

Primary attraction and random landing in host-selection by wood-feeding insects: a matter of scale?

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- Abstract**
- 1 Most plant-feeding insects show some degree of specialization and use a variety of cues to locate their host. Two main mechanisms of host location, primary attraction and random landing, have been investigated for such insects.
 - 2 Research has led to contradictory conclusions about those hypotheses, especially for wood-feeding insects; however, recent studies suggest that both mechanisms may take place in a single taxon but at different scales.
 - 3 We developed a field experiment to test the hypothesis that primary attraction occurs at larger scale and random landing at finer scale in wood-feeding insects. Landing rates, measured using sticky traps, were compared first between patches and then between individual trees according to their distance to a baited central tree.
 - 4 Polynomial functions describing landing rate to distance relationships were compared with a function produced by a null model describing what should occur under the random landing hypothesis. Scolytidae and Cerambycidae (Coleoptera) responded to volatiles at the patch scale, supporting the primary attraction hypothesis, but the landing patterns of some groups at finer scale matched closely the predictions of our null model, giving support to the random landing hypothesis.
 - 5 Our results show that the primary attraction and random landing hypotheses are not mutually exclusive and that prelanding use of host-produced volatile is scale-dependant. Scale considerations should thus be included in the study of prelanding host-selection of wood-feeding insects.

Keywords Cerambycidae, host volatiles, kairomones, Scolytidae, semiochemicals.

Introduction

Most plant-feeding insects show some degree of specialization in their host preferences. In most cases, a dispersal phase is necessary, and insects use a variety of cues to locate their host, most frequently either visual or olfactory (Bernays and Chapman, 1994). The use of volatiles produced and released by plants as attractants has received much attention (Metcalf, 1987).

Several species of wood-feeding insects lay their eggs exclusively on heavily stressed or recently dead trees (i.e.

secondary, or stressed-host insects), taking advantage of the weakened defense mechanisms and of the nutritional quality of the woody tissues, which at this point has not yet declined significantly (Wood, 1982; Hanks, 1999). Such resources are ephemeral and of unpredictable availability; stressed-host insects have thus evolved particularly efficient mechanisms helping them locating potential hosts. Numerous studies have been published on the use of volatiles by bark beetles (Coleoptera: Scolytidae) in particular (Person, 1931; McMullen and Atkins, 1962; Miller and Strickler, 1984; Raffa *et al.*, 1993; Byers, 1995; Pureswaran *et al.*, 2004). This is largely because species of this family can reach epidemic populations and kill healthy trees over large areas (Wallin and Raffa, 2004).

The importance of volatiles in host selection is generally acknowledged, but in which context these volatiles convey

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usable information during prelanding location processes is still unclear. Numerous laboratory experiments have demonstrated that host volatiles do play a role at some point in host selection by showing physiological responses to host volatiles in several species of bark beetles (Mustaparta *et al.*, 1979; Huber *et al.*, 2000; Pureswaran *et al.*, 2004) and longhorn beetles (Coleoptera: Cerambycidae) (Allison *et al.*, 2004). Field experiments comparing capture rates of baited traps to controls usually show strong responses of beetles to host-produced volatiles (Chénier and Philogène, 1989; Tunset *et al.*, 1993; Brattli *et al.*, 1998; Pureswaran and Borden, 2003), suggesting primary attraction (i.e. a positive response of insects to host-produced volatiles in the orientation of their flight; Person, 1931) is an important contributor in prelanding steps of host selection. However, other field studies have shown equivalent landing rates of bark beetles on neighbouring hosts and nonhosts trees (Goeden and Norris, 1965; Berryman and Ahsraf, 1970; Moeck *et al.*, 1981; Wood, 1982; Byers, 1995), and such studies are sometimes interpreted as suggesting random landing as the principal mechanism of host-finding. The random landing hypothesis states that insects fly and land on trees at random and then assess their quality as potential hosts using short-range olfactory and gustatory cues.

However, we should interpret these apparently contradictory results in the context of a multisteped host location sequence. At each of these steps, the relative importance of primary attraction and more random mechanisms may vary, and results supporting either of the two hypotheses could be seen for the same insect species depending on the scale at which host selection is considered. In a recent study, Saint-Germain *et al.* (2006) compared insect assemblages landing on contrasting snag types and stovepipes controls using sticky traps. Despite sampling five tree species and aluminium pipes painted black, no major differences in captured assemblage species composition were detected between the different treatments. However, the species and physiological state of neighbouring trees (within a radius of 3 m) had a significant influence on the captured assemblages. These results suggest that habitat patches may be located using host volatiles, but that individual potential hosts are then explored and assessed through random landing. Thus, in such cases, volatiles may be used to locate habitat patches but not to identify precise sources of volatiles at a finer scale.

