

Integration of visual and olfactory cues of hosts and non-hosts by three bark beetles (Coleoptera: Scolytidae)

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Abstract. 1. There has been a long-standing pre-occupation with how phytophagous insects use olfactory cues to discriminate hosts from non-hosts. Foragers, however, should use whatever cues are accurate and easily assessed, including visual cues.

2. It was hypothesised that three bark beetles, the mountain pine beetle (MPB), *Dendroctonus ponderosae* Hopkins, the Douglas-fir beetle (DFB), *D. pseudotsugae* Hopkins, and the western balsam bark beetle (WBBB), *Dryocoetes confusus* Swaine, integrate visual and olfactory information to avoid non-host angiosperms (e.g. paper birch, trembling aspen), that differ in visual and semiochemical profile from their respective host conifers (lodgepole pine, Douglas-fir, interior fir), and tested this hypothesis in a series of field trapping experiments.

3. All three species avoided attractant-baited, white (non-host simulating) multiple-funnel traps, and preferred attractant-baited black (host-simulating) traps. In experiments combining white, non-host traps with non-host angiosperm volatiles, bark beetles were repelled by these stimuli in an additive or redundant manner, confirming that these species could integrate visual and olfactory information to avoid non-host angiosperms while flying.

4. When antiaggregation pheromones were released from white traps, the DFB and MPB were repelled in an additive-redundant manner, suggesting that beetles can integrate diverse and potentially anomalous stimuli.

5. The MPB demonstrated the most consistent visual preferences, suggesting that it may be more of a 'visual specialist' than the DFB or WBBB, for which visual responses may be more contingent on olfactory inputs.

Key words. Bark beetles, Coleoptera, foraging behaviour, host–non-host discrimination, host selection, olfactory cues, Scolytidae, sensory integration, visual cues.

Introduction

Foraging insects assess their environment through different sensory modes (e.g. olfaction, vision, taste). Cues in each mode vary in both cost of assessment (e.g. after landing vs. in-flight) and in accuracy, and these factors should affect which mode is used (Fawcett & Johnstone, 2003). For instance, the same chemical may emanate from an acceptable host plant and one or more non-hosts (Eisner & Grant, 1981), and this overlap may lower the reliability of the cue. Many volatile green leaf alcohols and aldehydes are ubiquitous among numerous plant

species, yet many insects use these chemicals to find specific hosts (Visser, 1986). Monoterpenes are often stereotyped as volatiles of conifer bark and foliage, and are used in host selection by conifer-feeding insects, but they are also common in the tissues of non-host angiosperm trees (Byers, 2000; Huber *et al.*, 2000). Host odour specificity (Eisner & Grant, 1981), however, might be achieved through qualitative or quantitative blends of host volatiles (Pureswaran *et al.*, 2004; Pureswaran & Borden, 2005), and/or through the relative variability of compounds among hosts and non-hosts (Wright & Smith, 2004).

In contrast to odour, visual cues (form, colour, texture) have been presumed to 'lack the identifiable uniqueness required to explain the obvious discriminatory power of insects' (Thorsteinson, 1960). In some cases, however, host and non-host visual cues may be detectable, accurate, and used to

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discriminate a suitable host from a non-host (Prokopy & Owens, 1978; Prokopy *et al.*, 1983; Todd *et al.*, 1990; Henneman & Papaj, 1999). A few studies have investigated integration of visual and olfactory stimuli by insects. Preference of the coffee berry borer, *Hypothenemus hampei* Ferr., for red or white traps depends on the release rate of host-associated volatiles (Mathieu *et al.*, 1997). The parasitoid wasp *Diachasmimorpha juglandis* (Muesebeck) uses olfactory cues to find walnut fruit infested with host larvae, but does not discriminate between infested fruit and artificially damaged fruit, suggesting that this species could rely on available visual cues, which also synergise olfactory responses (Henneman *et al.*, 2002). Male gypsy moths, *Lymantria dispar* L. (Cardé & Hagaman, 1984; Charlton & Cardé, 1990) and adult *Manduca sexta* L. (Raguso & Willis, 2005) also appear to rely on visual and olfactory cues in an integrated fashion. Phytophagous insects would benefit both by identifying and avoiding non-hosts, as well as orienting to suitable hosts; however, it is rarely clear how sensory integration operates during each process (but see Prokopy *et al.*, 1983).

Conifer-colonising bark beetles feed and breed within the inner bark (phloem) of their host trees. Location of a suitable host is the single most important determinant of fitness for bark beetles (Raffa & Berryman, 1983), and many species avoid the costs of landing to determine host identity or quality by responding to olfactory cues while in flight (Moeck *et al.*, 1981; Wood, 1982; Borden *et al.*, 1986; Raffa *et al.*, 1993). Initial host location by some species is mediated by volatile, host tree semiochemicals. For example, Douglas-fir beetles (DFBs), *Dendroctonus pseudotsugae* Hopkins, are attracted to synthetic blends of Douglas-fir foliage and bole monoterpenes, although mountain pine beetles (MPBs), *D. ponderosae* Hopkins, are not (Pureswaran & Borden, 2005). There is, however, also some evidence of similar 'primary attraction' to host volatiles by the latter species, and several other bark beetles in Europe and North America (Byers *et al.*, 1985; Miller *et al.*, 1986; Syed & Graham, 1987; Schroeder & Lindelöw, 1989; Moeck & Simmons, 1991; Tunset *et al.*, 1993; Brattli *et al.*, 1998; Mac'asámano *et al.*, 1998). Several host-associated monoterpenes (Billings *et al.*, 1976; Borden *et al.*, 1987; Miller & Borden, 2000), and other host compounds such as ethanol (Furniss & Schmitz, 1971; Pitman *et al.*, 1975; Stock & Borden, 1983; Ross & Daterman, 1995), increase or synergise the attractiveness of bark beetle aggregation pheromones (Borden, 1985), which facilitate host selection by the majority of foragers.

