau and Colpitts 2004, O'Neal et al. 2004) and their flight dispersal (Riley et al. 1996, Roland et al. 1996, Boiteau and Colpitts 2001).

The critical role of minimal weight electronic tags was first highlighted in flight studies. Roland et al. (1996) developed a harmonic system to study flight-dispersing Lepidopterans that used light tags representing 0.10–0.90% of the insect body weight. Riley et al. (1996) used a 2.90 mg tag representing 1.5% of the body weight of the tracked bumblebees. The important flight behavior modifications that could result from the additional weight of the tag have been acknowledged (Riley et al. 1996) but remain undetermined. Boiteau and Colpitts (2001) found that the adult Colorado potato beetle, *Leptinotarsa decemlineata* (Say), was incapable of upward flight with weights 10.3 mg beyond their minimum daily body weight. They estimated that electronic tags should not weigh >23–33% of the potato beetle's body weight to have no or minimal impact on the number and quality of upward flights taken by the beetle.

The many muscles, joints, and appendages of insects provide flexibility, stability, and maneuverability extending beyond straight-ahead locomotion (Full et al. 2002). In most insects, the maximum tolerable tag payload for walking is therefore likely to be heavier than the maximum payload tolerable for flight. Changing the distribution of body mass by attaching an electronic tag could have an effect on the level of stability. In a walking insect, the center of mass moves with respect to the legs, and the likelihood of falling increases the closer the center of gravity comes to the edge of the triangle of support (Full et al. 2002). Reduction in stability or maneuverability can be expected to result in reduction in travel speed, distance traveled, and even refusal to travel.

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The dispersal ecology of these species relies on a poorly understood combination of flight and walking behaviors. In the case of the Colorado potato beetle, dispersal by walking is especially important for the colonization of rotated potato fields in the spring, foraging movements in the summer, and for their migration from a wide geographical area in late summer to overwintering sites (Weber and Ferro 1994; Boiteau et al. 2003).

The western corn rootworm, *Diabrotica virgifera virgifera* (LeConte), is very mobile and may stay within the emerging field with short visits to adjacent crops to feed and oviposit or disperse to fields shedding pollen (Drees et al. 1999). Rootworms walk up and down the corn stalk to feed on anthers, ear silk, or pollen deposits in leaf collars as well as to reproduce. Knowledge on rootworm walking activity is very limited and difficult to gather.

Walking behavior of plum curculio, *Conotrachelus nenuphar* (Herbst), adults marked with Zn65 has been studied in an experimental orchard (Lafleur et al. 1987). However, the use of such radioactive material is proscribed in commercial settings. Although there has been a great deal of effort directed toward development of effective tools to detect plum curculio activity within fruit orchards (Leskey et al. 2009), there is no reliable method at present. One of the key factors for development of an effective monitoring tool is a thorough understanding of plum curculio movement toward and within orchards and host trees. Adult plum curculios exhibit temperature-dependent movement; univoltine adults walk at temperatures below 20°C, while flight occurs at temperatures of ≥20°C or greater (Prokopy et al. 1999). Similarly, multivoltine adults also exhibited a strong propensity to fly at average daytime temperatures of 22°C based on pyramid trap captures targeting discrete movement patterns (Leskey 2006). Dispersal from overwintering sites into fruit orchards is strongly influenced by air temperatures early in the season (Piñero and Prokopy 2006) indicating that there may be much variation in terms of movement patterns toward host trees based on ambient temperature before fruit set. A harmonic radar detection system could provide much needed information on the relative role of walking and flight in the dispersal ecology of these species in real time and over a range of distances and locations.

The impact of the electronic tags was assessed in the laboratory by comparing the walking behavior of each beetle species with and without electronic tags in horizontal arenas using motion-monitoring equipment. All species are active climbers so a comparative test of the ability of the insects to climb with and without a tag on vertical surfaces was conducted.

Materials and Methods

Horizontal Walking Tests

The impact of tag weight on the walking activity of tracked Colorado potato beetles, plum curculios, and western corn rootworms was determined by comparing the distance, duration, and walking speed for each species with and without additional weights.