Few field studies were appropriately conceived to actually test primary attraction concurrently at more than one of the prelanding host selection steps. Hynum and Berryman (1980) and Moeck *et al.* (1981) compared landing rates on suitable hosts and neighbouring nonhosts and found no differences. However, they did not consider whether primary attraction occurred concurrently at a larger scale. To fully understand the role of host-produced volatiles in prelanding host location processes, these multiple steps must be considered together for the same taxa in a single study. Understanding prelanding host selection processes of wood-feeding insects is of primary importance because volatiles are commonly used in monitoring and mass-trapping procedures in the management of economically important bark beetle species (Borden *et al.*, 2003; Wermelinger, 2004; Progar, 2005; Faccoli and Stergulc, 2006).

The present study was designed to test primary attraction at two scales relevant to prelanding host location. We first compared landing rates of secondary wood-feeding insects between patches (approximately 400 m²), including control patches, patches with a mechanically killed tree in their centre (natural volatiles), and patches with a tree baited with a high-release commercial blend of ethanol and α -pinene in its centre. For this part of the study, we predicted, in accordance with the primary attraction hypothesis, higher landing rates in baited patches and lower rates in controls. In the second part of the study, we looked at landing rates of selected taxa at a finer scale. In the same patches, we looked at landing rates occurring on several healthy trees (nonhosts) in relation to their distance to the baited central tree. Here, we predicted significant landing rates on nonhost trees, in accordance to the random landing hypothesis.

Materials and methods

Study site

For this study, nine jack pine (*Pinus banksiana* Lambert)-dominated sites were selected in the Lake Duparquet Research and Teaching Forest (Université du Québec en Abitibi-Témiscamingue, 48°28'N, 79°16'W), Canada. This forest is situated in the boreal mixed-wood domain, and is dominated overall by trembling aspen (*Populus tremuloides* Michaux) and black spruce (*Picea mariana* (Miller)). Most of the nine sites were 4–10-ha stands isolated within an aspen-dominated matrix. Two sites were located in the same > 35-ha stand. All of the nine sites originated from the same 1923 fire (Bergeron *et al.*, 2004) and are of comparable structure, with some marginal components of trembling aspen and black spruce. The average jack pine stem density was estimated at 585.0 per ha using the point-centred quarter method (Pollard, 1971).

Sampling

In each of the nine plots, a tree was selected near the middle of the stand. In the four cardinal directions, distances of 2, 5 and 10 m were measured from the central tree (Fig. 1). For ten of these 12 points, the closest tree with a diameter at breast height \geq 20 cm was selected. All selected trees were apparently healthy jack pines. Plots were not established in the proximity of dying or recently dead pines. The exact distance between each tree and the central one was measured. When all of the nine plots had been established, each was randomly assigned a treatment. The treatments were: (i) controls; with nothing added to the plots; (ii) commercial bait (CB); a high-release commercial blend of ethanol and α -pinene (Phero Tech Inc., Canada) was fixed to the central tree; and (iii) mechanically killed (MK); a healthy jack pine was cut outside our sampling area the day before we started sampling and a 1.2-m bole segment was suspended in the middle of each plot. Each treatment was replicated three times ($n = 3$). Ethanol and α -pinene have been shown to act as attractants to a large number of wood-feeding species and often act synergistically

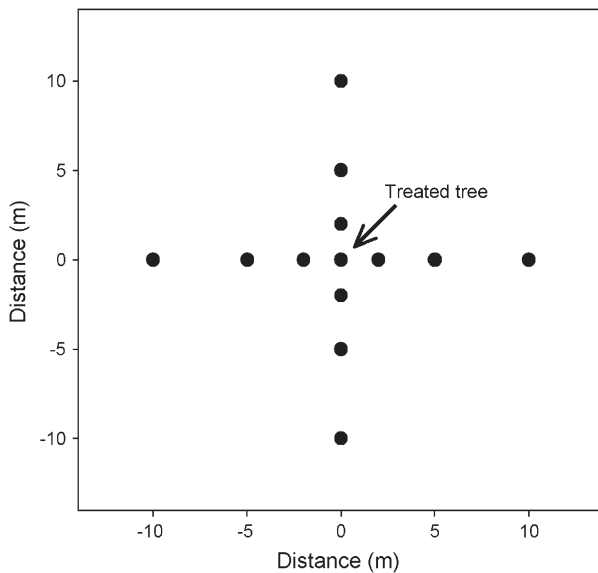


Figure 1 Sampling design used for each plot. A central tree was selected in the interior of the stand and was baited according to treatment. Ten other trees were chosen among the closest to points at 2, 5 and 10 m from the central tree in the four cardinal directions.

