

Dispersal of Warren Root Collar Weevils (Coleoptera: Curculionidae) in Three Types of Habitat

LAURA A. MACHIAL,^{1,2} B. STAFFAN LINDGREN,¹ ROBIN W. STEENWEG,¹
AND BRIAN H. AUKEMA^{1,3}

Environ. Entomol. 41(3): 578–586 (2012); DOI: <http://dx.doi.org/10.1603/EN11169>

ABSTRACT Warren root collar weevil, *Hyllobius warreni* Wood, is a native, flightless insect distributed throughout the boreal forest of North America. It is an emerging problem in young plantings of lodgepole pine, *Pinus contorta* variety *latifolia*, in western Canada, where larval feeding can kill young trees by girdling the root collar. Susceptible plantings are becoming more abundant following salvage harvesting and replanting activities in the wake of an ongoing epidemic of mountain pine beetle, *Dendroctonus ponderosae* (Hopkins). Previous studies using mark-trap-recapture methods found that movement rates of adult *H. warreni* were elevated in areas with high numbers of dead trees, consistent with a hypothesis that the insects immigrate from stands with high mountain pine beetle-caused tree mortality to young plantings in search of live hosts. Sampling methods were necessarily biased to insects captured in traps; however, potentially missing individuals that had died, left the study area, or simply remained stationary. Here, we used harmonic radar to examine weevil movement in three different habitats: open field, forest edge, and within a forest. We were able to reliably monitor all but two of 36 insects initially released, over 96 h (4 d). Weevils released in the open field had the highest rates of movement, followed by weevils released at the forest edge, then weevils released within the forest. Movement declined with decreasing ambient air temperature. Our results suggest that weevils tend to be relatively stationary in areas of live hosts, and hence may concentrate in a suitable area once such habitat is found.

KEY WORDS *Hyllobius warreni*, dispersal, harmonic radar, movement, sampling

Dispersal, the movement of a specified distance from one predefined habitat patch to another (Bennetts et al. 2001), is one of the most important life history processes that shape population dynamics and evolution (Hanski 1999, Bennetts et al. 2001). Knowledge of a species' dispersal patterns provides insight into how a population may respond to environmental changes such as habitat fragmentation, climate change, and incursions of invasive species (Dunning et al. 1995, Hanski 1999, Bowler and Benton 2004). Dispersal not only has direct impacts at the individual, population, and species levels, but also provides insight into how each level affects the others (Samietz and Berger 1997, Clobert et al. 2001, Bowler and Benton 2005, Coombs and Rodriguez 2007). The key to understanding dispersal, however, is through in-depth knowledge of how individuals move in natural settings (Samietz and Berger 1997, Turchin 1998, Clobert et al. 2001, Ramos-Fernandez et al. 2004). To best predict a population- or species-level response to disturbance, basic movement patterns of individuals within that population must be understood (Romero et al. 2010).

Warren root collar weevil (*Hyllobius warreni* Wood) (Coleoptera: Curculionidae) is a phytophagous insect native throughout Canada's boreal forests (Cerezke 1994). Much of the insect's biology and ecology was compiled in an excellent review by Cerezke (1994), so only a brief summary is provided here. Warren root collar weevil requires 2 yr to mature from an egg to an adult, and adult weevils can live up to 5 yr (Cerezke 1994). Adult weevils have a body length of 11.7–15.1 mm and are flightless. They are primarily active at night, when they ascend trees at dusk to feed on the branches, bark, and/or needles of coniferous trees (Warren 1956, 1966). Adult Warren root collar weevils overwinter within the top few centimeters of duff layer surface on the forest floor (Cerezke 1994). Female weevils deposit eggs at the root collar of host trees, or in the duff layer near a host tree. Developing larvae feed on the phloem around the host's large lateral roots and/or the root collar. As the insects mature, their feeding galleries become deeper, and they may score the xylem tissues (Warren 1956, Cerezke 1994). In British Columbia, the weevil's primary host is lodgepole pine, *Pinus contorta* variety *latifolia*, although they feed on a variety of hosts in the Pinaceae family including species of *Pinus*, *Picea*, *Abies*, *Larix*, and *Tsuga* (Warren 1956, Wood 1957, Whitney 1961,

¹ University of Northern British Columbia, 3333 University Way, Prince George, British Columbia, Canada, V2N 4Z9.

² Corresponding author, e-mail: lauramachial@gmail.com.

³ Department of Entomology, University of Minnesota, 1980 Folwell Ave, St. Paul, MN 55118.

Grant 1966, Wood and Van Sickle 1989, Cerezke 1994, Hopkins et al. 2009).

Historically, Warren root collar weevil was thought to be of minor economic concern to forests of western Canada. The feeding activity of adults typically causes only minor damage to hosts (Warren 1956, Cerezke 1994), although larval feeding on younger trees can girdle the roots and inflict mortality. Peak mortality occurs in stands 5–10 yr old, when trees have root collar diameters of <10 cm (Cerezke 1994). In recent years, feeding activity and subsequent mortality from this insect has increased (Schroff et al. 2006). This has coincided with an increase in replanted areas of young pine across the landscape in western Canada. These replantings have followed clear-cut salvage harvests of mature pine in the wake of an ongoing outbreak of mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae), that now extends over 16.3 million ha of forests of lodgepole pine since 1998 (Aukema et al. 2006, Walton 2010). Recently, Klingenberg et al. (2010b) noted an increase in mortality of trees within 100 m of unsalvaged stands affected by mountain pine beetle, and formulated a hypothesis that adult weevils migrate out of mature stands heavily affected by mountain pine beetle and concentrate in young regenerating forests in search of new hosts. This hypothesis was supported by data from a mark-recapture field experiment, in which the movement rates of the weevils were higher in areas of dead trees versus live trees (Klingenberg et al. 2010a).