Many species of coniferophagous beetles also detect and avoid volatile semiochemicals common to the bark and foliage of non-host angiosperm trees (Schroeder, 1992; Wilson *et al.*, 1996; Borden *et al.*, 1997, 1998; Birgersson *et al.*, 1998; Zhang *et al.*, 1999; Huber *et al.*, 2000; Huber & Borden, 2001, 2003), supporting the original hypothesis (Schroeder, 1992) that beetles also use olfactory cues to avoid non-hosts while flying. In general, when different non-host volatiles (NHVs) are combined into blends, there is an additive or redundant repellent effect on conifer-colonising bark beetles, which may be adaptive for avoidance of a variety of angiosperm taxa, particularly with overlap in the semiochemistry of hosts and non-hosts (Huber *et al.*, 2000).

As with other insects, bark beetles are thought to utilise visual cues such as vertical stem silhouettes only for 'landing and short range orientation' (Lanier, 1983; cf. Finch & Collier, 2000), and relatively few studies have investigated visual discrimination. Two bark beetles, *D. pseudotsugae* and *Ips paraconfusus* Lanier, have been shown to have at least two photoreceptors, one responding maximally to blue light ($\lambda_{\max} = 450$ nm), and the other to green light ($\lambda_{\max} = 520$ nm) (Groberman & Borden, 1982), although bark beetles probably have a third photoreceptor that responds to ultraviolet light (Droska *et al.*, 1983; Lin & Wu, 1992; Briscoe & Chittka, 2001). Pedestrian *D. pseudotsugae* and the striped ambrosia beetle *Trypodendron lineatum* Olivier are also photopositive to blue and green light in laboratory bioassays (Groberman & Borden, 1981), and bark beetles in general appear to be photopositive during the dispersal flight that precedes host selection (Atkins, 1966a; Shepherd, 1966). Bark and wood-boring beetles appear to prefer traps that may simulate host tree boles in form or hue (Kerck, 1972; Lindgren *et al.*, 1983). The MPB (Schonherr, 1977) and *T. lineatum* (Dubbel *et al.* 1985) also prefer dark-coloured sticky traps (black, brown, and red) and avoid landing on yellow or white cards (also see Entwistle, 1963). Similarly, the southern pine beetle, *D. frontalis* Zimm. (Strom *et al.*, 1999), and the western pine beetle, *D. brevicomis* LeConte (Strom *et al.*, 2001), both avoid white, attractant-baited multiple-funnel traps relative to black, baited traps. The southern pine beetle also avoids yellow, baited traps, although it does not discriminate among other colours (black, brown, blue, grey, green, or red; Strom & Goyer, 2001). The ecological significance of colour avoidance by bark beetles, however, remains essentially unexplored.

Black multiple-funnel traps (Lindgren, 1983) are widely used for experimentation with many coniferophagous beetles. The vertical silhouette created from the stacked funnels simulates a tree bole, and the reflectance spectrum of these traps is indistinguishable from that of most host conifers over the range of wavelengths visible to beetles (Campbell & Borden, 2005). The bark of two predominant non-hosts in northern temperate forests of North America, trembling aspen, *Populus tremuloides* Michx. and paper birch, *Betula papyrifera* Marsh, is white, however, and it was hypothesised that this quantitative difference in reflectance constitutes useful information to foraging beetles (Campbell & Borden, 2005). To test this hypothesis, we investigated: (i) whether the MPB, DFB, and western balsam bark beetle (WBBB), *Dryocoetes confusus* Swaine, would avoid traps simulating these non-hosts while foraging; (ii) how they would integrate putative visual and olfactory cues of these non-hosts; and (iii) how the first two species would integrate a visual non-host cue with beetle-produced antiaggregation pheromones.

Methods

Black and white 12-unit multiple-funnel traps (Phero Tech Inc., Delta, British Columbia, Canada) were used to mimic 'host conifer' and 'non-host angiosperm' boles respectively. White traps had higher reflectance, but similar spectral quality as the bark of non-hosts trembling aspen and paper birch, but unlike birch, did not reflect ultraviolet light (Campbell & Borden, 2005). All

experiments had a full factorial structure, with black and white traps and two or three levels of a semiochemical factor. Semiochemical treatments (see below, and Table 2 for details) always contained attractive pheromones and kairomones, so that responses could be interpreted in a host-seeking context. Semiochemicals were hung within the middle funnels of the traps, which were placed at least 15 m apart in randomised, complete linear blocks set up along logging roads, trails, and forest margins. A small block of Vapona No-pest® strip (Monsanto Canada Ltd, Mississauga, Ontario, Canada) was placed in each collecting cup to minimise escape and predation. Collected insects were frozen until counted; sex ratios were estimated by subsampling $n = 50$ (Lyon, 1958; Jantz & Johnsey, 1964; Bright, 1976).

Effect of a non-host visual cue

As detailed in Table 1, all species were assayed with an initial experiment that tested the prediction that beetles would avoid

white, baited traps and prefer black, baited traps. Black and white unbaited traps were included as controls, to give four treatments.

