

# Seeing the Forest Through the Trees: Differential Dispersal of *Hylobius warreni* Within Modified Forest Habitats

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**ABSTRACT** *Hylobius warreni* Wood, also known as the Warren root collar weevil, is a flightless insect that feeds on conifers throughout the boreal forests of Canada. Mature trees typically can withstand feeding, but larval feeding around the root collar may cause mortality to young trees. Recently, a large outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) has killed a high proportion of mature lodgepole pine (*Pinus contorta* Douglas variety *latifolia*) across British Columbia, Canada. This raises concerns that adult weevils may migrate from mature forests with reduced host pools into adjacent young forests that had been salvaged and replanted. To study movement of these walking weevils in different habitat types, we constructed three research plots consisting of various combinations of live-, dead-, and mixed (i.e., live and dead)-tree habitats. We observed dispersal patterns of individually labeled insects using a novel insect trap attached to the base of trees. Approximately 35% of insects were recaptured over 1 mo. Weevils were least likely to be recaptured proximate to the release location when released in a habitat with dead trees. Movement rates therein were almost double the rates of insects moving through live- or mixed-tree habitats. Our findings support the hypothesis that *H. warreni* may disperse out of habitats with dead trees into areas with higher proportions of green trees. Our findings are discussed in the context of habitat discrimination and potential increases in herbivory by *H. warreni* in western Canada given salvage harvesting activities after outbreaks of mountain pine beetle.

**KEY WORDS** *Hylobius warreni*, mark-recapture, mark-release, dispersal, matrix habitat

Elucidating processes that contribute to spatial patterns of the dispersal of insect herbivores is a challenge, as dispersal may depend on multiple and interacting factors, including the physiological status of the insects (e.g., reproductive status, energy reserves) and population density (e.g., migration, crowding). Habitat conditions, such as composition and quality of the habitat matrix or patches, may also affect insect dispersal (Nathan et al. 2003, Haynes and Cronin 2006). For example, within boreal forest ecosystems, habitat alterations such as clear-cut harvesting can affect the spatial distribution of insect assemblages (Welty and Houseweart 1985, Niemelä et al. 1993, Bengtsson et al. 1997, Örlander et al. 1997, Heliölä et al. 2001, Lemieux and Lindgren 2004, Phillips et al. 2006). Species perturbations in forested environments are not limited to anthropogenic impacts. For example, insect disturbances may affect the spatial or temporal dynamics of

other insects as well (Denno et al. 1995). Currently, for example, there is a large outbreak of mountain pine beetle, *Dendroctonus ponderosae* Hopkins, modifying the forest landscape in British Columbia, Canada (Aukema et al. 2006). This outbreak has precipitated concern regarding how major, sudden habitat changes may affect vertebrates such as woodland caribou *Rangifer tarandus caribou* Gmelin (McNay et al. 2006), but the effects on insect species are less well studied. The current study examines the effects of habitat quality on the spatial distribution and movement of Warren root collar weevil, *Hylobius warreni* Wood (Coleoptera: Curculionidae).

Much of the natural history and ecology of *H. warreni* has been summarized by the pioneering work of Warren (1960) and Cerezke (1994). In brief, *H. warreni* are found throughout the boreal forests of North America, feeding on a variety of conifer tree species. Adults feed on coniferous foliage above ground. Females lay up to 25 eggs per year in the duff layer around the root collar of trees. Upon eclosion, larvae feed on the phloem tissues of the root collar, protected by a hard casing consisting of a mix of frass and tree resin (Cerezke 1970). After 2 yr of feeding at the root collar, larvae pupate and adults emerge. In the spring months, adults feed nocturnally on young shoots of coniferous trees in preparation for mating and oviposition that occur throughout the summer and fall

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(Cerezke 1994). Adults may live for up to 5 yr, and remain flightless throughout their entire life cycles (Cerezke 1994).