(Chénier and Philogène, 1989; Kelsey and Joseph, 1997; Czokajlo and Teale, 1999; Sweeney *et al.*, 2004). The CB and MK treatments differ both in their release rates of volatiles (higher in CB) and in the spectrum of volatiles emitted (wider in MK). No attractants derived from bark beetle pheromones were added to CB because this study aimed to focus on primary attraction with as little interference as possible from secondary attraction (insect-produced kairomones).

For all nine plots, a 0.25-m² (approximately 60 × 40 cm) polyethylene sheet coated with Tree Tanglefoot Pest Barrier (The Tanglefoot Company, Grand Rapids, Michigan) was pinned between hips and shoulders height on each selected tree, including the central one, facing outward of the plot. Tree Tanglefoot is a substance designed to intercept crawling insects and, because none of its key components is volatile, it does not interfere with primary attraction. Such sticky traps are appropriate to sample insects as they land on a potential host (i.e. between prelanding and postlanding host assessment; Saint-Germain *et al.*, 2006). Sampling took place for 58 days from 19 June to 15 August 2005. Polyethylene sheets were replaced once during the sampling period. Sheets were taken to the laboratory and specimens were cleaned using Histo-Clear (histological cleaning agent; National Diagnostics, Atlanta, Georgia). All Coleoptera were identified to family, and wood-feeding individuals to species. Voucher specimens are deposited at the Lyman Entomological Museum (McGill University, Montreal, Canada).

Statistical analysis

For analytical purposes, number of captures was standardized as landing rates (number of insects per m² per week) for

each tree. To address our first objective (compare landing rates between patches), the tree-scale landing rates were pooled by patch. Pooled landing rates were compared for selected taxa between treatments with one-way analysis of variance (ANOVA). Tukey's honestly significant difference tests were used for *post hoc* multiple comparisons. For the second part of the study, we used polynomial linear regressions to correlate individual landing rates to distance of the trap to the central tree, but only for relevant taxa as identified from the first part of the study. For these regressions, the 33 trees of the appropriate treatment were considered in single analyses. ANOVA and regressions were performed using SPSS, version 10.0.5 (SPSS Inc., Chicago, Illinois).

Null model

If we assume that beetles attracted to volatiles converge from all directions towards the central tree and potentially land on any encountered tree before reaching the true source of volatiles (i.e. random landing at fine scale), then we must expect a 'concentration effect'. As they get closer to the centre, incoming beetles are restricted to fewer trees acting as potential hosts. We thus expect to have higher landing rates on trees near the centre compared with trees on the periphery of the plot. To account for this concentration effect, we formulated a null model for selected taxa presented in the results with which we compared the polynomial function obtained from real data and their 95% confidence intervals. A predicted landing rate was calculated for each sampled tree by dividing the total number of beetles (average landing rate found on central trees per treatment) by the average number of trees found in a 2-m wide circular band centred at the radius of the tree (Fig. 2A). The predicted landing rate (LR_{pred}) was calculated as follows for each sampled tree:

$$LR_{pred} = \frac{\bar{x}LR_{center}}{\left(\frac{((\pi(d+1)^2) - (\pi(d-1)^2))}{10000} \times D \right)}$$

where LR stands for landing rate, d is the distance between the sampled tree and the central tree (m) and D is jack pine stem density (per ha). If we calculate this null model for a central LR of 20 beetles, we obtain the relationship shown in Fig. 2(B) (cubic polynomial function). Differences between the predicted and observed functions would indicate higher efficiency on the part of the insect if the observed function fell below the predicted one, and lower efficiency (sometimes getting away from the source during random landing) if the observed function was above the predicted one.

Results

Analysis of plot-level landing rates

All families with sufficient landing rates (over 2/m²/week in at least one treatment) were compared between treatments