Effect of visual and olfactory host and non-host cues

A second series of experiments tested the predictions that beetles would avoid attractant-baited traps that also had either an angiosperm NHV stimulus or a non-host angiosperm visual stimulus (white colour), and that this discrimination would be greatest when both cues were present. The six treatments included: black and white attractant-baited traps, black and white traps with both an attractive bait and NHVs, and black and white unbaited control traps (Table 1). We tested NHVs with low to moderate behavioural activity (Wilson *et al.*, 1996; Borden *et al.*, 1998; Huber & Borden, 2001, 2003), which would be unlikely to overwhelm any visual-olfactory stimulus interaction. Two *host* volatiles were added in experiments with the

Table 1. Description of all experiments. Treatment combinations are listed at left, with experiments using those treatments enumerated for each primary target insect (including sample sizes and dates for each).

Treatments*	Interior DFB	Coastal DFB	WBBB	MPB
Effect of a non-host visual cue				
Black	Exp 1:	Exp 6:	Exp 8:	Exp 10:
Black + Bait	29 May–4 June, 2001	15 replicates:	22 June–14 July, 2002	18 July–15 August, 2001
White	$n = 14$	17 April–13 May;	$n = 15$	$n = 14$
White + Bait		6 replicates:		
		29 April–13 May 2002		
Effect of visual and olfactory host and non-host cues				
Black	Exp 2 (NHV 1):	Exp 7 (NHV2):	Exp 9 (HV):	Exp 11 (NHV2):
Black + Bait	1–11 June 2001	13 May–3 June 2002	14 July–15 August 2002	18 July–8 August 2001
Black + Bait + NHV	$n = 14$	$n = 15$	$n = 15$	$n = 14$
White	Exp 3 (NHV 2):			Exp 12 (NHV3):
White + Bait	$n = 8$: 18 June–6 July;			29 Aug–10 Sept 2001
White + Bait + NHV	$n = 8$: 6 July–11 Aug 2002			$n = 16$
Effect of visual and olfactory non-host cues and antiaggregation pheromones				
Black	Exp 4 (AA = MCH):			Exp 13 (AA = verbenone):
Black + Bait	11–22 June 2001			15–21 August 2001
Black + Bait + AA	$n = 15$			$n = 15$
White				
White + Bait				
White + Bait + AA				
Black	Exp 5 (AA = MCH; NHV1):			Exp 14
Black + Bait	3–6 July 2001			(AA = verbenone;
Black + Bait + NHV + AA	$n = 16$			NHV2): 15–21 August
White				2001 $n = 14$
White + Bait				
White + Bait + NHV + AA				

*Colour refers to trap colour, followed by abbreviations for semiochemical treatments: NHV = non-host volatile blend; HV = host volatile blend; AA = antiaggregation pheromones. Species-specific semiochemicals listed by experiment: NHV1 = benzyl alcohol + guaiacol; NHV2 = benzyl alcohol + hexanol; NHV3 = guaiacol; NHV5 = hexanol; HV = α -pinene + ethanol; MCH = antiaggregation pheromone of the Douglas-fir beetle; verbenone = antiaggregation pheromone of the mountain pine beetle. See Table 2 for semiochemical information. Locations in British Columbia, Canada: Interior DFB – Luluwassin Creek Forest Service Road (FSR) near the town of Lytton; coastal DFB – Malcolm Knapp University of British Columbia Research Forest, near Maple Ridge; WBBB – Buchanan FSR, Buck Mountain, near Kelowna; MPB – Opax Mountain, near Kamloops.

Table 2. Optical nature, purity, release devices, and rates for experimental semiochemicals.

Semiochemical*	Optical Nature %(+: -), where present	Chemical purity (%)	Release device†	Release rate‡ (mg 24 h ⁻¹)	Temp (°C)
Douglas-fir beetle bait					
frontalin	50 : 50	98	400 µl PE capillary tube	2	23
MCOL	50 : 50	97	PE bubblecap	2	20
ethanol		95	PVC pouch	30–50	20
Western balsam bark beetle bait					25
<i>exo</i> -brevicommin	50 : 50	98	1.5 ml PP tube in PE pouch	3	25
Mountain pine beetle bait					
<i>trans</i> -verbenol		90 <i>trans</i> , 7 <i>cis</i>	PE bubblecap	1.2	20
<i>exo</i> -brevicommin	50 : 50	98	PVC flexlure	0.2	20
myrcene		90	PE bottle	250	20
Antiaggregation pheromones and non-host volatiles					
MCH		98	Glass microcapillary tube§	0.307	23
verbenone	20 : 80	99	PE bubblecap	0.68	25
guaiacol		99	PE bubblecap	5	20
hexanol		99	PE bubblecap	4	20
benzyl alcohol		99	PE bubblecap	5	20

*All compounds were obtained from Phero Tech Inc. (7572 Progress Way, Delta, B.C. V4G1E9).

IUPAC names (where different from trivial names given above) follow. Frontalin, 1,5-dimethyl-6,8-dioxabicyclo[3.2.1]octane; MCOL, 1-methyl-2-cyclohexen-1-ol; *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; α -pinene, 2,6,6-trimethylbicyclo[3.1.1]hept-2-ene; MCH, 3-methyl-2-cyclohexen-1-one; verbenone (S)-(-)-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one; guaiacol, 2-methoxyphen-1-ol; hexanol, hexan-1-ol.

†Release device materials: PE, polyethylene; PVC, polyvinyl chloride; PP, polypropylene. All release devices were sealed except that for MCH.

‡Release rates determined by Phero Tech Inc., except for MCH and verbenone, determined at S.F.U.