Forest health issues with *H. warreni* are predominately related to larval feeding. Adult feeding is not detrimental to the tree host, but larval feeding may inhibit growth, or even result in tree death, by girdling of the stem and disrupting translocation (Cerezke 1974). Although insects do not feed on dead trees, larvae and pupae may mature on residual stumps after harvesting, thus supplying weevils to the regenerating forest. Populations are frequently maintained throughout the life of the stand (Cerezke 1973). Mortality to young trees by larval feeding may be exacerbated by root deformation resulting from planting practices (Robert and Lindgren 2006), as well as by root rots introduced at feeding scars (Whitney 1961, 1962).

*H. warreni* appears to be an emerging concern in forests in western Canada, particularly in areas with extensive ongoing reforestation or regeneration after the current outbreak of mountain pine beetle. Whereas a vast amount of research exists on the ecology and management of related *Hylobius* spp. such as *Hylobius pales* Herbst and *Hylobius radialis* Buchanan in the northeastern United States (Corneil and Wilson 1984, Hunt et al. 1993) and *Hylobius abietis* L. in northern Europe (Nordlander et al. 1997, Leather et al. 1999, Bylund et al. 2004, Nordlander et al. 2005, Wallertz et al. 2006), including studies on dispersal patterns (Rieske and Raffa 1990, Eidmann 1997), little information exists on the movement or dispersal patterns of *H. warreni* (Schroff et al. 2006). In this study, we examine the dispersal patterns and movement rates of *H. warreni* through different environments containing live and dead trees using a label, release, and recapture experiment using a novel trap. We hypothesize that weevils may exhibit the highest movement rates through habitats with dead trees, which, in natural settings could complicate reforestation efforts as a result of emigration from stands with high proportions of pine killed by *D. ponderosae*.

## Materials and Methods

**Trap Development and Collection of Insects.** *H. warreni* were collected daily from a  $\approx$ 15-yr-old pine forest near Prince George, British Columbia, Canada ( $53^{\circ}55'14''\text{N}$ ,  $122^{\circ}49'10''\text{W}$ ), using a Björklund funnel trap attached to the base of each tree (Björklund 2009). These traps exploit the insects' nocturnal feeding behavior and capture them alive, without chemicals, when they descend from the foliage to rest during dawn hours (Fig. 1). The trap was developed during the summer of 2006 in a plantation of 182 trees ranging in diameter from 3.8 to 13.7 cm (Fig. 2). The site was chosen because visual inspection revealed high levels of weevil activity, estimated at 0.5 insects per tree based on insect abundance-diameter relationships described in Fig. 15A of Cerezke (1994). The plantation consisted of planted lodgepole pine (*Pinus contorta* variety *latifolia*) with some natural ingress of

both interior hybrid spruce (*Picea glauca*  $\times$  *engelmannii*) and Douglas-fir (*Pseudotsuga menziesii*). Small gaps had formed where weevils had previously killed young trees, although only live trees were used for the study. A trap was placed on each tree, and the contents were emptied each morning. Weevils were returned to the plantation near the bases of the trees where they were captured. After settling on a working prototype and finding no evidence of avoidance behavior (Björklund 2009), we collected 300 weevils from 8 May 2007 to 5 June 2007. Insects were stored in growth chambers at  $7^{\circ}\text{C}$  to reduce the insects' metabolism until experiment initiation (Toivonen and Viiri 2006).

**Labeling of Insects.** Each weevil was labeled in the laboratory by etching the elytra, a technique used previously for other ground-dwelling arthropods (Winder 2004). We had previously experimented with latex paint, but the paint rubbed off over time as the insects burrowed through leaf litter. Insects were secured in petri dishes using plasticine (Flair Leisure Products, Surrey, United Kingdom) before etching labels into the elytra with a high speed Dremel rotary drill (engraving cutter bit number 106). To accentuate markings, elytral etchings were traced using nontoxic latex-based model paint (Humbrol Paints, Hornby Hobbies, Kent, United Kingdom). Each weevil was labeled with a unique dot-and-number code representing 0–99 in either blue, green, or yellow for tracing to specific release points. To investigate whether labeling affected insect survival, 12 labeled and 12 unlabeled weevils were placed in petri dishes (10-cm diameter) containing clippings of lodgepole pine and moistened filter paper. New lodgepole pine branches were added every week, and filter paper was moistened as necessary. Insect survival in the groups of labeled and unlabeled insects was monitored over a 2-wk period.

