

Close-range, in-flight integration of olfactory and visual information by a host-seeking bark beetle

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Abstract

A long-standing controversy questions whether foraging bark beetles assess the suitability of individual host trees using cues at close range while flying or engage in random landing followed by contact assessment. In most cases, visual discrimination mechanisms are ignored. We show that pheromone-responding mountain pine beetles (MPB), *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), can visually discriminate between 'host' (black) and 'non-host' (white) traps arranged in small clusters, in the absence of additional host olfactory information, and that males (but not females) demonstrate a greater preference for combined host visual and olfactory cues. However, white, non-host traps baited with a host volatile were as attractive as unbaited, black host traps. Our results support the hypotheses that when deciding to land, the MPBs integrate visual and olfactory information and can process cues in both sensory modes at relatively close range (≤ 2 m). Thus, host selection mechanisms in this species are unlikely to be random with respect to either sensory mode.

Introduction

When making foraging or oviposition decisions, insects may rely on multiple olfactory, visual, and acoustic cues, but should favour information that is the most accurate and least costly to assess (Fawcett & Johnstone, 2003). Potentially for these reasons, many foraging insects appear to rely on olfactory cues, which may be specific to hosts or non-hosts, and which in many cases can be detected while flying, thereby avoiding any predation risks or opportunity costs associated with landing and close assessment (Pyke et al., 1977). However, the accuracy of a semiochemical may be low, e.g., when it is emitted by both a host and a non-host (Eisner & Grant, 1981), and host-seeking insects could therefore benefit from integrating available visual cues into host selection decisions.

Host selection comprises a series of the most important life history decisions made by the mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) (Wood, 1982; Raffa & Berryman, 1983; Borden, 1997). Pioneer beetles locate host *Pinus* spp. (Pinaceae) either by primary attraction to olfactory cues (Gara et al.,

1984; Syed & Graham, 1987; Moeck & Simmons, 1991) or by 'random landing' on vertical stems, a counterintuitive strategy (Gries et al., 1989) that nonetheless has some theoretical (Byers, 1996) and empirical support (Hynum & Berryman, 1980; Moeck et al., 1981). The majority of beetles reduce foraging costs by locating hosts using pheromones produced by pioneers (Borden, 1985), in conjunction with synergistic host volatiles such as α -pinene, terpinolene, β -phellandrene, and myrcene (Pitman, 1969, 1971; Billings et al., 1976; Borden et al., 1987; Miller & Borden, 2000). However, it is unclear whether pheromone responders use these cues to assess trees at close range while flying. Studies of infestations of the southern pine beetle, *Dendroctonus frontalis* Zimmerman, suggest that pheromones and host kairomones function primarily as long-range attractants, with individual tree finding occurring by 'random' landing on both hosts and non-hosts (Gara et al., 1965; Payne, 1986, see also Lanier, 1983). In addition, the bark and foliage volatiles of non-host angiosperms repel the MPB (and many other bark beetles) from attractant-baited traps (Wilson et al., 1996; Borden et al., 1998; Huber & Borden, 2003; Zhang & Schlyter, 2004), host trees (Huber & Borden, 2001), and groups of trees in small plots (Borden et al., 2003), suggesting that non-host volatiles (NHVs) also operate as long- and mid-range cues.

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Implicit in discussions of host location (e.g., Borden et al., 1986; Payne, 1986; Gries et al., 1989; Byers, 1996) is the assumption that beetles also use visual cues. For instance, the so-called random landing hypothesis (Hynum & Berryman, 1980) implies that host-seeking beetles use visual cues such as an upright silhouette. In general, bark beetles such as the MPB appear to prefer traps that resemble their hosts in form, orientation (Billings et al., 1976; Safranyik et al., 2003), and hue (Strom et al., 1999, 2001). Complementing olfactory non-host avoidance, the MPBs also avoid traps that visually simulate non-hosts aspen and birch (Campbell & Borden, 2006), supporting the hypothesis that visual cues aid host and non-host discrimination (Campbell & Borden, 2005).