§Open glass tube mounted inside an open, 400 µl PE tube.

WBBB, because it does not respond well to traps baited only with the pheromone (+/-)-*exo*-brevicommin (Table 1).

Effects of visual and olfactory non-host cues and antiaggregation pheromones

In similar six-treatment experiments with the mountain pine and Douglas-fir beetles, we substituted these species' anti-aggregation pheromones for the NHVs, to test how beetles would integrate these stimuli, and also substituted a combination of antiaggregants and NHVs in a final two experiments (Table 1).

Statistical analyses

To improve normality and homoscedasticity, all catches were \log_{10} transformed (Zar, 1999). This reduced the difference between the largest and smallest treatment standard deviations to less than fourfold, which is considered appropriate for ANOVA (C.J. Schwarz, Department of Statistics and Actuarial Science, Simon Fraser University, pers. comm.). Log-transformation has the added advantage of allowing correct estimation of (non-additive) interactions when treatment effects are proportional to one another, and therefore act multiplicatively (as is the case when testing combinations of repellent stimuli). The responses of male and female beetles to the different stimuli were compared

by ANOVA (PROC GLM, SAS v.8.0) for two fixed effects (colour and semiochemical) and their interaction. Standard treatment means were similar to least squares means in all cases, and were compared by the REGW multiple-range test (Day & Quinn, 1989; SAS/STAT®, 1990). Although the absence of a significant ANOVA interaction could have permitted factor-specific comparison of means, the same REGW procedure was used to allow comparisons between sexes, and among experiments both within and across species. There was no treatment \times time interaction ($P > 0.05$) in any experiment with blocks in two time periods. All analyses considered block as a random effect, used Type III sums of squares, and experimentwise $\alpha = 0.05$.

Results

In describing lower catches, use of the terms 'repelled', 'avoided', 'disrupted', and 'deterred' is always relative to black, attractant-baited control traps.

Effect of a non-host visual cue

All three bark beetles avoided white, baited traps compared with black, baited traps (Experiments 1, 6, 8, 10; panel A in Figs 1–5). For interior and coastal DFBs (Experiments 1 and 6 respectively), there was a significant interaction of

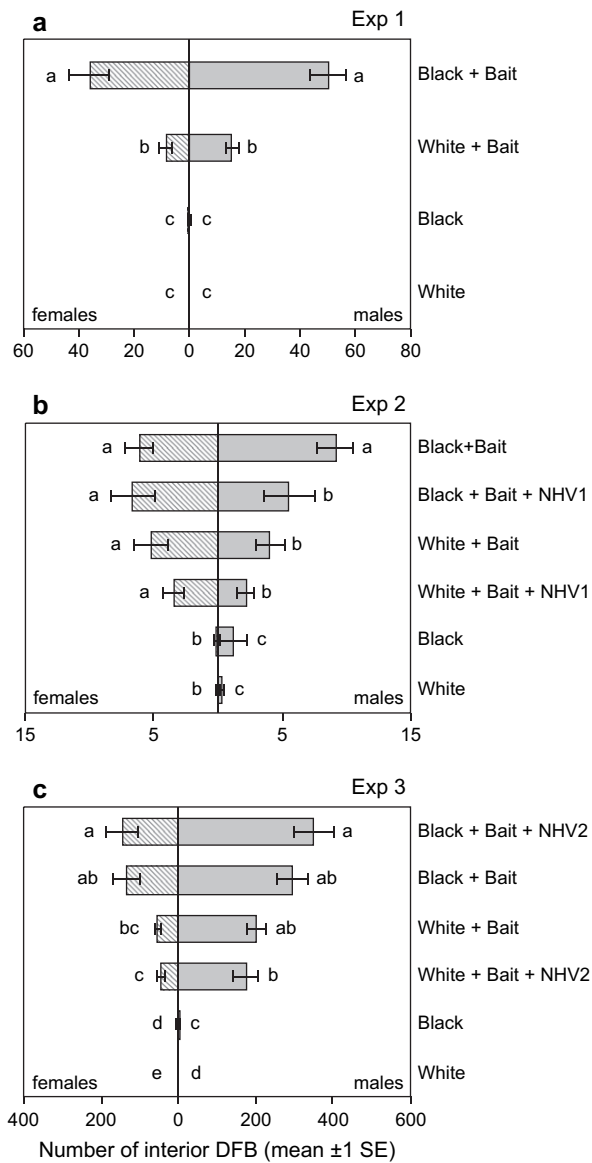


Fig. 1. Results of Experiments 1–3 for interior DFBs, demonstrating the effects of a non-host visual cue alone (a) and in combination with different non-host volatiles (b,c). In the treatment combinations listed on the right, white and black denote trap colours, bait is a combination of aggregation pheromones and ethanol, and NHV denotes non-host volatile combinations. Within an experiment and sex, means followed by the same letter are not significantly different (REGW test).

colour \times semiochemical for both sexes (Table 3), with more beetles caught in black over white traps only when the traps were baited (Figs 1a and 2a). There was no such interaction for the MPB (Experiment 10, Table 4), with significantly more beetles caught in black than white traps even when these were unbaited (Fig. 3a). For the WBBB (Experiment 8), there was a 65% reduction in catches (significant for females only) in white as opposed to black, baited traps for both sexes (Fig. 4a; Table 5). Significant numbers of the fir-colonising *Dryocoetes*