Insect Material and Treatments. Two-week old Colorado potato beetle adults were taken from the breeding colony at the Potato Research Centre of Agriculture and Agri-Food Canada, Fredericton, New Brunswick. They were maintained at room temperature (average: 23°C) on potato cultivar. Shepody for up to 2 more wk, Beetles were returned to their holding cage after the daily tests. All beetles tested were females to help standardize beetle size. Each beetle was marked using the method of Unruh and Chauvin (1993). Some of the same beetles were reused over time but never within the same day or over consecutive days. Treatments consisted of tagged and untagged beetles. A tag was placed on the pronotum of half of the beetles. Tagged and untagged beetles were tested alternately, over a period of 3 months. Each test day, two beetles were taken out of the holding cage and brought to the laboratory. The beetles tested in the morning had access to food up to the start of the test. In the afternoon, the test beetles had been left without food for 3 to 4 h before being placed in the arena. A total of 13 tagged and nine untagged beetles were evaluated in the morning experiment and nine tagged and 13 untagged beetles in the afternoon experiment.

Univoltine plum curculios adults were collected at the Agriculture and Agri-Food Canada experimental farm of Frelighsburg, QC, in June 2008. The individuals, sexed according to Thomson (1932), were kept in 1 liter jars in a rearing room at 22°C, 70% RH, 16L:8D, and fed with freshly cut apple pieces. The apple pieces were replaced twice a week. In preliminary assays conducted during their photophase, the activity of adults was intense and several adults flew out of the arena, impairing data acquisition with the Videomex. To address that point, the insects were acclimated to an inverse photoperiod so that assays were performed during the scotophase of the curculios. Curculios were prepared at the beginning of each assay and randomly assigned to six treatments: (1) Control (without glue or tag), (2) glue droplet on the pronotum, (3) copper tag, (4) copper/silver tag, (5) compact weight equivalent to that of copper tag, (6) compact weight equivalent to that of silver tags. In a given day, the treatments were assigned randomly. Compact metal masses close to the body of the insect were used to help determine if long dipole tags of similar masses have a negative impact on the stability of walking beetles.

Western corn rootworms were collected on the Central Experimental Farm of Ottawa, ON, in July 2007 and tests were carried out at Agriculture and Agri-Food Canada, Horticulture Research and Development Centre, Saint-Jean-sur-Richelieu, QC, Canada. Beetles were placed in cages held at 25°C, 70% RH, 16L:8D, and fed with organic romaine lettuce renewed every fourth day. Rootworm adults were sexed according to White (1977). Beetles were prepared at the beginning of each assay and randomly assigned to two treatments: (1) Control beetles (without glue or tag) and (2) beetles with tag.

Harmonic Radar Tags. Harmonic radar dipole tags were made on site using AWG #34 copper-coated steel wire measuring six and 6 mm on either side of a 1.0 mm diameter loop (3.47 mg; Boiteau and Colpitts 2001) for the Colorado potato beetle. Dipole tags for the plum curculio were also made on site using AWG#34 copper-coated steel wire and copper/silver plated 6% wire (AWG#41) measuring two and 6 mm on either side of a 1.0 mm loop (2.1 ± 0.02 mg). Compact metal masses consisting of sections of paper clip wire with average weight equivalent to that of copper or copper/silver tags were also made up for the plum curculio. Tags and compact masses (≈0.60 mg) were also made for the western corn rootworm using paper clip wire. Tags were attached vertically to the pronotum of adult Colorado potato beetles, plum curculios, and western corn rootworms using a small drop of glue (Crazy Glue evolved formula; Elmer's Products Canada, Corp., Scarborough, Ontario, Canada). The pronotum of the Colorado potato beetle was lightly sanded before applying the glue to remove waxes and increase the strength of the bond (Boiteau and Colpitts 2001).