When combined, NHVs repel beetles in additive and/or redundant fashions (Borden et al., 1998), and similar effects were demonstrated for visual and olfactory non-host stimuli (Campbell & Borden, 2006). However, visual and olfactory stimuli can also have synergistic (Slinker, 1998) effects on scolytid beetles, with certain host visual stimuli becoming attractive only when accompanied by host tree olfactory cues (Vité & Bakke, 1979; Borden et al., 1982; Lindgren et al., 1983; Campbell, 2004), and non-host colour only being repellent when accompanied by a non-host semiochemical (Campbell, 2004). Although these results imply complex integration of visual and olfactory information, it is still unknown whether bark beetles can use semiochemical or visual cues for short-range, in-flight host assessment, and the relative distance at which they switch between or integrate sensory modes. In this study, we physically separated the attractive pheromone components *trans*-verbenol (Pitman et al., 1968) and *exo*-brevicommin (Pitman, 1969; Borden et al., 1987) from the target trap silhouettes and assessed the behavioural responses of the MPB to host and non-host visual stimuli and a synergistic host tree volatile. We asked three questions.

1. Will pheromone-responding (host-seeking) MPBs prefer host-coloured to non-host-coloured, bole-simulating traps in a small area redolent with attractive semiochemicals?
2. How does the MPB integrate bimodal information when a host kairomone is added to traps resembling hosts and/or non-hosts?
3. What is the relative importance of visual and olfactory cues in eliciting landing?

Materials and methods

We conducted two field trapping experiments using 12-unit multiple-funnel traps (Phero Tech Inc., Delta, British Columbia, Canada), as these are thought to be perceived as tree boles by foraging beetles (Lindgren, 1983). Because they prevent beetles from taking off after landing, differences in catches reflect differences in landing decisions. We used black and white traps to mimic conifer and non-host angiosperm boles, respectively (Campbell & Borden, 2005). In experiment 1, MPBs were challenged to discriminate between black and white traps in small areas redolent with attractive semiochemicals. We erected a pole baited with three release devices of each of the MPB bait components (Table 1) at a height of 1.5–1.8 m, and two replicate black and two replicate white traps were alternately placed in a 2 m radius circle around the pheromone pole to create a ‘cluster’ of four traps. The position and colour of the first trap were determined by coin toss. Six clusters ran concurrently from 9 September to 8 October 2001 along Opax Mountain Forest Service Road (FSR) and adjacent skid trails and forest margins (near Kamloops, British Columbia) in an area heavily infested with the MPB.

In experiment 2, we examined the relative roles of silhouette colour and a key host semiochemical (myrcene) in eliciting landing by beetles that had responded to aggregation pheromone components (Table 1). Two release devices each of *trans*-verbenol and *exo*-brevicommin were hung from a central pole at 1.5–1.8 m, and alternating black and white traps were arranged in a ca. 2.5 m radius cluster as in experiment 1. Four semiochemical treatments were randomly assigned to clusters: (1) a myrcene release device on each black trap in a cluster, (2) myrcene on each white trap, (3)

Table 1 Optical nature, purity, release devices, and rates for semiochemicals

| Semiochemical ¹ | Chemical purity (%) | Release device | Release rate ² (mg per 24 h at 20 °C) |
|------------------------------|---------------------|-----------------------------|---|
| (±)- <i>trans</i> -verbenol | 90 (7% <i>cis</i>) | Polyethylene bubblecap | 1.2 |
| (±)- <i>exo</i> -brevicommin | 98 | Polyvinyl chloride flexlure | 0.2 |
| Myrcene | 90 | Polyethylene bottle | 250 |

¹All three compounds comprise the ‘MPB bait’ used in experiment 1. All compounds obtained from Phero Tech Inc., Delta, BC, Canada. IUPAC names: *exo*-brevicommin, *exo*-6-ethyl-trimethyl-7,8-dioxabicyclo[3.2.1]octane; *trans*-verbenol, *trans*-4,6,6-trimethylbicyclo[3.1.1]hept-3-ene-2-ol; myrcene, 7-methyl-3-methylene-1,6-octadiene.