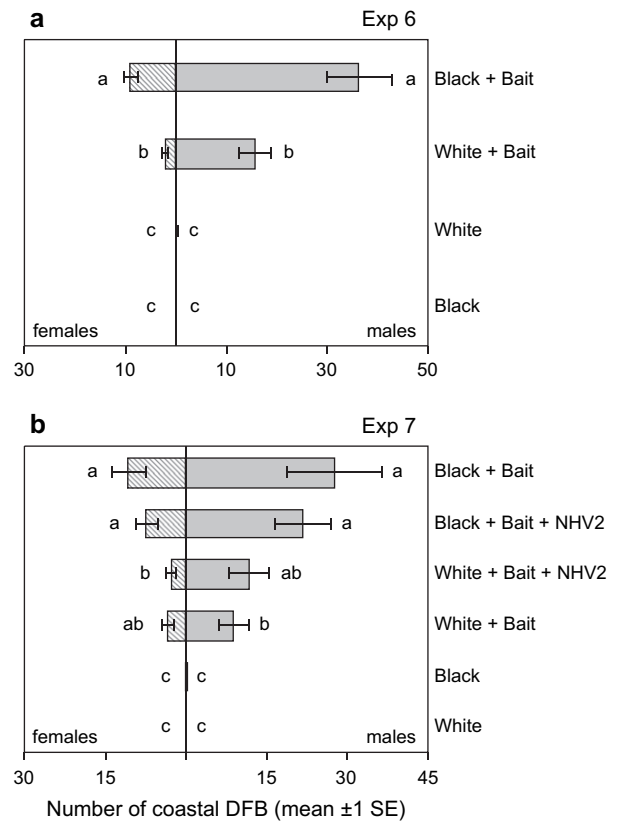


Fig. 2. Results of Experiments 6 and 7 for coastal DFBs, demonstrating the effects of a non-host visual cue alone (a) and in combination with a non-host volatile (b). In the treatment combinations listed on the right, white and black denote trap colours, bait is a combination of aggregation pheromones and ethanol, and NHV denotes non-host volatile blends. Within an experiment and sex, means followed by the same letter are not significantly different (REGW test).

autographus (Patzburg) were also caught in Experiment 8, and analysis of mixed sexes indicated a strong avoidance of white, baited traps (Fig. 5a; Table 5).

Effects of visual and olfactory host and non-host cues

Both the DFB and MPB avoided non-host visual and semiochemical stimuli (Experiments 2, 3, 7, 11, 12; panels B and C in Figs 1–3). In Experiment 2, attraction of male (but not female) DFBs to aggregation pheromones was significantly disrupted by both white traps and the addition of benzyl alcohol and guaiacol (Fig. 1b). These two stimuli combined had a redundant effect on catches, contributing to a significant semiochemical \times colour interaction (Table 3). In Experiment 3, black traps caught significantly more beetles than white traps (main effect of colour, Table 3), and females were significantly disrupted by the combination of white traps and NHVs; there was an additive effect of combining both types of stimuli, with some redundancy (Fig. 1c). In unbaited traps, significantly more beetles of both sexes were also caught in black over white traps. More

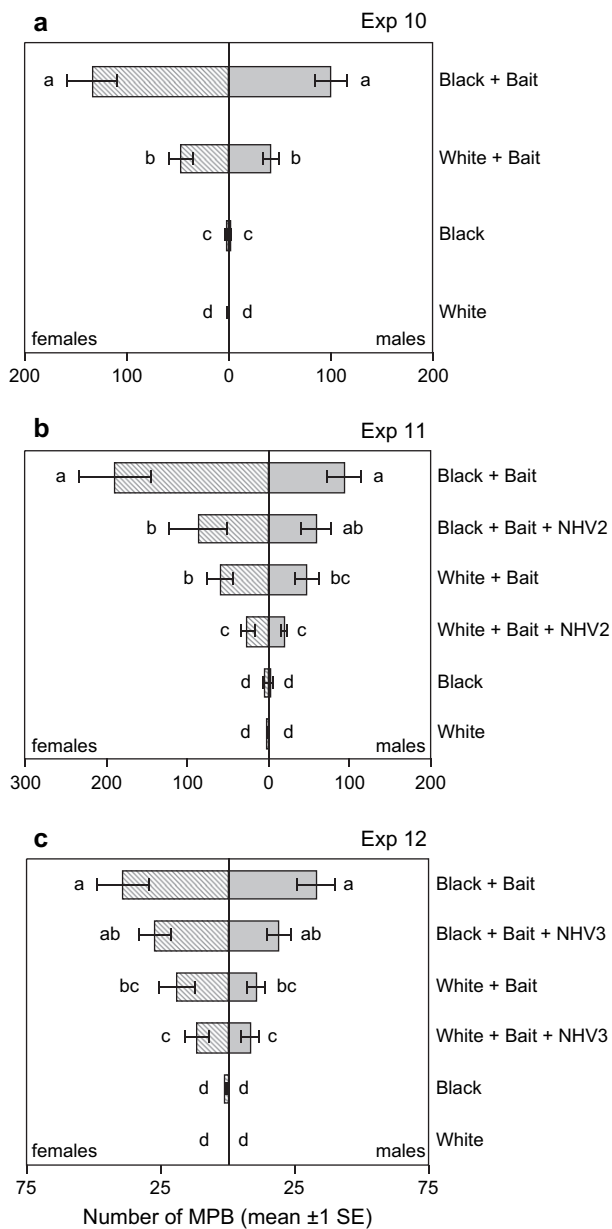


Fig. 3. Results of Experiments 10–12 for the MPB, demonstrating the effects of a non-host visual cue alone (a), and in combination with non-host volatiles (b,c). In the treatment combinations listed on the right, white and black denote trap colours, bait is a combination of aggregation pheromones and myrcene, and NHV denotes non-host volatile blends. Within an experiment and sex, means followed by the same letter are not significantly different (REGW test).

male and female coastal DFBs were caught in black than in white traps in Experiment 7 (significant colour effect, no interaction; Table 3). For females, there was an additive-redundant trend; only the white and NHV stimuli together significantly reduced catches relative to the black, baited controls. For males, only the non-host visual cue significantly reduced catches relative to the black, baited controls (Fig. 2b).