Monitoring. The walking tracks of Colorado potato beetles, plum curculios, and western corn rootworms were recorded live using a motion monitoring device (Videomex V, Version 2.12, Columbus Instruments, Columbus, OH). Assays for the Colorado potato beetle used an arena consisting of a 70 cm diameter wooden platform surrounded by a 6.8 cm high white metal edge. The arena was filled with white sand to a depth of 5 mm and evenly lighted from above. The plum curculio and western corn rootworm arena consisted of 10 cm petri dishes. The camera was placed 70 and 25 cm above arena's centers for Colorado potato beetle and plum curculios-western corn rootworms, respectively. Noise thresholds were updated manually before each trial. The ambulatory threshold and the stereotypic threshold were set at 5.3 and 2.6 mm, respectively, in the case of the Colorado potato beetle. Beetles were released individually at the center of each arena. The acquisition of plum curculio data in near darkness was made possible by illumination with two 11-watt safelights (Brightlab Universal Red Junior Safelight, CPM Delta 1 Inc., Dallas, TX) underneath the semitransparent arena to produce enough contrast for the system to distinguish between the curculio and the test arena.

The motion monitor measured and recorded distance (millimeters) and ambulatory time (seconds) during 36, 5-min long consecutive sessions for each Colorado potato beetle and for each 15 1-min long consecutive sessions per plum curculio female and for each 20 1-min long consecutive sessions per western corn rootworm beetle. Percentage of sessions with walking activity and average speed were calculated. Movement data in each 15 or 20 min trial were averaged for each individual. Speed of walking (centimeters per square) was calculated by dividing distance traveled by ambulatory time.

Data Analysis. Colorado potato beetle, plum curculio, and western corn rootworm data were subsequently analyzed using the GLM procedure (SAS Institute 2002) to construct ANOVA tables for the total distance moved (centimeters), total ambulatory time (seconds), and mean speed (centimeters per square). Initially, for the Colorado potato beetle, the models included treatment (tag and no tags) and time of testing (morning and afternoon) as class variables. As time of testing had no significant effect, the data were pooled for the final analysis. Dependent variable data were log-transformed as homogeneity-of-variance assumptions were violated according to Levene's test. For the plum curculio, dependent variable data met the homogeneity-of-variance assumptions according to Levene's Test. The average parameters reported were based on $n = 22$ females. For the western corn rootworm dependent variable data met the homogeneity-of-variance assumptions according to Levene's Test. Western corn rootworm data of distance traveled, ambulatory time, and speed were subsequently analyzed using unpaired *t*-tests with the software Graphpad Prism version 4.01 (Graphpad Software Inc., 2004).

Vertical Walking Tests

The impact of the weight of the tag on the ability of the insects to walk on a vertical structure was assessed for the Colorado potato beetle and the plum curculios. It was not assessed for the western corn rootworm because tags could not be glued to its pronotum without affecting survival (Boiteau et al. 2009).

Colorado Potato Beetle. The experimental setup consisted of a display board made of cardboard with three panels that folded out so that the board could stand up by itself on a table (Boiteau 2005). The display board was painted black and a 60-watt incandescent light was centered above it. A 19 cm high, HB #2 pencil was placed vertically at the center of the arena's floor. Each test beetle was placed at the base of the pencil, facing the pencil to allow climbing behavior. Beetles started climbing almost immediately and the time taken to climb up and down the pencil once was recorded using a stopwatch. Individuals that had not started to climb down 2 min after reaching the top of the pencil were gently pushed down using a fine brush. Beetles that refused to walk down were not considered in the analysis. Twenty beetles with and 20 without an electronic tag were used in the test. The dipole tags, consisted of a 2 mm proximal pole followed by a 1 mm diameter loop and a 6 mm pole made of gauge 34 copper wires. The tags were attached to the beetles in the manner described in the previous test. Tests were conducted at room temperature. The walking speed of beetles with and without tags was compared using a Student's *t*-test on untransformed data.