Despite the empirical support for the hypothesis provided by Klingenberg et al.'s field study (Klingenberg et al. 2010a), a number of questions remain. First, although the experiment was conducted in experimental field plots with transplanted live (≈ 5 yr old) and "dead" trees (i.e., dead branches inserted into the ground of similar height to live trees), the suitability for comparison to areas with larger trees is unknown. Second, the recapture method used a Björklund trap designed to exploit the insects' nocturnal feeding behavior (Björklund 2009). Although the novel trap yielded an exceptional recapture rate of 35%, the method risks biasing inference of movement rates to only those individuals engaged in tree-climbing (or, more specifically, tree-descending) behavior. Despite several comprehensive field and observational studies (Reid 1954, cited in Cerezke 1994, 1969, cited in Cerezke 1994, Hoover 2000), we still know little about diel activity periods, or, more broadly, the cues involved in host location that could affect trapping efficiency (Machial et al. 2012).

In this paper, we investigate movement of adult Warren root collar weevils in areas with mature trees, an open field, and a forest edge using harmonic radar, a survey method that does not depend on trapping. Harmonic radar is a detection system originally designed for locating avalanche victims (Mascanzoni and Wallin 1986). It is composed of two parts: a transceiver and a transponder (Mascanzoni and Wallin 1986). The transceiver emits an initial signal referred to as the first harmonic. The transponder is composed

of a Schottky barrier diode and a wire antenna. It receives the transmitted signal from the transceiver and then reemits a second signal at double the original frequency. The transponder is powered by the initial signal and therefore does not require an independent battery source (Mascanzoni and Wallin 1986, Brazeo et al. 2005). Harmonic radar permits the investigator to track the movement path of an individual insect and typically yields higher resight rates than traditional mark-recapture studies. More information can be obtained from fewer individuals, as individuals can be found at any spatial and temporal point in the study (Mascanzoni and Wallin 1986, Williams et al. 2004, Hedin et al. 2007, Boiteau et al. 2011, Chapman et al. 2011). Consequently, researchers can discern between insects that have died and those that have left the boundary of the study (Mascanzoni and Wallin 1986, Turchin 1998, Hall and Hadfield 2009). Warren root collar weevils are ideally suited to studies involving harmonic radar because the insects are cryptic, slow moving, and unable to fly (Brazeo et al. 2005, Vinatier et al. 2010).

Materials and Methods

Study Organisms. From 26 April through 18 August 2010, 519 adult Warren root collar weevils were collected from ≈ 600 lodgepole pine trees in eight 7–12 yr old stands in the Prince George, British Columbia, Canada, area ($53^{\circ} 46' N$ $122^{\circ} 43' W$). Each tree had a Björklund funnel trap installed following the protocol described by Björklund (2009). The traps were checked for weevils ≈ 4 times per week. The majority of the weevils were collected from two 20–25 yr-old stands at the Prince George Tree Improvement Station.

The sex of each weevil was determined using techniques described by Öhrn et al. (2008). In addition, internal markings on the eighth sternite were examined to increase confidence in the accuracy of the identification (G.R.H., M.D.K., and B.H.A., unpublished data). Male and female weevils were kept separate, in groups of eight, in plastic containers ($L \times W \times H$, $15 \times 15 \times 5$ cm). Approximately 2–5 pieces of lodgepole pine branches that were 5–12 cm in length were placed in each container for food, along with a moist paper towel (Toivonen and Viiri 2006, Hopkins et al. 2009). Food was changed as needed. The weevils were stored in an environmental growth chamber at 75% RH, and a photoperiod of 12 L:D h; to slow the weevils' metabolism the ambient temperature was set to $8^{\circ}C$ (Toivonen and Viiri 2006).

Thirty-six weevils were selected at random (18 males and 18 females) for behavioral trials toward the end of the summer while still active. (The majority of the insects from collections were used in separate host-orientation experiments to test vision and inform experimental design; Machial et al. 2012.) Each weevil received a unique marking designating its individuality, sex, and location of release. Insects were restrained in a petri dish using plasticine (Flair Leisure Products, Cheam, Surrey, England). The elytra were then

etched with a rotary drill sensu Klingenberg et al. (2010a) as modified from previous studies on ground dwelling Coleoptera (Winder 2004). Etchings were filled with nontoxic latex-based paint (Citadel Color, Lenton, Nottingham, England) to emphasize the markings (Klingenberg et al. 2010a). Previous work demonstrated that etched and/or colored weevils did not suffer higher mortality than their unlabeled counterparts (Klingenberg 2008).

Using a sanding tip on the rotary drill, a patch of hair was carefully removed from a 1×1 mm area in the middle of the elytra near the weevil's head to serve as a place to attach a transponder. A transponder, composed of a Schottky barrier diode (RECCO AB, Lidköping, Sweden) and 0.05×50 mm copper wire, was then attached using a cyanoacrylate glue (The Original Super Glue, Nailene, Irvine, CA) (Brazee et al. 2005, Boiteau et al. 2009). The 50 mm length of copper wire for the transponder was chosen because it was the shortest length that produced a detectable signal from 2 m distance. A 2 m detection distance was deemed appropriate because it reflected the average distance moved by adult Warren root collar weevils per night in previous trapping studies (Cerezke 1994, Klingenberg et al. 2010a). We had previously determined that the cyanoacrylate glue was not toxic by applying it to the elytra of 10 adult insects in the summer of 2009. All of these weevils were still alive in 2010 and did not show behavioral differences compared with weevils collected at the same time that had not had glue applied (L.M., unpublished data).

Following transponder attachment, we allowed the glue to set for 15 min before releasing weevils from the plasticine. Upon release, the insects were returned to their holding containers. Twenty-four hours before the start of the experiment, the containers were removed from the environmental growth chamber and placed next to a window to expose the insects to a natural photoperiod.

Study Sites. We replicated our tracking experiments in two similar stands of lodgepole pine trees at the Prince George Tree Improvement Station. One replicate was conducted at the Bulkley #228 PLI (interior lodgepole pine) Provenance seed orchard, while the other replicate was conducted at the Central Plateau-Finlay #223 PLI Provenance seed orchard. Both orchards were between 20–25 yr old. The trees had a mean tree height of 11 m and mean diameter at breast height (1.3 m) of 19 cm. The orchards had carbonyl (GardenTech, Palatine, IL) applied to the boles of select trees 13 mo prior as a preventative measure against attack by pine engravers, *Ips pini* Say (Coleoptera: Curculionidae: Scolytinae) and mountain pine beetle. The ground cover in both orchards was predominately sheep fescue, *Festuca ovina* L., and white Dutch clover, *Trifolium repens* L.