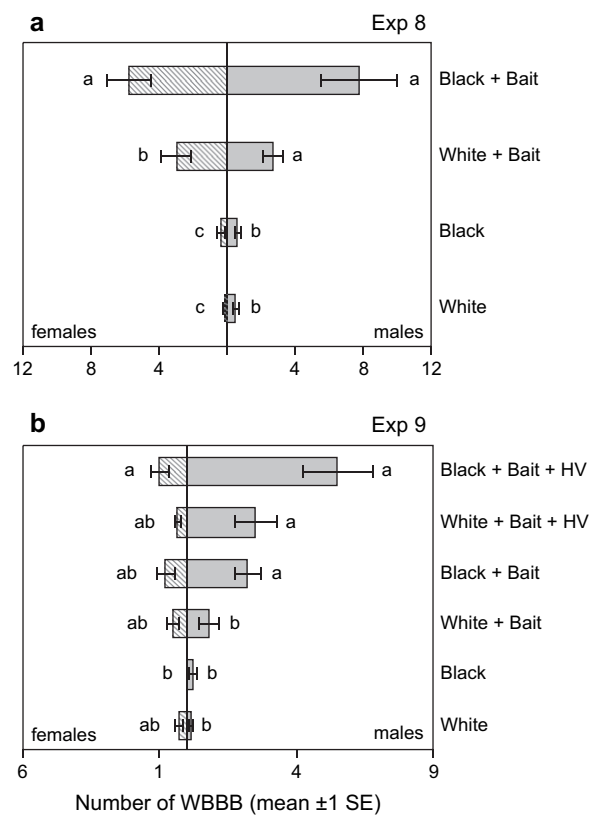


Fig. 4. Results of Experiments 8 and 9 for the WBBB, demonstrating the effects of a non-host visual cue alone (a) and in combination with host volatiles (b). In the treatment combinations listed on the right, white and black denote trap colours, bait is the aggregation pheromones and ethanol, and HV denotes the host volatile blend. Within an experiment and sex, means followed by the same letter are not significantly different (REGW test).

In Experiment 11, female MPBs were significantly deterred by both white traps and a blend of benzyl alcohol and hexanol; combining the two types of stimuli led to a further reduction (Fig. 3b). Males were deterred by the white traps (but not the NHVs), and there was evidence of redundancy when the two types of stimuli were combined (Fig. 3b). This redundancy, and the lack of differences between unbaited black and white traps for either sex, contributed to significant semiochemical \times visual interactions (Table 4). In Experiment 12, white traps deterred both sexes, but the NHV guaiacol did not significantly reduce responses to baited traps of either colour (Fig. 3c). Overall, female colour preference in Experiment 12 was similar across semiochemical treatments, although there was a significant interaction for males (Table 4).

Over twice as many male WBBBs were caught in traps baited with *exo*-brevicomin, α -pinene, and ethanol than in traps with *exo*-brevicomin alone, although this increase was only significant in white traps (Experiment 9; Fig. 4b). There was also a significant main effect of colour, and no interaction, indicating that males preferred black over white traps across all semiochemical treatments (Table 5). Few females were caught, and