Plum Curculio. Univoltine plum curculio adults of the summer generation were prepared and selected according to the same treatments as in the horizontal test. A 2.5 cm diameter by 22 cm height tube was constructed with a transparent plastic sheet. The tubes were fixed vertically to the center of a 9 cm diameter petri dish with Fun-Tak (Henkel Canada Corp.,

Table 1. Influence of electronic dipole tags on the horizontal walking parameters (means ± SEM) of adult Colorado potato beetles (A) over a 3 h period and (B) per 5 min session with activity in test arenas

Treatments	Distance ± SEM (cm)	Duration ± SEM (s)	Speed ± SEM (cm/s)
A: Over a 3 h period			
Tag	1235.12 ± 196.33a	1477.68 ± 232.32a	0.83 ± 0.010b
No tag	2770.95 ± 486.43a	3027.76 ± 515.39a	0.90 ± 0.016a
B: Per 5 min active sessions			
Tag	75.78 ± 5.05b	90.98 ± 5.55a	0.82 ± 0.011b
No tag	114.47 ± 11.92a	125.54 ± 11.74a	0.89 ± 0.015a

Within a treatment, means followed by the same letters are not significantly different ($P < 0.05$) (tag vs no tag comparisons).

Brampton, ON, Canada) laid on a table. A climb was considered successful if the individual reached a reference mark set 19 cm above the petri dish. An 11-watt safelight was placed over the tube to allow an observer to determine the movements in near darkness. The top of the tube was capped with a fresh piece of apple to confine the arena within the tube and stimulate movement. Observations were done simultaneously in six tubes, one per treatment. One adult was put on the petri dish and its walking behavior was followed during 20 min. Ten males and 10 females were tested three times for each treatment. The parameters observed were: percent of climbing success (climbing over the 19 cm mark), time required to climb at the 19 cm mark, and speed of walking. Data were analyzed using the GLM procedure (SAS Institute 2002) and all pair wise comparisons of means were performed with the LSMEANS statement. Dependent variable data were not transformed as homogeneity-of-variance assumptions were not violated according to Levene's Test.

Results

Horizontal Walking Tests

Colorado Potato Beetle. Attaching a 3.47 mg electronic tag, developed to track the Colorado potato beetle (Boiteau and Colpitts 2001), to the pronotum of female Colorado potato beetle did not significantly reduce the mean total distance and mean total time spent walking over a 3 h period compared with those without tags ($F = 2.88$; df = 1, 41; $P = 0.0974$ for distance; $F = 2.24$; df = 1, 42; $P = 0.1417$ for duration) (Table 1A). However, the mean walking speed for tagged beetles was significantly lower than for untagged beetles ($F = 13.41$; df = 1, 41; $P = 0.0007$).

Beetles with tags tended to have fewer observation periods with walking activity (15.18 ± 1.95 SEM) than beetles without tags (20.81 ± 2.72 SEM) although not significantly so ($t = 1.21$; df = 41; $P > 0.232$). In those observation periods with walking activity, the mean walking distance for beetles with tags for each 5 min observation period was significantly lower than for those without tags ($F = 4.09$; df = 1, 41; $P > 0.049$). The mean walking time was also lower but not significantly different ($F = 2.48$; df = 1, 41; $P = 0.123$) (Table 1B).

Plum Curculio. Attaching tags or weights to overwintered univoltine female plum curculios did not significantly reduce the distance or time spent walking (distance: $F = 1.18$; df = 5, 131; $P = 0.3236$; time: $F = 1.14$; df = 5, 131; $P = 0.3434$) (Table 2). A similar trend was observed with walking speed which was significantly reduced only by the addition of 0.55 mg elongated silver tags ($F = 2.93$; df = 5, 131; $P = 0.0155$) but not by the other weights. Attaching a long dipole tag had the same impact on the walking parameters as the short, compact tag of the same weight. The glue alone did not have a significant impact.

Corn Rootworm. The mean distance walked and the mean time spent walking with and without the 0.6 mg weight did not differ significantly for western corn rootworm adults. However, the mean speed of walking was significantly higher (14%) for rootworms with a weight than without a weight (Table 3). The proportion of sessions where walking took place was similar between males or females with or without weights.