Trees within the orchards were spaced ≈ 5 m apart. Each tree within the orchards had a unique tag and was mapped on a grid with alphabetically labeled tree rows and numerically labeled columns. The Bulkley orchard was 250×160 m, labeled A-FF and 1–50. The Central Plateau-Finlay orchard was 200×150 m, la-

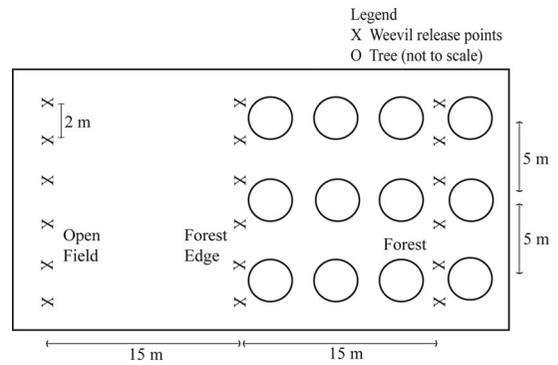


Fig. 1. Schematic diagram of experimental design for investigating movement of adult Warren root collar weevil. The experiment was composed of three transects, open field, forest edge, and forest, that were spaced 15 m apart. Trees within the forest habitat were ≈ 5 m apart. Six weevils, initially placed 2 m apart, were released per transect. The experiment was replicated in two plantations 29 August through 2 September 2010, Prince George, British Columbia, Canada. Note that drawing is not to exact scale.

beled A-DD and 1–40. A 50×100 m area in the SW corner of the Central Plateau-Finlay orchard was not planted. In both the Bulkley and Central Plateau-Finlay seed orchards, our experiments were conducted between rows P-R and columns 1–4. In the Bulkley orchard, two trees were removed from the grid because they had been attacked by *I. pini*. In the Central Plateau-Finlay orchard, one tree had been removed from the grid because of graft incompatibility.

Experimental Design. Our goal was to examine movement in three habitat types: open field, forest edge, and forest. We conducted our experiment by initially placing a weevil every 2 m along 12 m of the stand edge (six weevils total; 'forest edge' treatment) (Fig. 1). Simultaneously, we placed two sets of six weevils along two similar lines parallel to the stand edge; one 15 m away from the edge in the open field ('open field' treatment), and another 15 m into the orchard among the trees ('forest' treatment) (Fig. 1). The open field transects, located in a grassy field, did not have a canopy cover. The forest edge transects located 50 cm from the tree line toward the open field, had a mean (\pm SE) canopy cover of 48.6% ($\pm 7.3\%$). The mean (\pm SE) canopy cover of the forest transect was 58.8% ($\pm 4.0\%$). Canopy cover was determined by taking a picture of the canopy 50 cm above the ground at each spot where a weevil was released. A transparent grid was then placed over each picture, and percent canopy cover was estimated. Pictures were taken at each release point, and canopy estimates were pooled to determine mean cover for each transect.

When placing weevils along the transects, male and female weevils were released in alternating order and were placed on the ground randomly facing N, NE, E, SE, S, SW, W, or NW. A ground staple (Ground Staple Burlap Landscape, Quest Plastic, Mississauga, Ontario, Canada) was placed 2.5 cm north of each released

weevil. A small piece of flagging tape, labeled with the weevil's corresponding identification code, was attached to the ground staple.

Insect Release and Tracking. Weevils were initially released in both seed orchards at dusk (≈ 2100 h). After 1 h, each spot where a weevil had been released was revisited with a RECCO Detector (R9, RECCO AB, Lidingö, Sweden). The transceiver emitted a signal of 917 MHz, deemed the first harmonic. When the signal encountered a transponder on a weevil, a second signal was reemitted at 1834 MHz. The operator of the transceiver identified the second signal as an audible beep that became louder with increasing proximity. To locate each weevil, the transceiver operator began searching ≈ 2 m north of where the insect was last located. Searching involved holding the transceiver 50 cm above the ground and gradually moving toward the spot where the weevil had been last seen, using protocol adapted from the detector instruction guide (RECCO Technology 2010). The operator moved the transceiver in a slow sweeping motion: first in a north-south direction, and then in an east-west direction, while approaching the release spot. When a signal from a weevil was detected, the operator would decrease the size of the sweeps to hone in on the signal. After locating the spot with the strongest signal, the operator would turn off the transceiver and switch to a visual search. At night, a head lamp (TIKKA², Petzl America, Clearfield, UT) was used to aid in weevil location.

When the weevil was located, the distance from the ground staple was measured, taking into consideration the initial distance between the staple and the weevil. Movement was recorded as the distance moved along an XY coordinate plane (+y designated as movement north and +x designated as movement east). After the distance moved was recorded, the ground staple was repositioned 2.5 cm north from where the insect was found. During the first 24 h this procedure was repeated at 2300, 0700, 0800, and 1400 h to better gauge when weevils move; based on these observations this procedure was repeated in the morning and night each day at ≈ 0800 and 2100 h for the remainder of the experiment. The experiment was conducted from 29 August through 2 September 2010.

Statistical Analysis. Effects of habitat type (open field, forest edge, or forest) on the probability of adult Warren root collar weevil moving versus remaining stationary since the preceding check was analyzed using a generalized linear mixed-effects analysis of variance (ANOVA) with a binary response. A term for habitat type was fitted as a fixed-effect factor. Random effects included terms for the orchard site and weevil. To determine if weevils released in different habitats preferentially moved in one of the four cardinal directions (N, E, S, and W) a χ^2 contingency analysis was conducted for each habitat type.