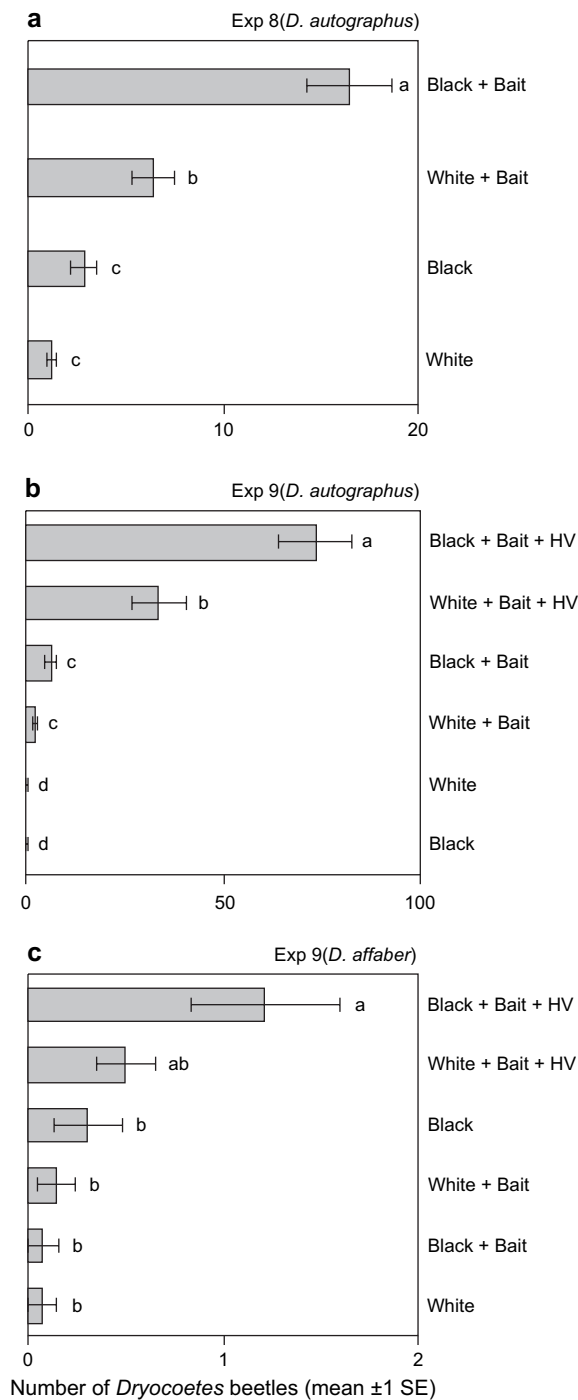


Fig. 5. Catches of mixed sexes of *Dryocoetes autographus* and *Dr. affaber* in Experiments 8 and 9, demonstrating the effects of a non-host visual cue alone (a) and in combination with host volatiles (b,c). In the treatment combinations listed on the right, white and black denote trap colours, bait is the aggregation pheromone (+/-)-*exo*-brevicomin, and HV denotes the host volatile blend. Within an experiment and species, means followed by the same letter are not significantly different (REGW test).

the only significant difference was between catches in black, unbaited traps, and black traps baited with *exo*-brevicomin and the host volatiles; there was only a weakly significant effect of semiochemical treatment overall (Table 5). In this experiment, *Dr. autographus* (mixed sexes) did not discriminate between black and white traps baited with *exo*-brevicomin; they did prefer black over white traps when these were baited with both *exo*-brevicomin and host volatiles (Fig. 5b), contributing to a significant visual \times olfactory cue interaction (Table 5). The host semiochemicals attracted greater numbers of beetles to traps of both colours relative to all other treatments. Similarly, with *Dr. affaber* (Mannerheim) (Experiment 9), the difference between black and white traps was greater (over twofold) in traps baited with *exo*-brevicomin and the host volatiles than in traps with only the pheromone. Only black traps with the pheromone and host volatiles caught significantly more beetles than the unbaited traps (Fig. 5c).

Effects of visual and olfactory non-host cues and antiaggregation pheromones

The DFB (Experiment 4; Fig. 6a; Table 3) and the MPB (Experiment 13; Fig. 7a; Table 4) both strongly avoided the black, attractant baited traps that also released their antiaggregation pheromones. They also avoided white, baited traps; avoidance by the DFB was strongest when the two stimuli were combined. In the presence of the potent antiaggregation pheromones, colour was effectively redundant. Similarly, verbenone always reduced catches of female MPBs to levels not significantly different from those in the unbaited control traps. There was a significant semiochemical \times visual interaction for the DFB, but not the MPB (Tables 3 and 4).

Similarly, in Experiment 5 (Fig. 6b), addition of MCH + NHV1 reduced DFB catches of both sexes significantly, with female catches being as low as those in the unbaited traps. As in Experiment 4, the non-host visual stimulus was redundant with the addition of the MCH + NHV1 blend, contributing to a significant interaction for females (Table 3). For the MPB, addition of verbenone + NHV2 in Experiment 14 reduced catches of females to levels no different from those in the unbaited control traps (Fig. 7b). There was an effect of colour overall, and no interaction (Table 5), although by multiple pairwise tests, the repellency of the white stimulus again appeared redundant in combination with the powerful antiaggregant + NHV blend (Fig. 7b).

Discussion

These results support the prediction that coniferophagous beetles should prefer host model (black) traps, and avoid non-host (white) traps. All three bark beetles colonise conifers with dark grey to black bark, but must be able to distinguish their hosts from a variety of coniferous and hardwood non-hosts. While the volatile signatures of trees are important in non-host angiosperm discrimination by many bark beetles (Zhang & Schlyter, 2004), beetles may also use the distinctive visual appearance of at least

Table 3. ANOVA of the response of the Douglas-fir beetle to visual and olfactory stimuli.

Exp.	Source of variation	d.f.	Males			Females		
			MS	F	P	MS	F	P
1	Colour	1	1.0812	22.76	< 0.0001	1.5863	20.56	< 0.0001
	Semiochemical	1	24.5213	516.24	< 0.0001	14.6656	190.07	< 0.0001
	Colour × Semio	1	0.7703	16.22	0.0003	1.0382	13.46	0.0008
	Error	37	0.0475			0.0772		
2	Colour	1	0.8707	9.94	0.0025	0.1532	2.65	0.1089
	Semiochemical	2	3.0667	35.00	< 0.0001	4.0334	69.63	< 0.0001
	Colour × Semio	2	0.3220	3.67	0.0310	0.0803	1.39	0.2575
	Error	62	0.0876			0.0579		
3	Colour	1	1.4422	21.42	< 0.0001	2.3300	20.18	< 0.0001
	Semiochemical	2	42.1231	625.51	< 0.0001	22.6100	195.86	< 0.0001
	Colour × Semio	2	0.0484	0.72	0.4905	0.0009	0.01	0.9918
	Error	73	0.0673			0.1154		
4	Colour	1	1.3312	28.23	< 0.0001	1.8756	39.49	< 0.0001
	Semiochemical	2	40.7078	862.99	< 0.0001	21.7579	458.14	< 0.0001
	Colour × Semio	2	0.2483	5.26	0.0075	0.4064	8.56	0.0005
	Error	68	0.0472			0.0475		
5	Colour	1	0.1339	1.33	0.2527	0.5086	8.49	0.0048
	Semiochemical	2	25.9393	257.69	< 0.0001	13.5671	226.45	< 0.0001
	Colour × Semio	2	0.1576	1.57	0.2164	0.2559	4.27	0.0178
	Error	69	0.1007			0.0599		
6	Colour	1	0.6295	7.68	0.0075	1.2226	28.17	< 0.0001
	Semiochemical	1	29.0083	353.70	< 0.0001	8.359	192.59	< 0.0001
	Colour × Semio	1	0.6504	7.93	0.0066	1.2405	28.58	< 0.0001
	Error	59	0.0820			0.0434		
7	Colour	1	1.3447	11.67	0.0011	0.9350	10.29	0.0020
	Semiochemical	2	8.8722	76.99	< 0.0001	3.7124	40.86	< 0.0001
	Colour × Semio	2	0.2175	1.89	0.1592	0.2048	2.25	0.1126
	Error	69	0.1152			0.0909		