Table 2. Influence of dipole tags and compact weights on the horizontal walking parameters (means ± SEM) of overwintered univoltine female plum curculio (n = 22) in test arenas

Treatments	Distance ± SEM (cm)	Duration of walking ± SEM (s)	Speed of walking ± SEM (cm/s)
Control	36.5 ± 6.2a	27.6 ± 3.5a	1.22 ± 0.09a
Glue	21.1 ± 5.3a	18.3 ± 3.3a	0.89 ± 0.08ab
Tag-Cu, 2.1 mg	26.7 ± 3.5a	25.3 ± 3.1a	1.02 ± 0.07ab
Tag-Ag, 0.55 mg	22.5 ± 5.4a	20.7 ± 3.9a	0.78 ± 0.10b
Weight 2.1 mg	28.9 ± 6.7a	24.2 ± 3.3a	1.02 ± 0.13ab
Weight 0.55 mg	22.6 ± 3.9a	19.9 ± 3.0a	0.85 ± 0.08ab

Means in a column followed by the different letters are significantly different ($P < 0.05$, Tukey's Studentized Range (HSD) test).

Table 3. Influence of dipole tags on the walking parameters (means ± SEM) of western corn rootworm adults in test arenas

Treatments (n)	Distance ± SEM (cm)	Duration of walking ± SEM (s)	Speed of walking ± SEM (cm/s)
Control (13)	22.03 ± 1.58	28.79 ± 1.56	0.74 ± 0.03
Weight, 6 mg (19)	23.75 ± 1.46	27.33 ± 1.19	0.84 ± 0.03
t-test (df)	0.74 (328)	0.77 (328)	2.11 (328)
P value	0.230	0.220	0.017

Mortality was high with western corn rootworm dying within 20 min after being glued. Because of the heavy mortality, sexes were combined in the table.

Table 4. Impact of dipole tag or compact wt on the vertical climbing parameters of summer generation univoltine (A) male (n = 10) and (B) female (n = 10) plum curculios in a 22 mm long plastic tube (n = 30 trials/treatment)

Treatments	Successful climb (%)	Duration of climb ± SEM (s)	Speed of climb ± SEM (cm/s)
A: Male			
Control	33.3 ± 8.8a	27.7 ± 3.9a	0.81 ± 0.10b
Glue	20.0 ± 7.4a	20.7 ± 5.5a	1.18 ± 0.20a
Tag-Cu, 2.1 mg	36.7 ± 8.9a	40.6 ± 7.3a	0.63 ± 0.11b
Tag-Ag, 0.55 mg	40.0 ± 9.1a	27.4 ± 3.2a	0.79 ± 0.08b
Weight 2.1 mg	36.7 ± 8.9a	34.1 ± 3.6a	0.63 ± 0.07b
Weight 0.55 mg	40.0 ± 9.1a	36.0 ± 7.2a	0.75 ± 0.11b
B: Female			
Control	73.3 ± 8.2a	31.4 ± 2.9a	0.75 ± 0.08a
Glue	63.3 ± 8.9a,b	27.16 ± 2.6a	0.80 ± 0.07a
Tag-Cu, 2.1 mg	33.3 ± 8.8c	32.1 ± 6.4a	0.76 ± 0.12a
Tag-Ag, 0.55 mg	43.3 ± 9.2bc	42.3 ± 10.8a	0.64 ± 0.08a
Weight 2.1 mg	30.0 ± 8.5c	47.7 ± 8.5a	0.55 ± 0.12a
Weight 0.55 mg	20.0 ± 7.4c	27.5 ± 6.0a	0.84 ± 0.15a

Means in a column followed by the same letters are not significantly different ($P < 0.05$, LSMEANS).