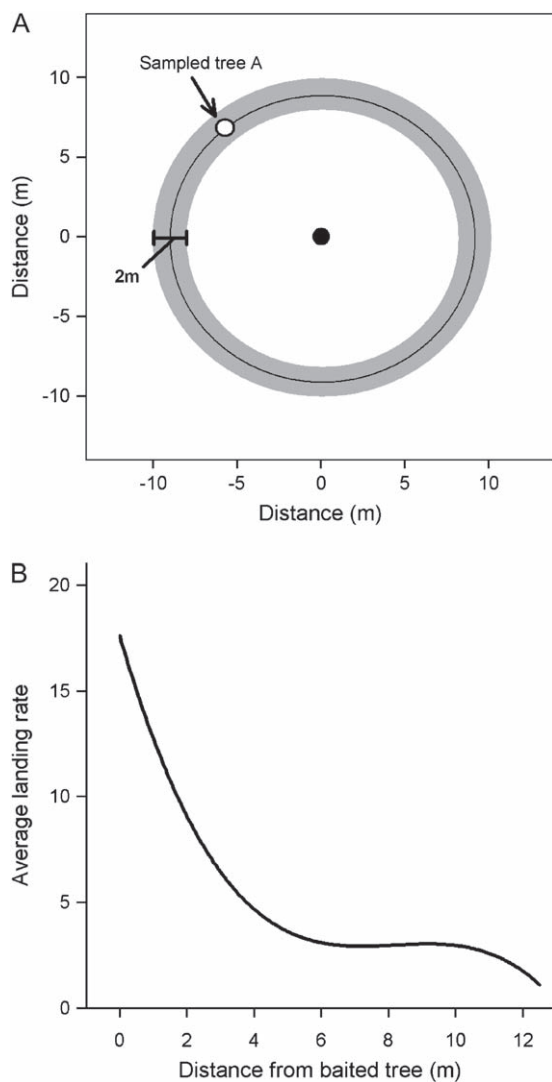


Figure 2 Calculation of the correction factor used for the null model. (A) For any given distance from the central tree, the area of a 2-m wide band is calculated. The number of trees to be expected on that surface is determined using the tree density estimate. In this example, the tree is at 9 m from the centre, the area of the band is 113.1 m² and we expect to find an average of 6.62 trees in that area (113.1/10000 × 584). (B) Number of insects expected to land on a given tree according to its distance from the central tree as predicted by our null model. For each distance, this number is calculated as the total number of insects (20 in this case) divided by number of trees expected as calculated in (A).

with ANOVA (Table 1). Among wood-feeding families, landing rates of Cerambycidae were significantly higher in CB and MK plots than in controls ($F_{2,6} = 5.66$; $P = 0.0415$), whereas rates of Scolytidae were significantly higher only in CB ($F_{2,6} = 16.95$; $P = 0.0034$) (Table 1; Fig. 3). Among those two families, Cerambycid *Xylotrechus undulatus* ($F_{2,6} = 6.25$; $P = 0.0341$), and Scolytids *Dryocoetes autographus* ($F_{2,6} = 24.14$; $P = 0.0014$) and *Hylurgops pinifex* ($F_{2,6} = 5.86$; $P = 0.0389$; Fig. 3) all had significantly higher landing rates in CB plots (Table 1). For families belonging to other

trophic groups, only predatory Lycidae ($F_{2,6} = 7.08$; $P = 0.0264$; higher in controls), Nitidulidae of the genus *Eपुरaea* ($F_{2,6} = 12.42$; $P = 0.0074$; higher in MK; Fig. 3) and detritus-feeding *Scaptia sericea* ($F_{2,6} = 15.14$; $P = 0.0045$; higher in MK; Fig. 3) showed significant differences between treatments (Table 1). Landing rates of other groups showed no response to treatments (e.g. Elateridae, Fig. 3).

Analysis of tree-level landing rates

Analysis at tree-scale was performed for Scolytidae (CB), Cerambycidae (CB), melandryids *Serropalpus coxalis* (CB) and *S. sericea* (MK), and *Eपुरaea* nitidulids (MK) (Fig. 4). We opted to settle with family level analyses in several cases because of insufficient landing rates from individual species. Relationships between tree-specific landing rates and distance to the centre were best described in all cases (except for *Scaptia* with nonsignificant relationships) with cubic polynomial functions. Scolytidae landing rates were highest in the first 3-m (polynomial function: $F_{3,29} = 28.60$; $P < 0.001$; $r^2 = 0.747$), and the observed function falls below the function predicted by the null model (not included in the 95% confidence intervals) (Fig. 4A). For Cerambycidae and *Serropalpus*, the observed functions were significant (Cerambycidae: $F_{3,29} = 10.15$; $P < 0.001$; $r^2 = 0.512$; *Serropalpus*: $F_{3,29} = 11.94$; $P < 0.001$; $r^2 = 0.553$) but were closely fitted with the predicted functions (Fig. 4B,C). *Eपुरaea* showed a response similar to the Scolytidae, with the observed function being distinct and below the predicted function ($F_{3,29} = 13.14$; $P < 0.001$; $r^2 = 0.576$; Fig. 4D). For *S. sericea*, all relationships were nonsignificant (Fig. 4E).

Discussion

The present study provides support for both the primary attraction and random landing hypotheses for the same taxon as host-selection was considered at multiple scales. Furthermore, the efficiency with which insects were able to locate the source of volatiles within a patch varied between taxa of the same functional group.