A mixed-effects ANOVA model was used to investigate the effects of habitat type, time of day (i.e., day vs. night), and sex on the total net displacement and mean distanced traveled of adult Warren root collar weevils. An analysis of covariance (ANCOVA) in a

mixed-effects framework was used to investigate the effects of habitat type, temperature, and time since release on the movement rates (cm/h) of Warren root collar weevils. Fixed effects included terms for habitat type (a factor), and covariates of ambient air temperature and time since release of weevils. Hourly temperature data were obtained from the National Climate Data and Information Archive (Environment Canada 2010). A reciprocal transformation ($1/x$) was used to fit the variable for time since release, as exploratory data analysis indicated that movement rates tended to exponentially decay over time. Random effects included terms for orchard site and weevil.

Because some insects require a settling time upon release before resuming normal activity, we also executed the above analyses excluding the first 12 h of data as a putative settling time. For the ANOVA and ANCOVA analyses, we used graphical inspection of residual plots to examine model assumptions, namely equal variances and normal distribution of residuals. A $\log(y+1)$ transformation on our response variables was performed to satisfy these assumptions. Where significant differences between habitat treatments existed (using $\alpha = 0.05$), means comparisons were performed using protected *t*-tests (Carmer and Swanson 1973). All data analyses were performed using R 2.12.2 (R Core Development Team 2011).

Results

We were able to relocate 34 of the 36 insects released over the full 96 h of the experiments. Of the two insects that did not finish the experiments, one was never relocated, while the other was lost at $t = 23$ h. Each weevil was checked ≈ 15 times over the course of the experiment and all tracked insects exhibited some movement. The farthest distance moved during the 4 d of the experiment was 3.3 m by a weevil in the open field. The shortest distance moved was only 5 cm by a weevil in the forest. We found that all analyses of movement metrics were robust to exclusion of the first 12 h of data as a putative settling time; hence, all results reported below reflect the full complement of data collected.

On average, weevils were found to have changed positions since their last check ≈ 1 in three times, although this varied with type of habitat ($F_{2,31} = 3.65$, $P = 0.038$; Fig. 2). Weevils in the open field moved $\approx 15\%$ more often than weevils in the forest ($F_{1,30} = 10.56$, $P = 0.003$; Fig. 2). Weevils released in the forest edge habitat did not differ in the number of times that they moved compared with weevils in the open field or in the forest. Insects did not display a directional preference, instead moving randomly in all four cardinal directions independent of habitat type (open field: $\chi^2 = 7.27$, $df = 3$, $P = 0.06$; forest edge: $\chi^2 = 2.17$, $df = 3$, $P = 0.54$; forest: $\chi^2 = 4.53$, $df = 3$, $P = 0.21$). The effects of habitat type on mean net displacement ($F_{2,31} = 3.69$; $P = 0.038$), that is, the final displacement of a weevil at the end of the experiment from its original release point, as well as total distance moved ($F_{2,31} = 7.61$; $P = 0.002$), that is, the sum of its move-

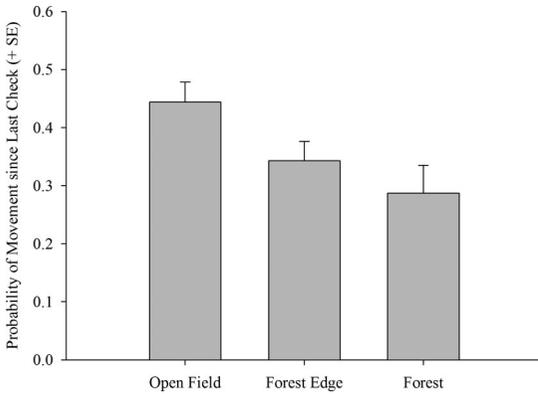


Fig. 2. Probability (+SE) that adult Warren root collar weevils moved since previous check in three habitat types: open field, forest edge, and forest. The statistical differences between the three habitat types are indicated by different lower case letters. The experiment was conducted from 29 August through 2 September 2010, Prince George, British Columbia, Canada; $n = 12$ weevils per treatment (6 insects \times 2 replicates).

ments between checks, were consistent with the patterns observed in frequency of movement. Weevils released in the open field exhibited the highest net displacement (Fig. 3A) and total (Fig. 3B) movements. These distances, generally less than 1 m over 4 d, were $>3.5\times$ greater than the movements exhibited by weevils in the forest habitat (Fig. 3). Total movement was not affected by time of day (day/night: $F_{1,33} = 1.67$; $P = 0.205$) or sex of insects ($F_{1,30} = 0.09$; $P = 0.77$).

When movement rate (cm/h) was examined with respect to habitat, temperature, and time variables collectively, we found that the movement rates of adult Warren root collar weevils differed among habitat types ($F_{2,31} = 6.95$; $P = 0.0032$), declined with decreased ambient air temperature ($F_{1,428} = 6.02$; $P = 0.0146$), and declined with lapsed time from initial release ($F_{1,428} = 205.0$; $P < 0.0001$). For clarity, we report each variable analyzed separately.

Adult Warren root collar weevils released in the open field habitat had a mean movement rate almost $4\times$ greater than movement displayed by weevils released in the forest habitat (Fig. 4). The mean speed of insects released in the open field was 2.5 cm/h (± 0.57 cm/h SE). The greatest speed demonstrated by an individual insect was 63 cm/h in the open field habitat. Movement rates for weevils in the forest edge habitat were not significantly different from those released in open field or forest habitat.

Movement rate of adult weevils tended to increase with increasing ambient air temperature (Fig. 5). For every degree that temperature increased, weevil movement increased by ≈ 0.2 cm per h. Weevils appeared active even at low temperatures, however. For example, the individual that moved 63 cm/h did so when the ambient temperature was only 6°C.

Overall, movement rates of weevils steadily decreased with time from release of weevils (Fig. 6).