The sexes of weevils released for the experiment were not identified, because at the time of these experiments, a noninvasive technique for sexing had not yet been developed for this species (Cerezke 1994, but now see Öhrn et al. 2008). Dissections of 12 randomly selected weevils captured in the same forest used to obtain weevils for this experiment revealed approximately equal proportions of males and females (7:5), consistent with previous field observations (Stark 1959, Warren 1960, Cerezke 1994).

**Plot Design and Insect Release.** We established three experimental plots at the Prince George Tree Improvement Station, British Columbia, Canada ( $53^{\circ}46'18''\text{N}$ ,  $122^{\circ}43'4''\text{W}$ ), with a mix of different habitat types. The plots were established within uniform grassy areas at least 20 m from any trees, to reduce potential migration of unlabeled, feral weevils into the experimental plots. Plots were 22 m in width and 44 m in length, divided into four adjacent sections 11 m in length. In each plot, the middle and outer sections were planted with different combinations of live and dead trees to simulate different habitat types. Live lodgepole pine trees were  $\approx$ 5 yr of age and 1.25 m in height, suitable for both a food source and reproduction for the insects (Cerezke 1994). Surrogate dead



Fig. 1. Photo of Björklund funnel trap. Detailed instructions on its construction can be found in Björklund (2009).

trees were established by planting dead branches of lodgepole pine of similar size as the live trees, upright into the ground. After planting, each plot contained 200 trees at 2-m spacing (Fig. 3). Trees were transplanted from a tree nursery with leftover planting stock for the Prince George region and watered with a drip irrigation line for 2 wk before the introduction of the insects.

The first plot simulated a forest of dead trees adjacent to live trees and was planted live:dead:dead:live (Fig. 3A). The second plot simulated a forest with live trees, adjacent to one with dead trees, an exact opposite scheme to the previous (Fig. 3B). The four 11-m sections were planted dead:live:live:dead. Finally, the third plot simulated a stand with a high percentage of dead trees adjacent to a stand with solely dead trees (Fig. 3C). The layout was similar to the first plot, but half of the live trees were replaced with surrogate dead trees so that there was a 4-m spacing of live trees. Hence, the sections appeared dead:mixed:mixed:dead. In summary, each plot had 10 rows of 20 trees with each of the four adjacent sections in each plot con-

taining 10 rows of five trees. Plots were separated by a minimum of 10 m.

In each plot, a Björklund funnel trap (Björklund 2009) was installed on each live tree and each dead tree. Traps were placed on dead trees as well as live trees because previous laboratory assays indicated that weevils may be as likely to climb dead versus live trees (M.D.K. and B.H.A., unpublished data).

On 14 June 2007,  $\approx 100$  labeled weevils were released along a center line in each of the plots (95, 92, and 101 insects in each of the plots of Fig. 3, A, B, and C, respectively). Plots received unequal numbers because of mislabeling and weevil escapes in the laboratory postlabeling. This total density of  $\approx 100$  weevils per plot, or 0.5 insects per tree, is within the range of field densities described in Cerezke (1994) (i.e., 0.03–2.55 insects per tree in lodgepole pine), and reflects the estimated field density of insects in the plantation used for trap development. Approximately 10 weevils were released every 2 m. Weevil captures were recorded daily on each tree for 8 d and then checked approximately every other day until 13 July for a total



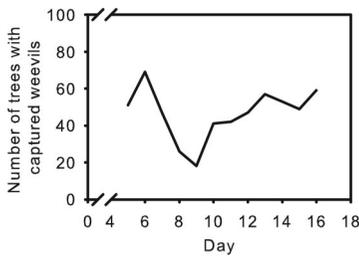


Fig. 4. Number of trees with trapped weevils over a representative 12-d period during trap development (30 May–11 June 2006). The first 5 d are excluded as not all traps were installed. See Björklund (2009) for more details.