Wood-feeding insects did respond to host-produced volatiles at the patch scale in our study because higher landing rates were observed in patches baited with host-produced semiochemicals in major groups of wood-feeding insects and several individual species. Scolytidae were significantly attracted to the 'commercial bait' patches, whereas Cerambycidae were attracted to both 'commercial bait' and 'mechanically killed tree' patches. A clear difference in release rate between the two treatments could explain the different responses of two groups, which are otherwise frequently found together in recently dead trees (i.e. *X. undulatus* and *Dryocoetes affaber*). The high-release commercial bait is expected to produce a stronger volatile concentration gradient, on which some Scolytidae may be more dependant than Cerambycidae. Byers *et al.* (1989) showed that the effective attraction radius of a baited trap varies considerably

Table 1 Dominant taxa captured with average landing rates (\pm standard error) for each treatment, and results from one-way analysis of variance and Tukey–Kramer *post hoc* tests

Taxon	Commercial bait	Mechanically killed	Control	<i>F</i>	<i>P</i>
Wood-feeding groups					
Cerambycidae	4.51 \pm 1.4 ^a	3.97 \pm 1.32 ^a	0.8 \pm 0.32 ^b	5.66	0.042
<i>Asemum striatum</i> (L.)	1.46 \pm 1.2	0	0		NS
<i>Clytus ruricola</i> (Olivier)	0.65 \pm 0.16	0.49 \pm 0.28	0.16 \pm 0.16		NS
<i>Psenocerus supernotatus</i> (Say)	0.65 \pm 0.16	0.65 \pm 0.33	0		NS
<i>Xylotrechus undulatus</i> (Say)	0.81 \pm 0.33 ^a	0 b	0 b	6.25	0.034
Others	1.14 \pm 0.71	1.3 \pm 0.33	0.65 \pm 0.16		NS
Curculionidae	6.76 \pm 0.97	5.47 \pm 2.44	2.9 \pm 0.28		NS
Melandryidae	53.5 \pm 13.0	28.8 \pm 10.4	30.5 \pm 3.88		NS
<i>Melandrya connectens</i> (Newman)	8.71 \pm 2.57	5.33 \pm 0.73	3.22 \pm 1.06		NS
<i>Serropalpus coxalis</i> Mank	34.3 \pm 12.7	14.3 \pm 7.72	13.9 \pm 5.23		NS
Scolytidae	9.69 \pm 1.86 ^a	2.13 \pm 0.59 ^b	1.93 \pm 1.0 ^b	16.95	0.004
<i>Dryocoetes affaber</i> (Mannerheim)	0.49 \pm 0.49	0	0		NS
<i>Dryocoetes autographus</i> (Ratz.)	2.11 \pm 0.43	0	0	24.14	0.002
<i>Hylurgops pinifex</i> (Fitch)	3.86 \pm 0.74 ^a	0.97 \pm 0.28 ^b	0.32 \pm 0.32 ^b	5.86	0.039
Others	2.44 \pm 0.84	0.65 \pm 0.43	1.3 \pm 0.86		NS
Others					
Alleculidae	2.9 \pm 1.7	5.94 \pm 0.23	3.06 \pm 0.58		NS
Cantharidae	43.9 \pm 5.34	107.0 \pm 22.2	70.8 \pm 13.6		NS
Cucujidae	1.16 \pm 0.46	2.45 \pm 0.76	2.25 \pm 0.64		NS
Elateridae	73.1 \pm 11.9	74.0 \pm 12.6	70.6 \pm 6.66		NS
Endomychidae	11.3 \pm 3.28	13.0 \pm 5.16	18.7 \pm 8.49		NS
Eucinetidae	9.84 \pm 2.75	5.47 \pm 0.58	6.99 \pm 2.43		NS
Lampyridae	35.0 \pm 10.9	33.4 \pm 2.55	16.2 \pm 4.61		NS
Lathridiidae	70.5 \pm 9.63	78.7 \pm 5.34	67.2 \pm 4.35		NS
Lycidae	6.15 \pm 1.4 ^{a,b}	4.18 \pm 0.43 ^a	8.75 \pm 0.46 ^b	7.08	0.026
Melyridae	22.4 \pm 4.71	61.1 \pm 15.8	30.9 \pm 16.9		NS
Mordellidae	10.2 \pm 0.98	11.3 \pm 1.51	7.64 \pm 2.09		NS
Nitidulidae					
<i>Eपुरaea</i> spp.	9.05 \pm 2.28 ^a	16.1 \pm 1.26 ^b	4.83 \pm 1.0 ^a	12.42	0.007
Melandryidae					
<i>Scraptia sericea</i> (Melsheimer)	10.4 \pm 1.69 ^a	19.1 \pm 1.78 ^b	8.53 \pm 0.58 ^a	15.14	0.005
Staphylinidae	49.5 \pm 10.9	38.1 \pm 5.43	29.2 \pm 7.75		NS
Throscidae	6.96 \pm 1.89	11.7 \pm 2.11	8.57 \pm 3.05		NS

For each treatment $n = 3$.