Vertical Walking Tests

Colorado Potato Beetle. The mean vertical upward walking speed of female Colorado potato beetles with tags (0.68 ± 0.06 cm/s) was not significantly different (t = 1.46; df = 38; P = 0.151) from that of potato beetles without tags (0.79 ± 0.05 cm/s). The mean vertical downward walking speed was slower than upward but the speed of potato beetles with tags (0.48 ± 0.04 cm/s) was not significantly different (t = 2.06; df = 24; P = 0.142) from that of potato beetles without tags (0.58 ± 0.05 cm/s).

Plum Curculio. The tags or compact weights equivalent to the mass of the tags did not significantly (F = 0.74; df = 5, 179; P = 0.596) affect the ability of males to climb the vertical pole in the experimental setup although very few males ascended the vertical pole in general including only 33.3% of the control group. However, 73.3% of females in the control group climbed the vertical pole and there were significant differences among treatments with those females with tags and compact weights having significantly lower percentages of successful climbs (F = 5.83; df = 5, 179; $P < 0.0001$) (Table 4). The time required to successfully complete a climb was not significantly affected by additional tags or weights (male: F = 1.43; df = 5, 61; P = 0.228; female: F = 1.68; df = 5, 77; P = 0.151). Furthermore, the mean vertical walking speed of females was not significantly affected by the added weights (F = 1.00; df = 5, 77; P = 0.424) but the vertical walking speed of males was (F = 2.41; df = 5, 61; P = 0.048).

Discussion

The weight of the tag is a critical parameter in the use of harmonic radars for insect tracking. Our results showed that the response of walking insects to the additional weight of tags is variable within and between species.

Results showed that the type and level of impact of a tag can vary according to the type of response of each sex or each species to different stimuli. For example, female plum curculios climbed a vertical pole more frequently than males. This is consistent with results in laboratory trials with the univoltine strain (Lamothe et al. 2008) in which significantly more females than males were captured in small pyramidal traps during scotophase (indicating a greater likelihood of females traversing a vertical trap surface compared with males), although there was no significant differences in captures during photophase (Lamothe et al. 2008). In our study, the addition of weights reduced the ability of females to climb the pole compared with males who were less likely to climb the pole in general. Multivoltine female plum curculios showed a climbing response similar to that of males in a parallel study (Boiteau et al. 2009). The ability of Colorado potato beetles to climb up or down was not assessed specifically but we noted that only a few individuals, with or without a tag, failed to climb the pole when placed at its base. The potato beetles normally do not climb downward especially in environments, such as this one, where the downward climb is against a light gradient. As a result, essentially all beetles, whether they had a weight or not, had to be gently probed with the paintbrush to engage in their downward climb.

The selection of tag weights and design cannot be based only on the absence of a visible impact on the walking activity of the tracked insect species. In the case of the Colorado potato beetle, tags representing 2.2% of the average body weight that had no visible (positive or negative) impact on the walking behavior of the adults were found to significantly reduce the mean walking speed by 8%. In the case of the plum curculio, 0.55 mg tags representing 3.9% of the average body weight that had no visible impact on the walking behavior of the adults were also found to significantly reduce the mean walking speed by 36%. However, heavier 2.1 mg tags and weights representing 14.7% of the plum curculio average body weight were found to reduce the mean walking speed by only 16% and nonsignificantly. In the case of the western corn rootworm, the mean walking speed was actually significantly increased by 14% by 0.6 mg weights representing 5% of the average weight of the insect. It is not clear, with the western corn rootworm, if the increase is attributable to the stress of the extra weight or to the latent lethal effect of the glue used to attach the tags as shown in Boiteau et al. (2009). Although the overall goal is to minimize the tag weight to body weight ratio, there is no single ratio that ensures that a tag will not adversely affect the walking parameters of the species tracked. The ratio will have to be determined for each species.

The study has demonstrated that tag weight can have a quantifiable impact on walking behavior and that the impact is not necessarily to reduce but can also be to increase locomotion parameters such as walking speed.