The probability of capture is distinct from movement rate. To examine potential differences in movement rates when weevils were released into live, dead, or mixed habitats, we analyzed the distance traveled along the  $x$ -axis versus number of days after release for all initial captures. This analysis was restricted to capture events recorded within the first 11 d of the experiment, because >80% of the capture events occurred within this time. Moreover, this restriction excluded subsequent captures for any given insect to avoid potential capture bias (i.e., a few insects were captured more than once; see “Results”). Different analysis of covariance parameterizations, depending on which terms are included, yield ecological models with various meanings. For example, models exhibiting uniform or disparate intercepts and slopes can be constructed by including or omitting the covariate, time (i.e., yielding slope estimates of movement rate(s) in meters per day), the factor, habitat type (i.e., providing additive a priori distance(s) moved by the insects immediately upon release at  $t = 0$ , depending on habitat types), and the covariate by factor interaction (i.e., yielding nonparallel lines, or dissimilar movement rates between habitat types). We fit a variety of analysis of covariance models, including one that forced a common intercept through zero (indicating stationary insects immediately upon release). The model with the highest adjusted  $R^2$  was chosen as the most suitable model, in conjunction with examinations of residual plots to assess assumptions of normality of errors and homoscedasticity. Where differences among movement rates existed, a comparison of movement rates between dead-tree versus live- and mixed-tree habitat types was performed using a linear contrast, setting  $\alpha = 0.05$ . All data analyses were conducted in R v.2.6.2 (R Development Core Team 2008).

## Results

**Trap Development.** The Björklund funnel trap captured weevils across the natural plantation, with between 10 and 38% of the trees harboring a captured weevil on any given day (Fig. 4). Captures did not decline over a 12-d period after all traps were deployed (Fig. 4). Weevils were captured on all but the smallest trees (3.8 cm), as the minimum diameter of trees harboring trapped weevils was 4.3 cm. On aver-

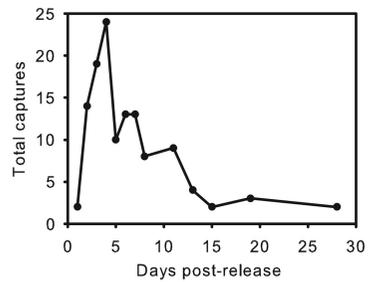


Fig. 5. Total number of *H. warreni* captures after initial release on 14 June 2007. Captures are summed over all plots.

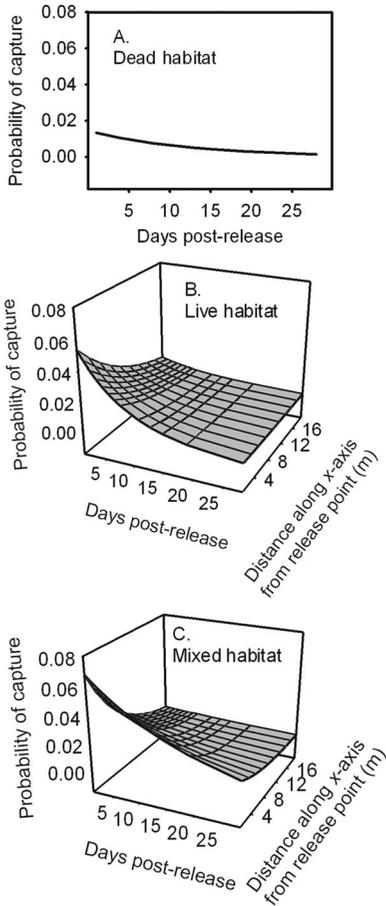
age, weevils were captured on trees 9.2 cm in diameter, which was 1.1 cm larger than trees with traps without weevils ( $F = 121.12$ ;  $df = 1, 2171$ ;  $P < 0.0001$ ).