NS, Not significant.

depending on the release rate of the attractants and on the identity of the insect species considered. Some nonwood-feeding groups were also attracted to the ‘mechanically killed tree’ patches. Nitidulidae of the genus *Eपुरaea* were probably attracted to volatiles not contained in the commercial blend but produced by the mechanically killed tree. *Eपुरaea* is a species-rich genus within which differences in behaviour can be expected; however, Schröder and Lindelöw (1989) have shown that species of *Eपुरaea* respond to the same compounds as some bark beetles do, suggesting that they may be predatory on these beetles. Because very little information is available on the ecology of *Scraptia*, it is difficult to explain its attraction for the ‘mechanically killed tree’ patches.

Results from the second part of our study shows that all taxa for which the primary attraction hypothesis was

supported at patch scale landed to varying degrees on nonhost trees, at higher rates than landings observed in control patches, showing some degree of random landing within patches. The observed landing rate to distance function for Cerambycidae closely fitted the function predicted by our null model. This suggests that cerambycids are rather inefficient at locating the source of volatiles in a within-patch context. This result clearly indicates that these insects cannot rely on host volatiles to discriminate before landing between several potential hosts, even if primary attraction was shown in the same group at a larger scale. The melandryid *Serropalpus*, for which trends but no significant differences were observed in analyses at the patch level, had a significant polynomial landing rate to distance function, and showed the same pattern as the Cerambycidae. Scolytidae, and to a larger degree

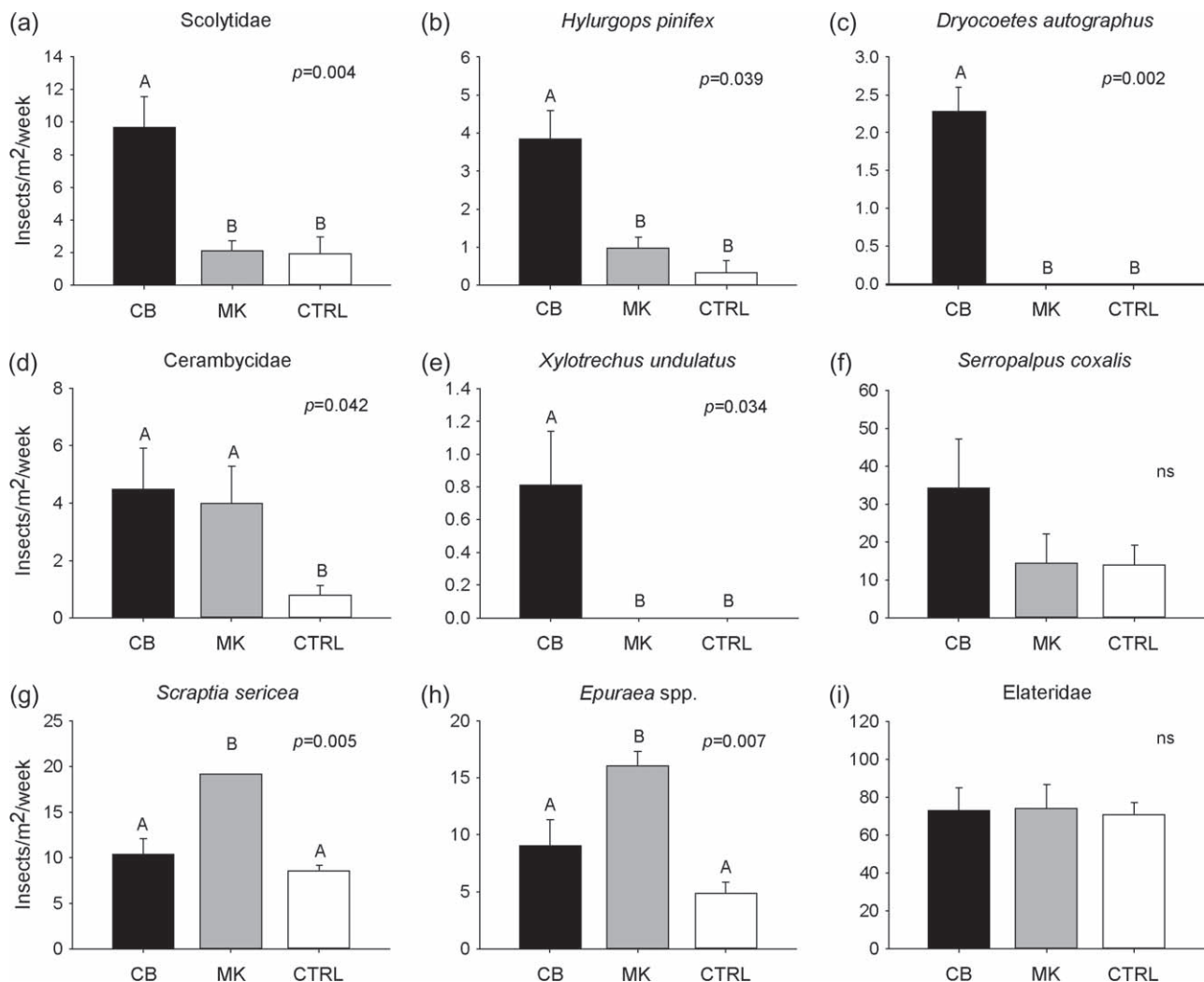


Figure 3 Comparison of landing rates of selected taxa according to treatment. For this analysis, landing rates on all trees were pooled by plot. Results of a one-way analysis of variance are shown. Error bars illustrate standard error. For all treatments, $n = 3$. CB, Commercial bait; MK, mechanically killed tree; CTRL, control.