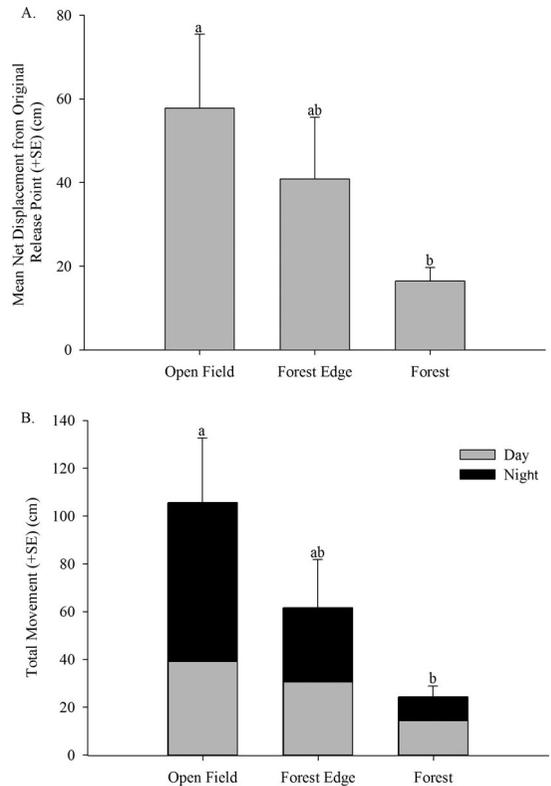


Fig. 3. (A) Mean net displacement from original release point (+SE) and (B). Total movement (+SE) (cm) of individual adult Warren root collar weevils released in one of three habitat types: open field, forest edge, or forest. The statistical difference between habitat types are indicated by different lower case letters. The experiment was conducted from 29 August through 2 September 2010, Prince George, British Columbia, Canada; $n = 12$ weevils per treatment (6 insects \times 2 replicates). In part B, mean total movement during day and night is displayed within each bar, although these differences were not statistically significant.

Initial movement rate averaged 5 cm/h, but this slowed considerably over the 4 d we tracked the insects. At the last observation on day 4, 26 of the 36 weevils had remained stationary for at least 24 h.

Discussion

Our results extend the findings of Klingenberg et al. (2010a) by demonstrating that Warren root collar weevils show elevated rates of movement not only in areas of dead hosts, but also in areas devoid of trees, compared with vicinities containing live host trees. This behavior mirrors that of other ground-walking beetles that move from habitats with poor or marginal food sources (Baars 1979, Wallin and Ekbohm 1988, Charrier et al. 1997, Kindvall et al. 1999). Escape and avoidance behavior is characterized by beetles covering long distances in a relatively constant direction (Baars 1979, Wallin 1991). Conversely, beetles in preferred habitats, such as those with an abundance of food or shelter, tend to travel shorter distances, and

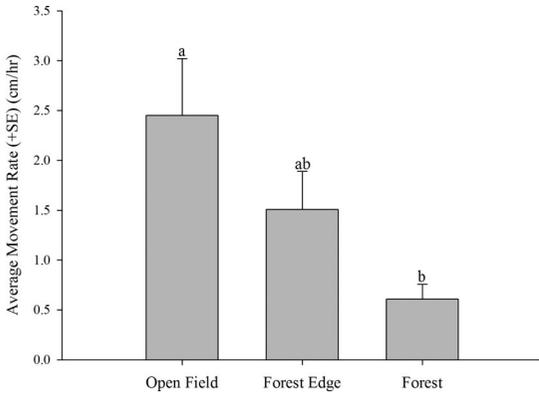


Fig. 4. Average movement rates (\pm SE) (cm/h) of adult Warren root collar weevils released in open field, forest edge, and forest habitat types. The experiment was conducted from 29 August through 2 September 2010, Prince George, British Columbia, Canada; $n = 12$ weevils per treatment (6 insects \times 2 replicates). Statistical difference between movement rates is indicated by different lower case letters.

may continually change directions and/or have longer residency times in such patches (Baars 1979, Wallin 1991, Romero et al. 2010). In our system, there was almost no litter layer in the open field where the grass was short and the ground was hard. Within the forest, litter was deeper and the ground softer. There, weevils could burrow more easily for cover and may not have felt the same urgency to move.

Decreased movement rates over time from release could reflect a decline in diel activity with progression of the fall season (Cerezke 1994), or simply be an artifact of the experimental design. Insects such as flea beetles, *Phyllotreta* spp., for example, may exhibit an initial increase in movement simply as a result of being

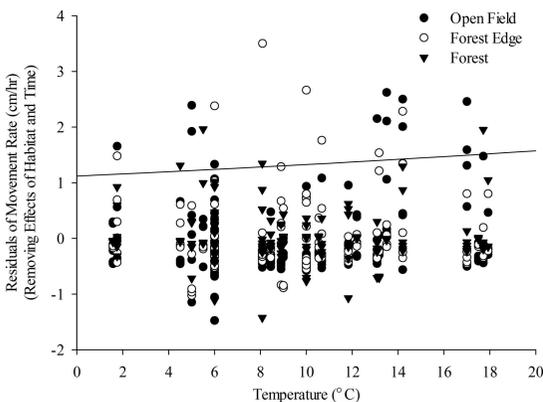


Fig. 5. Trends in adult Warren root collar weevil movement rate (cm/h) in three types of habitat (open field, forest edge, and forest) as a function of ambient air temperature ($^{\circ}$ C). Residuals of movement rate reflect the signal after removing the effect of habitat type; equation of trend line is $y = \exp(0.114 + 0.017x) - 1$; $F_{1,428} = 6.02$, $P = 0.0146$. The experiment was conducted from 29 August through 2 September 2010, Prince George, British Columbia, Canada; $n = 12$ weevils per treatment (6 insects \times 2 replicates).