²Release rates determined by Phero Tech Inc.

myrcene on all four traps, and (4) no myrcene (control). Sixteen complete, four-cluster blocks were set up along forest margins on East Gate FSR (two blocks) and Sunday Summit (14 blocks), both near Princeton, BC; seven replicates ran from 22 to 29 August, and nine replicates ran from 29 August to 4 October 2002. In both studies, clusters were 20 m apart, and a small block of dichlorvos-impregnated plastic (Vapona No-pest® strip, Monsanto Canada Ltd, Mississauga, Ontario, Canada) was placed in each collecting cup to minimize escape and predation. Insects were collected and frozen until counted; sex ratios (Lyon, 1958) were determined by subsampling 50 insects.

Statistical analyses

In experiment 1, we compared proportional catches of each sex in black and white traps using χ^2 tests (Zar, 1999) (PROC FREQ, SAS v.8) of each cluster. For each cluster in experiment 2, catches in the two traps of each colour were averaged and log transformed to improve normality and homoscedasticity (Zar, 1999). We tested the effect of semiochemical treatment by analysis of variance (ANOVA) of the cluster totals and tested for differences in discrimination among semiochemical treatments by ANOVA of the mean proportional difference between catches in black and white traps (PROC GLM). In both cases, the four treatment means were then compared by the Ryan-Einot-Gabriel-Welsch (REGW) multiple-range test (Day & Quinn, 1989; SAS, 1990). Within each semiochemical treatment group, we also tested for differences between 'black' and 'white' trap catches by ANOVA. Low catches in the two East Gate replicates provided insufficient power to detect a treatment*location interaction; however, removal of these

replicates did not affect the results, and all 16 replicates were analysed together. There was no treatment*time interaction for Sunday Summit clusters ($P_{\text{males}} = 0.8140$, $P_{\text{females}} = 0.9176$). We treated block as a random effect, used Type III sums of squares, and experimentwise $\alpha = 0.05$.

Results

In experiment 1, females discriminated more acutely than males (Figure 1). Males preferred black to white traps in three of six clusters, whereas females preferred black traps in all but one cluster, in which they preferred white traps.

In experiment 2, catches of each sex were highest in clusters with myrcene on traps of both colours (all four traps), followed by clusters with myrcene on either black or white traps, and very few beetles were caught in clusters without myrcene ($F_{\text{males}} = 27.52$, $F_{\text{females}} = 21.90$, both $P < 0.0001$) (Figure 2). The mean proportional difference between catches in black and white traps also differed among treatments ($F_{\text{males}} = 17.06$, $F_{\text{females}} = 18.41$, both $P < 0.0001$) (Figure 3). Male discrimination was greatest in clusters with myrcene on black traps only, followed by clusters with myrcene on all four traps or without myrcene. Female discrimination was equally great in clusters with myrcene on black traps and on traps of both colours (Figure 3). Within-treatment differences between black and white traps were significant in the myrcene-on-both ($F_{\text{males}} = 35.35$, $F_{\text{females}} = 44.69$, both $P < 0.0001$) and myrcene-on-black ($F_{\text{males}} = 43.03$, $F_{\text{females}} = 40.81$, both $P < 0.0001$) clusters, but not in clusters with myrcene-on-white ($F_{\text{males}} = 0.01$, $P = 0.9916$; $F_{\text{females}} = 2.17$, $P = 0.1612$) or no-myrcene ($F_{\text{males}} = 2.12$, $P = 0.1656$; $F_{\text{females}} = 0.13$, $P = 0.7200$) clusters (Figure 2).