Nitidulidae, had an observed function below the predicted function and were thus more efficient at locating the source of volatiles than Cerambycidae, although a non-negligible proportion of landing on nonhosts was still observed.

These findings bring us back to the contradictory results often reported from laboratory and field experiments when dealing with primary attraction and random landing. Such contradictions are reported in the literature within single species. Examples of this can be found for the bark beetles *Scolytus ventralis* LeConte and *Dendroctonus ponderosae* Hopkins. In laboratory bioassays, *S. ventralis* has been found to respond physiologically to 19 compounds released by its host (*Abies grandis* Lindley) when under heavy stress, thus showing some form of primary attraction (Macias-Samano *et al.*, 1998). However, in field surveys during which both healthy and stressed trees were examined locally, 74% of the trees examined showed signs of postlanding host assessment (gallery initiation), whereas completed galleries, and thus

host acceptance, were found on only 3.5% of the trees (Berryman and Ahsraf, 1970). The authors thus concluded that host selection in *S. ventralis* was random prior to the aggregation phase. The same can be seen for *D. ponderosae*: this species has been shown to react to several host-produced monoterpenes (Pureswaran *et al.*, 2004) but a field study using baited traps showed no significant response to host volatiles in this species at close range (Pureswaran and Borden, 2005). These two examples suggest that olfactory information is not necessarily usable at all scales during host-selection, as shown by our results. Most studies supporting the random landing hypothesis sampled hosts and nonhosts within the same patch, and were thus able to detect any erroneous landings by beetles that were initially attracted by good hosts present in their proximity (Goeden and Norris, 1965; Berryman and Ahsraf, 1970; Hynum and Berryman, 1980; Witanachchi and Morgan, 1981). Field experiments relying only on baited traps are unable to detect such random