**Dispersal in Habitats of Different Types.** The elytral etching and labeling technique did not reduce the survival of weevils. In our preliminary laboratory assay, no mortality was observed in either the labeled or unlabeled groups after a period of 2 wk.

A total of 101 of the 288 weevils initially released was recaptured over the 28 d, a recovery rate of 35.1% (Fig. 5). Twelve of these weevils were captured more than once. One weevil was captured four times, and one weevil was captured three times in total. The number of weevils captured peaked on the fourth day of the experiment, whereas the last recorded capture occurred on day 19. During the course of the experiment, weevils were captured throughout each of the three plots on 13.5% of the total trees. The first place in which a weevil was captured ranged between 1 and 17 m from the initial release locations (Fig. 3). On average, weevils, released into habitats with live trees, moved 6.9 m, compared with 9.6 m when released into a habitat of dead trees. Insects released in a habitat of mixed live and dead trees moved, on average, 5.7 m before their first capture. The furthest that any weevil moved in 1 d was 15 m.

In general, weevil capture was associated with two variables: displacement along the  $x$ -axis from the release line and time since initial release (Fig. 6). The probabilities of capture declined with distance from the release line and days since release when weevils were released in the live and mixed habitats (Fig. 6, B and C). In the plot where weevils were released among dead trees, however, only time since release was a significant predictor of likelihood of a tree capturing an insect (Fig. 6A). Variables that were not significant in explaining the likelihood of insect capture included distance along the  $y$ -axis to the nearest margin, initial density of weevils released, direction from the release line, presence of bark beetles in the stems of live trees, and the status of individual trees (live/dead).

Movement rate, defined as the relationship between distance in the  $x$  direction traveled from the release line and time since release to initial capture, varied between the experimental habitat types (Fig. 7). The model represented in this figure exhibits a common intercept among the three central habitat types in

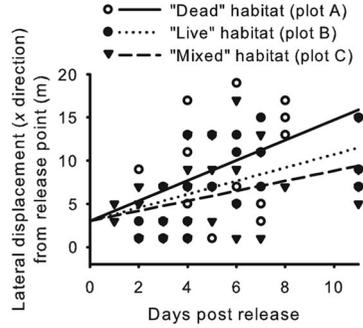


**Fig. 6.** Effect of time since initial release (in days) and horizontal distance from release line (in meters) on the probability of capturing a weevil on an individual tree in three experimental plots. Each figure label refers to habitat type in center of plot where the insects were released (see Fig. 3). Equations for each plot are (A)  $y = -4.23 \pm 0.34 - 0.081 \pm 0.040$  (time); (B)  $y = -2.65 \pm 0.37 - 0.10 \pm 0.034$  (distance)  $- 0.13 \pm 0.040$  (time); (C)  $y = -2.42 \pm 0.30 - 0.15 \pm 0.031$  (distance)  $- 0.057 \pm 0.024$  (time). For all equations, probabilities may be obtained by back transforming values  $\exp^y / 1 + \exp^y$  (i.e., back transforming the logit link characteristic of logistic regression).

each plot of  $3.02 \pm 0.99$  m. That is, when the insects were released, they appeared to travel 3 m a priori. Movement rates varied among habitat types ( $F = 4.26$ ;  $df = 2, 85$ ;  $P = 0.0173$ ). Weevils exhibited the highest movement rates when released into dead habitat (center of plot A in Fig. 3), moving at  $1.17 \pm 0.23$  m/d. This was significantly higher than movement rates through live ( $0.77 \pm 0.21$  m/d) and mixed habitat ( $0.58 \pm 0.18$  m/d) (centers of plots B and C, respectively, in Fig. 4) ( $t = 2.73$ ;  $df = 86$ ;  $P = 0.0077$ ).