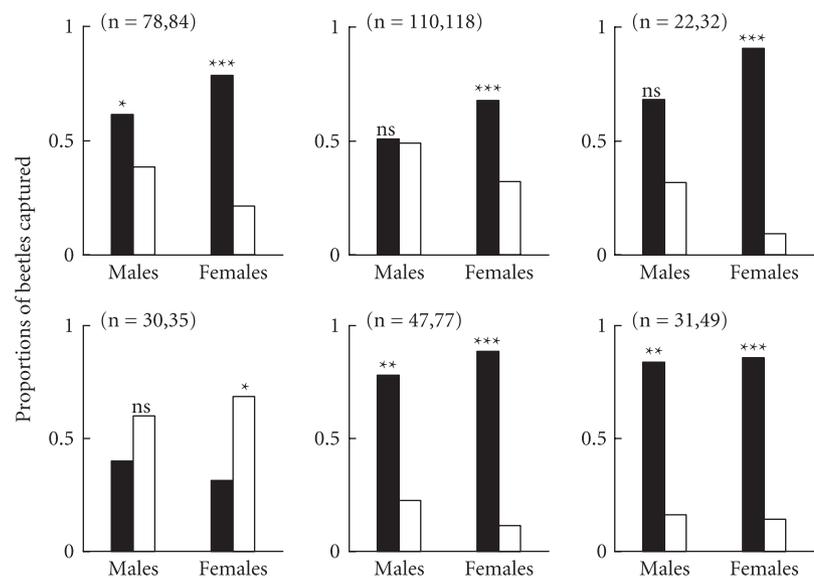


Figure 1 Proportions of *Dendroctonus ponderosae* caught in black (dark bars) and white (white bars) traps in the six clusters of experiment 1. Total catches of males and females are, respectively, given in parentheses. For χ^2 tests, * indicates $P < 0.05$, ** $P < 0.001$, *** $P \leq 0.0001$, and ns indicates no significant difference.

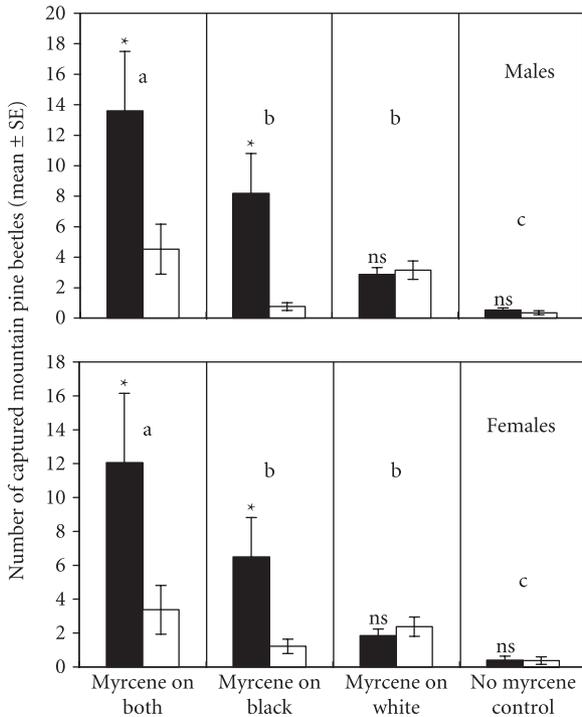


Figure 2 Catches of *Dendroctonus ponderosae* in pheromone-baited clusters of traps in experiment 2. Dark and white bars are catches in black and white traps, respectively. For each sex, semiochemical treatments with the same letter had total catches (sum of catches in black and white traps) that were not significantly different (REGW test). Within each treatment and sex, * denotes significantly greater catches ($P < 0.0001$) in black traps and ns indicates no significant difference between colours.

Discussion

Experiment 1 demonstrated that MPBs, particularly host-seeking females, generally prefer host- to non-host-coloured traps in a small area redolent with attractive semiochemicals. This preference was variable (Figure 1), but corresponds with earlier experiments (Campbell & Borden, 2006), in which we found consistent avoidance of attractant-baited, white (non-host) traps by the MPB, the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, and the western balsam bark beetle, *Dryocoetes confusus* Swaine. Because there were no anomalous combinations of host semiochemicals and non-host colour or volatiles, experiment 1 constitutes a more realistic test of visual preferences, and these results support a functional interpretation of visual preference (Campbell & Borden, 2006).

Experiment 2 was designed to elucidate the interplay of visual and olfactory host cues, and non-host colour, when the attractive pheromone components were decoupled from the ‘tree’ stimuli. The results clearly confirm that the MPB

could visually avoid non-host angiosperms while foraging, and led to the following hypothetical synthesis of bimodal sensory integration and behavioural responses by this species.