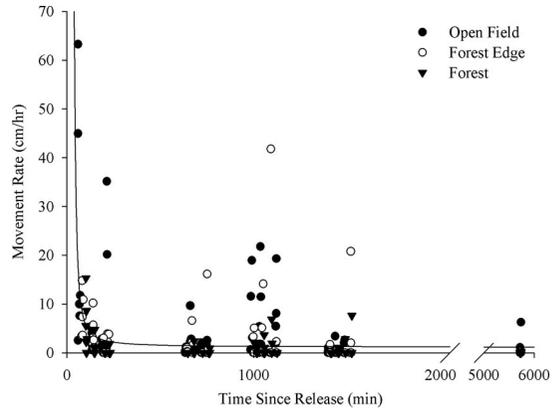


Fig. 6. Decay of movement rates (cm/h) of adult Warren root collar weevils following initial release in three types of habitat: open field, forest edge, and forest. For clarity, data from $t = 2,000$ min to 5,000 min is not displayed, but is included in analysis estimating line of best fit; $y = \exp(0.114 + 165*(1/x)) - 1$. The experiment was conducted from 29 August through 2 September 2010, Prince George, British Columbia, Canada; $n = 12$ weevils per treatment (6 insects \times 2 replicates).

marked and handled (Banks et al. 1985, Southwood and Henderson 2000). Because our results were robust to the exclusion of a 12-h settlement time, it is likely that all movement simply reflected habitat-dependent dispersal. The decline in movement rate through time likely reflected the successful location of suitable shelter by the insects. Similar movement in search of suitable microhabitats and shelter immediately upon release has been noted in radio telemetry studies with another duff-dwelling arthropod, the banana weevil, *Cosmopolites sordidus* (Germar) (Venetier 2010).

Our study adds another species to the list of insects that have been successfully tracked using harmonic radar. One of the largest hindrances in the development of harmonic radar technology for tracking insects has been negotiating a compromise between transponder detection and durability (Neal et al. 2004). We attempted to minimize this problem by using an antenna length that had a maximum detection range of ≈ 2 m, reflecting previous estimates of the average distance that Warren root collar weevils move per day (Cerezke 1994, Klingenberg et al. 2010a). As a result, we were able to use an antenna shorter than those previously used in other insect-tracking studies (Mascanzoni and Wallin 1986, Wallin and Ekbohm 1994, Roland et al. 1996). The short antenna decreased the weight of our transponders so that they were $\approx 10\%$ of the weevils' body mass. This is a lower transponder-to-weevil ratio of weights than those considered acceptable in other studies (Boiteau and Colpitts 2001, Brazee et al. 2005, Boiteau et al. 2010, Vinatier et al. 2010), and should have minimized behavioral changes such as hindrances of movement.

Over the duration of the study, we accounted for the movement behavior of all but two of the weevils

released. Because of the high success rate relocating weevils using this nontrapping sampling method, we estimate that most of the 65% of insects not relocated in Klingenberg et al. (2010a) did not leave their study area but simply found shelter in the duff layer. Our estimates of overall movements are considerably less than the 2 m/night suggested by previous studies (Cerezke 1994, Klingenberg et al. 2010a) for two reasons. First, previous studies were conducted earlier in the summer, when the insects are engaged in feeding or mate-finding behavior before oviposition (Cerezke 1994). Second, previous estimates may have been biased toward a subpopulation of insects more prone to moving and being captured in traps.

For a number of pine weevil species, optimal temperature ranges for activity, feeding, and oviposition are between 20–30°C (Christiansen and Bakke 1968, Taylor and Franklin 1970, Corneil and Wilson 1984a,b, Leather et al. 1994). In this experiment, the ambient air temperature ranged from 1–23°C, with an average of 10.6°C. Thus, temperatures were only briefly within the putative optimal range. Insect activity generally slows at lower temperatures; Warren root collar weevils exhibit little to no activity at 2.2°C, for example (Reid 1954, cited in Cerezke 1994). Similarly, a small number of *Hylobius pales* (Herbst) adults are active at 1.1°C, but movements are slow and infrequent (Taylor and Franklin 1970). Factors that typically govern insect behavior can change or even cease to be effective below certain temperature thresholds. For example, Corneil and Wilson (1984b) found that *H. pales* ignored decreases in light that, at higher temperatures, triggered the nocturnal portion of their daily cycle (e.g., ascending trees to feed) at temperatures below 10°C. Similarly, *Hylobius radialis* (Buchana) stopped climbing trees at dusk when temperatures dropped to 4°C (Wilson 1968). In our study, low temperatures may have obfuscated typical diurnal cycles. Warren root collar weevil is considered to be a nocturnally active insect (Cerezke 1994), but we found no difference between day and night total movements (Fig. 3B).

Reduced movement once burrowed into the duff layer suggests that weevils may concentrate in areas of live trees, such as in plantings of young pine when located next to forests with high numbers of mature, dead trees caused by mountain pine beetle (Klingenberg et al. 2010b). Despite increasing knowledge about patterns of movement by adult insects in different environments, we still know little about the diversity of cues involved in host location although initial research indicates that vision plays a key role in host orientation (Machial et al. 2012). Nonetheless, we are unsure of the relative importance of shelter versus host-seeking (for food and/or oviposition sites) as motivators for locomotion for this insect. Greater understanding of host orientation behavior should be a priority of future research, as it may lead to better management strategies in areas where required (Machial et al. 2012).

Acknowledgments

We thank Genny Michiel (University of Northern British Columbia) for excellent field and laboratory assistance, and the Prince George Tree Improvement Station for research space. Special thanks to N. Björklund, H. Bylund, H. Nordhem, and G. Nordlander of the Swedish Hylobius Research Program for their training and guidance using harmonic radar technology during a research training visit by L.A.M. to Sweden in May 2010, supported by a Graduate Research Travel Scholarship from UNBC. E. B. Radcliffe (University of Minnesota) provided valuable comments on earlier drafts of this manuscript. Funding for this project was provided by NSERC CGS and a UNBC Research Seed Grant to L.A.M., NSERC Research Tools and Instruments Grant to B.S.L., and NSERC Discovery Grant to B.H.A.