**Discussion**

Our results demonstrate that habitat quality, defined as varying composition of live versus dead trees,



**Fig. 7.** Movement rates of *H. warreni* released into the center of three experimental plots with combinations of dead-, live-, and mixed-tree habitats (see Fig. 3). Model contains the covariate for time and the time  $\times$  habitat type interaction ( $F = 9.16$ ;  $df = 3, 85$ ;  $P < 0.0001$ ;  $R^2_{adj} = 0.24$ ). See text for the equations of lines. There are 88 insects included in this analysis, although some symbols may overlap.

affects the movement and distribution of *H. warreni*. Movement rates are elevated in the plot with dead trees in the center and lower in plots with live trees in the center, providing evidence that *H. warreni* may migrate away from areas with high proportions of dead trees and concentrate in areas with live trees. These findings are important within the context of the recent outbreak of mountain pine beetle in British Columbia, which now encompasses >13 million ha of mature lodgepole pine forests (Westfall and Ebata 2009). In many areas, extensive salvage harvesting and reforestation efforts have created circumstances in which young lodgepole pine forests are planted adjacent to unharvested, mature forests containing high proportions of trees recently killed by mountain pine beetle. In many areas, a gradient of young-tree mortality caused by *H. warreni* exists from mature forest boundaries into young replantings (Klingenberg 2008). The current study lends support to a proposed mechanism, i.e., that *H. warreni* are migrating out of mature stands heavily affected by mountain pine beetle (i.e., those with few live hosts), and concentrating in these young, regenerating forests. Because almost all coniferous forests contain endemic populations of *H. warreni* (Cerezke 1967), and recent estimates of tree mortality in the central interior of British Columbia reach as high as 16% (Schroff et al. 2006), the migration of *H. warreni* into young forests may add to pressures from residual populations completing development on residual stumps after harvesting operations (Cerezke 1973).

Our results that rates of displacement along the x-axis from the release line were highest when released into a plot with a high proportion of dead trees in the center ( $1.17$  m/night) versus those with proportions of live trees ( $0.77$  and  $0.58$  m/night) in the center suggest that movement of *H. warreni* is predominantly related to host selection for feeding and/or oviposition. Comparisons with field data in mature forests of live lodgepole pine, presumably a better food resource than the juvenile trees we trans-

planted, support this hypothesis. For example, previous studies have indicated that *H. warreni* disperse 2.3 m, on average, during one night, in mature pine forests with tree spacing similar to our experimental plots (2.5 m) (Cerezke 1994). Assuming movements in random directions among hosts, the distribution of lateral movement distances can be obtained from the equation  $2.3 \text{ m} \sin(\theta)$ , where  $\theta \approx$  uniform (0, 90). Given equal probabilities of movement in either of two lateral directions, a random sample of seven lateral displacements from this distribution yields a 1-wk total lateral displacement of 3.46 m, or an average lateral movement rate of 0.5 m/night. If weevils stay stationary for one or more nights, which is likely on mature hosts that accommodate higher levels of feeding and oviposition (Cerezke 1994; N.B., unpublished data), realized lateral movement rates would be  $<0.5$  m/night. Such estimates, combined with our findings that movement rate is highest when released into a habitat with a high proportion of dead trees (1.17 m/night), provide evidence that dispersal of adult *H. warreni* is predominantly characterized by host-seeking behavior.

Other behaviors that may be associated with insect movement include a priori dispersal, immediately upon release, as an escape response or to reduce crowding. For example, the initial lateral distance traveled by an insect before capture, regardless of habitat type, was 3 m (i.e., intercept in Fig. 7). This distance is consistent with distance to a proximate tree from the release line, as the first two rows of trees were located at 1 and 3 m from the release line (Fig. 3). We lack data, however, on how fluctuating population densities at a larger scale (e.g., entire forest level) might affect movement rates via crowding or interspecific competition for food or oviposition site resources. As a result of interspecific competition, for example, movement rates in field settings may be depressed when insect levels reach a point of saturation in a young forest.