Long-range orientation to groups of target silhouettes is apparently mediated by an attractive kairomone (myrcene), consistent with the general expectation that olfactory cues mediate long-range behavioural responses (Dethier, 1982; Lanier, 1983; Prokopy, 1986; Finch & Collier, 2000). There were twice as many male and female beetles in clusters with myrcene on both black and white traps (four release devices) than in clusters with myrcene on black traps only (two release devices), similar catches in the two treatments with myrcene on only one trap colour, and significantly lower catches (<1 beetle on average) in clusters without myrcene, suggesting that neither the two pheromone components nor the traps were attractive in the absence of

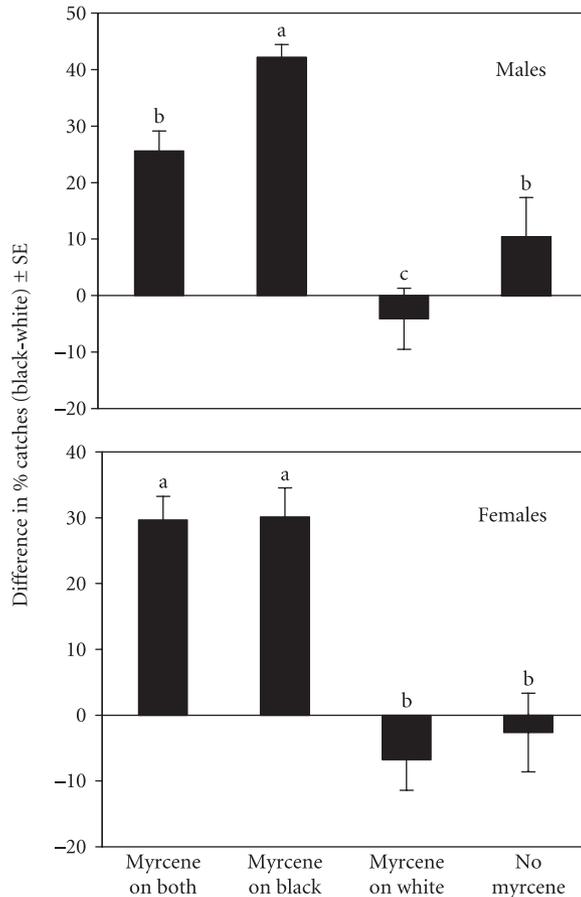


Figure 3 Differences in visual discrimination by *Dendroctonus ponderosae* among semiochemical treatments in experiment 2. Bars represent the mean percentage difference between black and white catches in each treatment. For each sex, bars with the same letter are not significantly different (REGW test).

a host olfactory stimulus. While myrcene is not the only host volatile that synergizes the attractiveness of *exobrevicomin* and *trans-verbenol* (Billings et al., 1976; Miller & Borden, 2000), it provided a suitable model stimulus (Pureswaran, 2003) for testing visual stimuli. This dose-dependent effect corroborates previous results (Borden et al., 1987; Miller & Borden, 2000; BS Lindgren, Faculty of Forestry, University of Northern British Columbia, Prince George, BC, pers. comm.).

Having responded to and entered a cluster, beetles then chose to land by integrating visual and olfactory information. In clusters with myrcene on traps of both colours (where semiochemical information was equal among traps), beetles chose black traps more often than white, corroborating the results of experiment 1. Discrimination was enhanced in clusters with myrcene on only black traps, where the response to the combined host visual and olfactory cues was so pronounced that the catches in white traps were almost as low as those in white traps in control clusters. However, in clusters with myrcene on white traps only, there were equal catches of beetles in black and white traps, indicating that in-flight discrimination using visual information can depend on the presence of kairomones, which may be more accurate signals of host suitability and identity, and override visual stimuli even at close range. A complementary interpretation is that myrcene's attractiveness was exactly negated by the repellency of the non-host visual cue. The similar total catches in myrcene-on-black and myrcene-on-white clusters support the hypothesis that this integration occurred within, rather than outside, the clusters. Thus, the host volatile myrcene appeared to function as both a long-range attractant to the clusters, and a close-range cue for beetles that entered clusters.