References Cited

- Aukema, B. H., A. L. Carroll, J. Zhu, K. F. Raffa, T. A. Sickle, and S. W. Taylor. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: spatiotemporal development and spatial synchrony within the present outbreak. *Ecography* 29: 427–441.
- Baars, M. 1979. Patterns of movement of radioactive carabid beetles. *Oecologia* 44: 125–140.
- Banks, H. T., P. M. Kareiva, and P. K. Lamm. 1985. Modeling insect dispersal and estimating parameters when mark-release techniques may cause initial disturbances. *J. Math. Biol.* 22: 259–277.
- Bennets, R. E., J. D. Nichols, J. D. Lebreton, R. Pradel, J. E. Hines, and W. M. Kitchens. 2001. Methods for estimating dispersal probabilities and related parameters, pp. 3–17. *In* J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols (eds.), *Dispersal*. Oxford University Press, New York.
- Björklund, N. 2009. Non-destructive tree-trunk funnel trap for capturing *Hylobius warreni* (Coleoptera: Curculionidae) ascending stems of trees. *Can. Entomol.* 141: 422–424.
- Boiteau, G., and B. G. Colpitts. 2001. Electronic tags for the tracking of insects in flight: effect of weight on flight performance of adult Colorado potato beetles. *Entomol. Exp. Appl.* 100: 187–193.
- Boiteau, G., F. Meloche, C. Vincent, and T. C. Leskey. 2009. Effectiveness of glues used for harmonic radar tag attachment and impact on survival and behavior of three insect pests. *Environ. Entomol.* 38: 168–75.
- Boiteau, G., C. Vincent, F. Meloche, and T. C. Leskey. 2010. Harmonic radar: assessing the impact of tag weight on walking activity of Colorado potato beetle, plum curculio, and western corn rootworm. *J. Econ. Entomol.* 103: 63–69.
- Boiteau, G., C. Vincent, F. Meloche, T. C. Leskey, and B. G. Colpitts. 2011. Harmonic radar: efficacy at detecting and recovering insects on agricultural host plants. *Pest Manage. Sci.* 67: 213–219.
- Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol. Rev. Cambridge Philos. Soc.* 80: 205–25.
- Brazee, R., E. Miller, M. Reding, M. Klein, B. Nudd, and H. Zhu. 2005. A transponder for harmonic radar tracking of the black vine weevil in behavioral research. *Trans. ASAE* 48: 831–838.
- Carmer, S. G., and M. R. Swanson. 1973. An evaluation of ten pairwise multiple comparison procedures by Monte Carlo methods. *J. Am. Stat. Assoc.* 68: 66.

- Cerezke, H. 1969. The distribution and abundance of the root weevil, *Hylobius warreni* Wood, in relation to lodgepole pine stand conditions in Alberta. Ph.D. dissertation, University of British Columbia, Vancouver, British Columbia, Canada.
- Cerezke, H. 1994. Warren rootcollar weevil, *Hylobius warreni* Wood (Coleoptera: Curculionidae), in Canada: ecology, behavior, damage relationships, and management. *Can. Entomol.* 126: 1383–1442.
- Chapman, J. W., V. A. Drake, and D. R. Reynolds. 2011. Recent insights from radar studies of insect flight. *Annu. Rev. Entomol.* 56: 337–356.
- Charrier, S. 1997. Movements of *Abax parallelepipedus* (Coleoptera, Carabidae) in woody habitats of a hedgerow network landscape: a radio-tracing study. *Agric. Ecosyst. Environ.* 61: 133–144.
- Christiansen, E., and A. Bakke. 1968. Temperature preference in adults of *Hylobius abietis* L. (Coleoptera: Curculionidae) during feeding and oviposition. *Nor. For. Res. Inst.* 62: 83–89.
- Clobert, J., J. O. Wolff, J. D. Nichols, E. Danchin, and A. A. Dhondt. 2001. Introduction, pp. xvii–xxi. In J. Clobert, E. Danchin, A. A. Dhondt, and J. D. Nichols (eds.), *Dispersal*. Oxford University Press, New York.
- Coombs, M. F., and M. A. Rodríguez. 2007. A field test of simple dispersal models as predictors of movement in a cohort of lake-dwelling brook charr. *J. Anim. Ecol.* 76: 45–57.
- Corneil, J. A., and L. F. Wilson. 1984a. Dispersion and seasonal activity of the pales weevil, *Hylobius pales* (Coleoptera: Curculionidae), in Michigan Christmas tree plantations. *Can. Entomol.* 116: 711–717.
- Corneil, J. A., and L. F. Wilson. 1984b. Some light and temperature effects on the behavior of the adult Pales weevil, *Hylobius pales* (Coleoptera: Curculionidae). *Gt. Lakes Entomol.* 17: 225–228.
- Dunning, J. B., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecol. Appl.* 5: 3.
- Environment Canada. 2010. National climate data and information archive. (www.climate.weatheroffice.gc.ca).
- Grant, J. 1966. The hosts and distribution of the root weevils *Hylobius pinicola* (Couper) and *H. warreni* Wood in British Columbia. *J. Entomol. Soc. B. C.* 63: 3–5.
- Hall, K. T., and M. G. Hadfield. 2009. Application of harmonic radar technology to monitor tree snail dispersal. *Invertebr. Biol.* 128: 9–15.
- Hanski, I. I. 1999. *Metapopulation ecology*. Oxford University Press, New York.
- Hedin, J., T. Ranius, S. G. Nilsson, and H. G. Smith. 2007. Restricted dispersal in a flying beetle assessed by telemetry. *Biodiversity Conserv.* 17: 675–684.
- Hoover, S. 2000. What do weevils do all night? The adult feeding and host selection behaviour and diurnal activity of *Hylobius warreni* Wood (Coleoptera: Curculionidae). Undergraduate thesis, University of Northern British Columbia, Prince George, British Columbia, Canada.
- Hopkins, G., M. D. Klingenberg, and B. H. Aukema. 2009. Temptations of weevil: feeding and ovipositional behaviour of *Hylobius warreni* Wood on host and nonhost bark in laboratory bioassays. *Agric. For. Entomol.* 11: 397–403.
- Kindvall, O., G. Nordlander, and H. Nordenhem. 1999. Movement behaviour of the pine weevil *Hylobius abietis* in relation to soil type: an arena experiment. *Entomol. Exp. Appl.* 95: 53–61.
- Klingenberg, M. D. 2008. Spatiotemporal associations between forests impacted by mountain pine beetle and adjacent replantings impacted by Warren root collar weevil. M.S. thesis, University of Northern British Columbia, Prince George, British Columbia, Canada.
- Klingenberg, M. D., N. Björklund, and B. H. Aukema. 2010a. Seeing the forest through the trees: differential dispersal of *Hylobius warreni* within modified forest habitats. *Environ. Entomol.* 39: 898–906.
- Klingenberg, M. D., B. S. Lindgren, M. P. Gillingham, and B. H. Aukema. 2010b. Management response to one insect pest may increase vulnerability to another. *J. Appl. Ecol.* 47: 566–574.
- Leather, S. R., S. I. Ahmed, and L. Hogan. 1994. Adult feeding preferences of the large pine weevil, *Hylobius abietis* (Coleoptera: Curculionidae). *Eur. J. Entomol.* 91: 385–385.
- Machial, L. A., B. S. Lindgren, and B. H. Aukema. 2012. The role of vision in host orientation behaviour of Warren root collar weevil, *Hylobius warreni* Wood (Coleoptera: Curculionidae). *Agr. For. Entomol.* (DOI: 10.1111/j.1461-9563.2012.00568x).
- Mascanzoni, D., and H. Wallin. 1986. The harmonic radar: a new method of tracing insects in the field. *Ecol. Entomol.* 11: 387–390.
- Neal, M.E.O., D. A. Landis, and E. Rothwell. 2004. Tracking insects with harmonic radar: a case study. *Am. Entomol.* 50: 212–218.
- Öhrn, P., M. D. Klingenberg, G. Hopkins, and N. Björklund. Two non-destructive techniques for determining the sex of live adult *Hylobius warreni*. *Can. Entomol.* 140: 617–620, 2008.
- R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. (<http://www.R-project.org>).
- Ramos-Fernandez, G., L. J. Mateos, O. Miramontes, G. Cocho, H. Larralde, and B. Ayala-Orozco. 2004. Levy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behav. Ecol. Sociobiol.* 55: 223–230.
- Reid, R. W. 1954. Summary of observations on *Hypomolyx* sp., 1952–1953. Canada Agriculture, Forest Biology Division, Calgary, Alberta, Canada. Unpublished file report.
- RECCO Technology. 2010. R9 detector user's guide, pp. 1–47. RECCO® AB, Lidingö Sweden.
- Roland, J., G. McKinnon, C. Backhouse, and P. D. Taylor. 1996. Even smaller radar tags on insects. *Nature* 381: 120.
- Romero, S. A., J. F. Campbell, J. R. Nechols, and K. A. With. 2010. Movement behavior of red flour beetle: response to habitat cues and patch boundaries. *Environ. Entomol.* 39: 919–929.
- Samietz, J., and U. Berger. 1997. Evaluation of movement parameters in insects: bias and robustness with regard to resight numbers. *Oecologia* 110: 40–49.
- Schroff, A., B. S. Lindgren, and M. P. Gillingham. 2006. Random acts of weevil: a spatial analysis of *Hylobius warreni* attack on *Pinus contorta* var. *latifolia* in the sub-boreal spruce zone of Northern Br. Columbia. *For. Ecol. Manage.* 227: 42–49.
- Southwood, R., and P. A. Henderson. 2000. *Ecological methods*. Blackwell, Malden, MA.
- Taylor, Jr., J. W., and R. T. Franklin. 1970. Biology of *Hylobius pales* (Coleoptera: Curculionidae) in the Georgia Piedmont. *Can. Entomol.* 102: 729–735.