Temporally, the probability of a tree capturing a weevil declined during the course of the experiment in all three plots as the insects dispersed, and weevils were progressively less likely to be captured within a habitat patch. Previously, it was thought that adult *H. warreni* may move up to 13 m during one season (Henigman et al. 2001). Given that females are engaged in host-seeking and ovipositional behavior for  $\approx 100$  d in the summer months (Cerezke 1994), and our findings that insects can move up to 10–15 m in one night, it is not improbable that these insects may move 50–100 m a year or more, especially when suitable hosts are scarce.

Spatially, the probability of individual trees capturing weevils was highest closest to the release line in plots with live trees closest to the release location. The lack of such a spatial effect when insects were released into a habitat with dead trees (Fig. 6A) was most likely because of the rapidity with which the insects moved away from the release line (Fig. 7). An alternative, but not mutually exclusive, explanation is that the lack of a distance effect in that plot is an artifact of capture

bias on live versus dead trees, as both plots where distance effects were exhibited contained live trees proximate to the release lines. Because *H. warreni* do not feed on dead trees, insects would most likely arrest more frequently at live trees, thus decreasing apparent movement rates. We note, however, that insects were occasionally trapped on dead trees in the mixed habitat, such that there was no statistical difference between live and dead trees for the probability of capture within that plot.

We cannot preclude the possibility that predation or parasitism, especially if varying across habitat types, may have affected trap captures and introduced a small degree of sampling bias within our results. Insects may exhibit higher movement rates in open spaces to escape predation, for example (Denno et al. 1990). Moreover, it is possible that the labeling technique increased visual apparency to predators such as birds. We consider this possibility unlikely, however, as adult *H. warreni* typically feed at night and are concealed in the duff during the day.

Several assumptions underlie the interpretation of dispersal patterns observed. First, we assume that there are no adverse effects of the elytral etching technique for marking insects. Second, we assume that the habitat constructed reflects young stands of lodgepole pine, the most abundant species of pine in western Canada and primary host of mountain pine beetle (Safranyik et al. 1974, Amman and Cole 1983). Third, we assume that the habitat was sufficiently large to allow meaningful observation of dispersal patterns. Fourth, we assume that our sampling method, the newly designed Björklund funnel trap, was unbiased in various habitat types.

This study represents the first deployment of the novel Björklund funnel trap for large-scale trapping of a walking weevil. In the present work, maximum trap efficiency during the trap development portion of the study was similar to the total recapture rate during the dispersal study (35%), although capture efficiencies of the Björklund trap may range as high as 75% (Björklund 2009). Such capture efficiencies compare favorably to other types of traps for weevils, including a more labor-intensive ladder trap (43% efficiency; Cerezke 1994), a shelterboard trap for *H. abietis* and *Hylobius pinastri* Gyll (up to 75%; Nordlander 1987, Eidmann 1997), baited pitfall traps for *H. pales* and *Pachylobius picivorus* (Germar) ( $\sim 35\%$ ; Rieske and Raffa 1990, Fettig et al. 1998), and an interception trap placed on trunks against *Tomicus piniperda* (L.) (66%; Ye et al. 2002). Studies with *H. radialis* in the eastern United States and *H. abietis* in Europe using established trapping methodologies have facilitated discovery of chemical attractants such as ethanol and terpenes (Hunt and Raffa 1989, Nordlander 1990, Hoffman et al. 1997, Björklund et al. 2005). Although no chemical host-seeking cues have been discovered for *H. warreni* to date, such compounds, if discovered, could improve future trap efficacy. Future capture and release studies using the Björklund funnel trap may identify possible chemical attractants or antifeedants (Månsson et al. 2005), refine trap efficacy (Rieske

and Raffa 1999), and provide population estimates within forest habitats (Rieske and Raffa 1993). Such research could facilitate a better understanding of the biological mechanisms controlling *H. warreni* dispersal and host selection.

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