The key question becomes whether or not the significant changes in travel speed observed in the study would affect the walking and climbing activity to the point that it would alter the normal dispersal of the tracked insects when using the radar tracking technology. The question is not an easy one to answer but available evidence suggests that the effect would be acceptable. The horizontal walking speed changes obtained for insects with tags remained well within the range of speeds reported in other field and laboratory studies, at least for the Colorado potato beetle (0.82 cm/s for beetle with tag). The mean walking speed of the Colorado potato beetle free of any additional weights has been estimated or measured in different studies to reach as low as 0.44 cm/s and as high as 2.12 cm/s (Boiteau et al. 2003). Some records reflect sprinting speeds (Baker et al. 2007) and others different types of natural or artificial environments (Boiteau et al. 2003). There are no published records for the walking speed of the plum curculio or the western corn rootworm to compare our data with. It is only known that in apple orchards, marked adults marked with Zn65 can cover mean distances ranging from 350 cm/d in early September to 20 cm/d in late October (Lafleur et al. 1987). However, the range of walking speeds obtained here for plum curculios with tags (0.78–1.02 cm/s) and without tags (0.89–1.22 cm/s) is similar to that for Colorado potato beetles in optimal (laboratory) conditions. The mean walking speed of the western corn rootworm with tag (0.84 cm/s) and without tag (0.74 cm/s) is also similar to that for Colorado potato beetles. No studies actually documented vertical movement. Our study is the first to determine climbing ability and speed of Colorado potato beetle and plum curculio. Walking Colorado potato beetles (with or without tag/weights) confronted to a vertical gradient reduced their horizontal walking speed by the same 18% to walk up the pole and by a further 29% and 27%, respectively, to climb down the pole in the setup. The vertical travel speed of the female plum curculio was not significantly affected either by the presence of a tag but that of males was. The impact of the tags on the ability of the western corn rootworms to climb remains unknown because of the difficulty encountered in trying to attach a weight on the insect. The toxic nature of the glue used to attach the tag on the rootworm (Boiteau et al. 2009) may have affected the behavioral response measured. Thus, alternative bonding methods will have to be considered.

Although tag weight may occasionally have a significant impact on walking speed, they are but one of numerous constraints that insects come across in their environment. They represent an additional constraint to consider during the interpretation of the data. Pelletier and Caissie (2001) showed that Colorado potato beetles significantly reduced their walking speed when they had to drag weights corresponding to the gravitational force of a 20° or more slope. The dorsal tags studied here significantly reduced the walking speed of two of the species studied and can therefore be considered similar to the environmental constraints that beetles encounter such as a slight slope in the land.

Given that travel speeds, even when significantly impacted, remained within expected or realistic ranges and that distance and duration were not generally significantly affected by the presence of a tag, it is unlikely that the impact of the tag would adversely affect the insect from moving to the required habitat, obtaining food or shelter or mate, or other life needs. The use of trailing tags would seem less likely to affect the walking stability of insects than vertical tags. However, the comparison of tags and equivalent masses added to the back of plum curculios did not suggest that the walking behavior of the insects was substantially improved by a short, condensed weight compared with an elongated structure of identical mass. It may be that the substantial extension of the legs beyond the body itself provides insects even as narrow as the western corn rootworm with enough stability to compensate for the elongated tag towering above the insect. In practice, results suggest that the weights tested with male plum curculios are appropriate and will require only a slight reduction for females. It is possible that the large variability of the data obtained from Colorado potato beetles walking on a horizontal surface may have been partially because of the inability of the insects to adhere properly to the sand substrate in the test arena. The weight of the dipole tags used for the Colorado potato beetle in this study (3.47 mg) has now been reduced to 2.4 ± 0.001 mg (Boiteau et al. 2009). The shorter and lighter tags now available, in combination with the firm soil structure found within the field compared with sand used in test arenas are expected to help reduce the small negative effects of the additional weights on the performance of walking tracked Colorado potato beetles. The impact of the substrate on walking dispersal parameters of insects in the landscape warrants more investigation. An underestimation of the frequency of dispersal for beetles with tags is possible although the momentary differences may average out over a period of time.

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