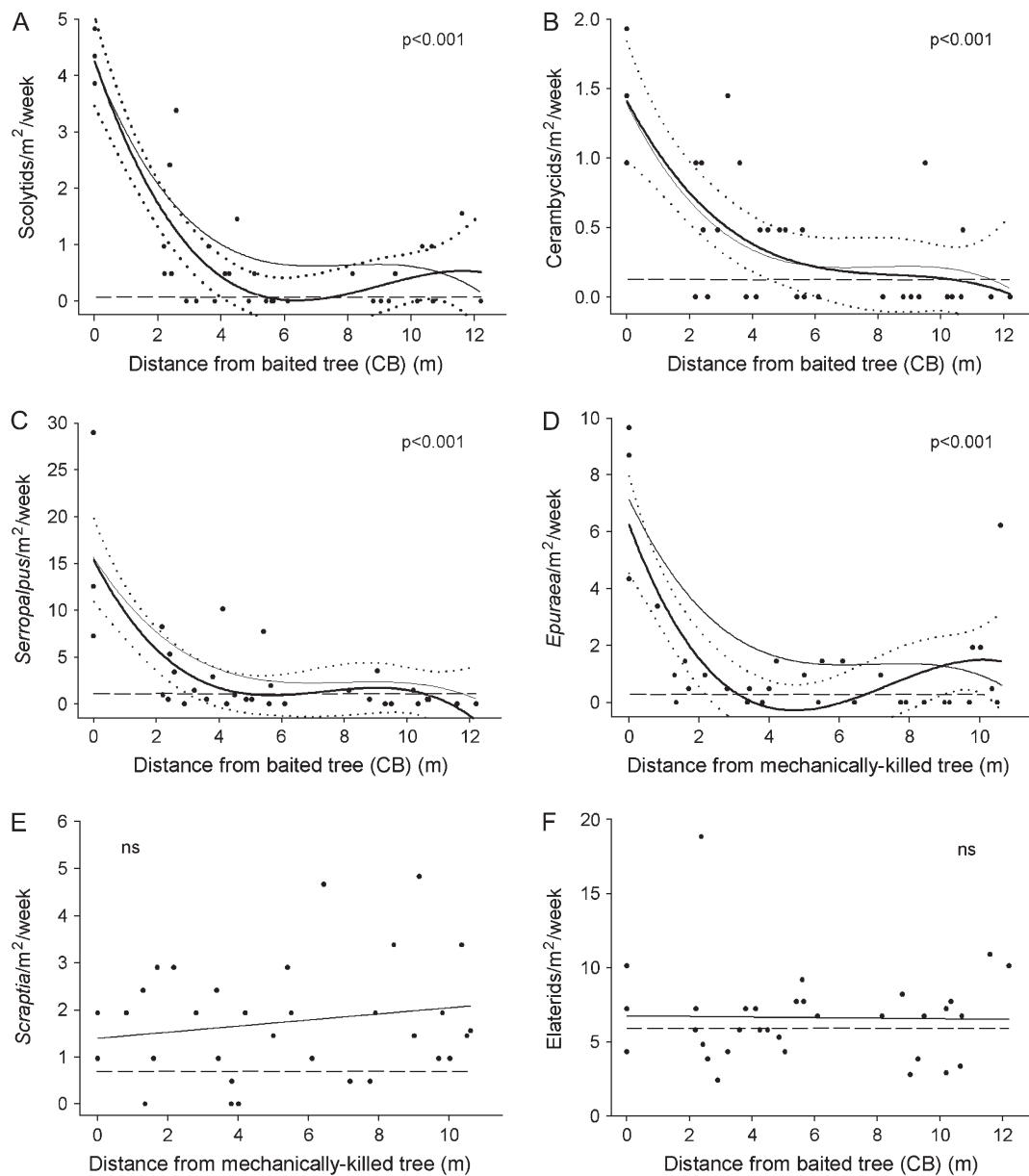


Figure 4 Landing rates of selected taxa, (A) Scolytidae; (B) Cerambycidae; (C), *Serropalpus*; (D), *Epuraea* spp. (Nitidulidae); (E), *Scaptia sericea*; (F), Elateridae, according to distance from central tree for the relevant treatments. Results from the three plots are pooled in all figures. The dark line shows the most significant polynomial function describing the relationship. The dotted lines show 95% confidence intervals (A–D). The thin line shows what would be expected if converging insects would land successively on every tree encountered (null model) (A–D). The dashed line shows landing rates observed for same taxa in control plots. CB, Commercial bait; MK, mechanically killed tree; CTRL, control.

landings and may have erroneously concluded unequivocal primary attraction at close range (Tunset *et al.*, 1993; Brattli *et al.*, 1998), whereas laboratory studies provide no information whatsoever on the scale at which volatiles might be used. The question is thus not whether there is primary attraction or not, but rather at which scale the insect can make good use of host-released volatiles.

The differential efficiency of insects in using volatile information at different scales that we observed could be explained by an increased difficulty of extracting directional

information from the host-volatiles present in the air in some ranges. Unfortunately, little information is currently available on the shape of the relationship between volatile concentration in air and distance from the host. Some authors suggest that such gradients are unlikely to exist over a few centimeters because of air turbulence (Bernays and Chapman, 1994). Instead, insects flying upwind will intermittently come in contact with air pockets containing volatiles in varying concentrations. In such a context, it would be even more difficult for the insect to assess the exact location of the host without

frequent random landings. The currently available information on the processes of in-flight host-finding is thus consistent with our view of a multiscaled differential prelanding host-selection strategy, which is also supported by our results.

Some of the results presented in this study are composite responses (family level analyses that generally include a few species). However, within-family variations in host-selection behaviour are usually correlated with the physiological state of the preferred host (Wood, 1982). Because all the bark beetle species captured within the present study are secondary in nature, fewer variations in behaviour among these species can be expected, and the situation is similar for Cerambycidae. We therefore conclude that family-level analyses still convey relevant information. Results shown for some individual species suggest that such differential strategy could be a common phenomenon, if not a generality. Our results indicate that our understanding of host-selection can be improved by including scale considerations in an empirical approach; it is clear that studies looking at the use of volatiles at a single scale provide fragmentary information. In the present study, we limited our efforts at comparing between- vs. within-patch use of volatiles but the main ideas presented here could be expanded at larger scales to provide a more comprehensive understanding of dispersal and host selection, from landscape scale to tree scale. In addition, the results from our study could be applied to mass-trapping experiments and to the use of nonhost antagonistic volatiles, of which the efficiency should also be considered at multiple scales.

Acknowledgements

We would like to thank A. Webb and V. Evans for their participation in field work, and E. Bolduc for her contribution to cleaning the specimens. Comments from two anonymous reviewers helped improve the manuscript. This project was funded by the UQAM-UQAT NSERC industrial chair in sustainable forest management, the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) – Programme Action Concertées – Fonds forestiers (P. Drapeau), a FQRNT new researcher grant (C. Buddle) and a Discovery grant (C. Buddle) from the Natural Science and Engineering Research Council of Canada (NSERC).

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Accepted 12 January 2007

First published online 10 April 2007