- Toivonen, R., and H. Viiri. 2006. Adult large pine weevils *Hylobius abietis* feed on silver birch *Betula pendula* even in the presence of conifer seedlings. *Agric. For. Entomol.* 8: 121–128.
- Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in plants and animals. Sinauer, Sunderland, MA.
- Vinatier, F., A. Chailleux, P. F. Duyck, F. Salmon, F. Lescourret, and P. Tixier. 2010. Radiotelemetry unravels movements of a walking insect species in heterogeneous environments. *Anim. Behav.* 80: 221–229.
- Wallin, H. 1991. Movement patterns and foraging tactics of a caterpillar hunter inhabiting alfalfa fields. *Funct. Ecol.* 5: 740.
- Wallin, H., and B. S. Ekbohm. 1988. Movements of carabid beetles (Coleoptera: Carabidae) inhabiting cereal fields: a field tracing study. *Oecologia* 77: 39–43.
- Walton, A. 2010. BC ministry of forest and range, provincial-level projection of the current mountain pine beetle outbreak. Victoria, British Columbia, Canada. (<http://www.for.gov.bc.ca/hre/bcmpb/BCMPB.v7.BeetleProjection.Update.pdf>).
- Warner, R. E. 1966. A review of the *Hylobius* of North America, with a new species injurious to slash pine (Coleoptera: Curculionidae). *Col. Bull.* 20: 65–81.
- Warren, G. L. 1956. The effect of some site factors on the abundance of *Hypomolyx piceus* (Coleoptera: Curculionidae). *Ecology* 37: 132–139.
- Whitney, R. D. 1961. Root wounds and associated root rots of white spruce. *For. Chron.* 37: 401–411.
- Williams, D. W., G. Li, and R. Gao. 2004. Tracking movements of individual *Anoplophora glabripennis* (Coleoptera: Cerambycidae) adults: application of harmonic radar. *Environ. Entomol.* 33: 644–649.
- Wilson, L. F. 1968. Diel periodicity and survival behavior of pine root collar weevil adults under various light and temperature conditions. *Ann. Entomol. Soc. Am.* 61: 1490–1495.
- Winder, L. 2004. Marking by abrasion or branding and recapturing carabid beetles in studies of their movement. *Int. J. Pest Manage.* 50: 161–164.
- Wood, C. S., and G.A.V. Sickle. 1989. Forest insect and disease conditions British Columbia and Yukon 1989. Victoria, British Columbia, Canada.
- Wood, S. L. 1957. The North American allies of *Hylobius piceus* (De Geer) (Coleoptera: Curculionidae). *Can. Entomol.* 89: 37–43.

Received 14 July 2011; accepted 18 April 2012.