The significant treatment effect on the percent differences between black and white trap catches (Figure 3) also supports the hypothesis that visual and olfactory information is integrated during landing decisions, and the contingency of visual responses on olfactory cues strongly suggests that integration can be synergistic. The heightened discrimination by male MPBs when host volatile and visual stimuli were combined (myrcene-on-black clusters) affirms that they assessed individual traps for both olfactory and visual information within the small clusters. Conversely, females preferred black to white traps to the same extent whether myrcene was on all four traps, or only black traps (Figure 3), suggesting that females may process information at a greater distance than males. There may also be redundancy in bimodal host stimuli. Females may (1) orient to host odours, (2) perceive visual stimuli (black tree silhouette) associated with those odours (e.g., outside the cluster), and (3) decide to land, with subsequent, close-range olfactory cues within the cluster being redundant. In a similar

fashion, visual and olfactory non-host stimuli are redundant in repelling the MPBs (Campbell & Borden, 2006). In clusters with myrcene only on white traps, this sequence of stimulus integration would have been disrupted at step 2 by the decoupling of the host visual and olfactory stimuli, prompting a close-range assessment of olfactory cues that negated the visual preference. Continuous, close-range assessment of target silhouettes might be adaptive for males searching for close-range pheromones or acoustic signals for mating (Rudinsky, 1973; Rudinsky & Michael, 1973; Ryker & Rudinsky, 1976). Females, with a greater reproductive investment than males, might benefit more from avoiding the costs of close-range 'fly by' assessments once an appropriate combination of host visual and olfactory stimuli is perceived.

Models of host selection have speculated that bark beetle landing decisions are either (1) based on assessment of potential host identity and quality (e.g., Gries et al., 1989) or (2) random before (Hynum & Berryman, 1980; Byers, 1996) or after (Payne, 1986) initial attraction to olfactory stimuli. In the case of the MPB, both NHVs and visual stimuli can disrupt responses to aggregation pheromones (Borden et al., 1998; Campbell & Borden, 2006). Our results suggest that beetles could enter a mixed stand of host pine and non-host angiosperms that contained a beetle-attacked tree (and were redolent with attractive pheromones), and orient to individual trees using vision where there was no discriminating olfactory information, but could also assess the trees within the stand at relatively close flying range using olfaction. This supports the hypothesis that pheromone-responding beetles continue to utilize information in multiple sensory modes as they search for an individual host, as opposed to landing randomly on stems after pheromone detection (e.g., Payne, 1986). These results also raise the question as to why host-seeking pioneer beetles should use random landing in the absence of pheromones (Elkington & Wood, 1980; Hynum & Berryman, 1980). If they are indeed capable of close-range appraisal of individual trees, then pioneers in particular might benefit from such assessment.

While there is limited evidence of sensory integration by foraging insects, a few species have been shown to rely on visual cues, but prioritize olfactory information. The parasitoid wasp, *Diachasmimorpha longicaudata* (Ashmead) (Jang et al., 2000), the dipteran parasitoid, *Apocephalus paraponerae* Borgmeier (Morehead & Feener, 2000), the wild hawkmoth, *Manduca sexta* L. (Raguso & Willis, 2005), and the plum curculio, *Conotrachelus nenuphar* (Herbst) (Butkewich & Prokopy, 1993), all orient to host visual cues, but final host acceptance is mediated by short range odour detection. Apple maggots, *Rhagoletis pomonella* (Walsh), appear to locate individual trees by

olfaction, and then locate individual fruit by visual cues. As visual cues become less apparent (colour or density of host fruit), flies start to integrate olfactory cues (Aluja & Prokopy, 1993). Finally, the haematophagous bug, *Triatoma infestans* (Klug), aggregates preferentially on black patches for 'shelter'. However, when presented with black, empty patches and red patches with conspecific faecal scent cues, bugs prefer the red patches; when blue is substituted for red, visual preference is negated (equal); and when faecal cues are on both coloured and black patches, bugs revert to preferring black (Reisenman et al., 2000), suggesting an integration of olfactory and visual cues that is consistent with our results. Where chemical cues are more accurate host indicators than visual cues, foragers would benefit from prioritizing olfactory information up to the point of landing (Fawcett & Johnstone, 2003). This is the first time this ability has been shown for bark beetles, and the results suggest a flexible continuum of sensory integration during host selection, with different modes predominating at, rather than restricted to (e.g., Lanier, 1983), different stages of this process.

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