two predominant angiosperm genera to identify them as non-hosts (Campbell & Borden, 2005) and avoid them.

The avoidance of white traps by the two *Dendroctonus* species is consistent with similar results for *D. frontalis* and *D. brevicomis* (Strom *et al.*, 1999, 2001). The former species also avoided yellow traps, but did not discriminate among black, blue, brown, grey, green, or red traps (Strom & Goyer, 2001). Schonherr (1977) also found a preference for black and brown traps by *D. ponderosae* and *Ips montanus* (Eichhoff) and an avoidance of white, yellow, and orange traps, but did not statistically evaluate these responses by species or sex. Similarly, Dubbel *et al.* (1985) found that *Ips typographus* avoided white, pheromone-baited traps, although neither Schonherr (1977) nor Dubbel *et al.* (1985) used bole-simulating traps. Goyer *et al.* (2004), however, found that unidentified *Ips* species arrived more frequently at painted black than at painted white logs.

When the visual stimulus was combined with olfactory cues of non-host angiosperms, there was an additively repellent effect in most cases, with evidence of considerable redundancy. This additive-redundant trend is consistent with similar findings by Borden *et al.* (1998), Huber and Borden (2003), and Zhang and Schlyter (2003), for combinations of repellent non-host angiosperm volatiles. Borden *et al.* (1998) hypothesised that this was because coniferophagous beetles should have evolved a generalised avoidance of multicomponent angiosperm volatile blends (rather

than specific compounds) and that additivity or redundancy of non-host chemicals should be favoured over a synergistic response that might deter beetles from too wide an area (e.g. mixed stands containing suitable hosts). We suggest that this hypothesis should be extended to include visual stimuli. Beetles would benefit from an integrated response to cues from both sensory modes, and redundancy of the effects of tree stimuli across sensory modes would allow beetles to switch between cues depending on their accuracy (Fawcett & Johnstone, 2003). For instance, visual and olfactory cues may be differentially apparent in different environments (e.g. mixed stands, different stand densities) (Endler, 1993). In cases where chemical cues alone were too complex or too evenly distributed to allow discrimination, visual cues could facilitate in-flight discrimination (Campbell & Borden, 2006), at least between conifers and angiosperms. Discrimination between host and non-host conifers would be unlikely to be accomplished using visual cues given the spectral similarity among most conifers in the study area (Campbell & Borden, 2005), and where accomplished in flight, may occur on a quantitative semiochemical basis (Pureswaran & Borden, 2005). Overall, our results indicate that bark beetles can integrate diverse combinations of repellent stimuli in a putatively adaptive manner.

The MPB exhibited the most consistent avoidance of white traps, and it and the DFB preferred black to white *unbaited* traps in one experiment each (Figs 1c and 3a). The ANOVA results

Table 4. ANOVA of the response of the mountain pine beetle to visual and olfactory stimuli.

Exp.	Source of variation	d.f.	Males			Females		
			MS	F	P	MS	F	P
10	Colour	1	1.9068	32.89	< 0.0001	2.3177	28.37	< 0.0001
	Semiochemical	1	30.0615	518.55	< 0.0001	29.4071	359.96	< 0.0001
	Colour × Semio	1	0.0599	1.03	0.3159	0.2647	3.24	0.0800
	Error	37	0.0580			0.0817		
11	Colour	1	1.3866	10.73	0.0017	2.3056	18.91	< 0.0001
	Semiochemical	2	16.3140	126.20	< 0.0001	18.4953	151.66	< 0.0001
	Colour × Semio	2	0.4118	3.19	0.0482	0.5977	4.90	0.0106
	Error	62	0.1293			0.1220		
12	Colour	1	1.8228	19.47	< 0.0001	2.1090	23.21	< 0.0001
	Semiochemical	2	8.7796	93.79	< 0.0001	11.6760	128.51	< 0.0001
	Colour × Semio	2	0.5267	5.63	0.0055	0.0507	0.56	0.575
	Error	68	0.0936			0.0909		
13	Colour	1	1.3163	10.40	0.0019	0.6658	5.87	0.018
	Semiochemical	2	12.6890	100.27	< 0.0001	9.9452	87.74	< 0.0001
	Colour × Semio	2	0.2906	2.30	0.1082	0.2727	2.41	0.0977
	Error	69	0.1265			0.1134		
14	Colour	1	0.9643	10.66	0.0018	0.7548	6.34	0.0144
	Semiochemical	2	29.3913	325.06	< 0.0001	29.6266	248.78	< 0.0001
	Colour × Semio	2	0.0390	0.43	0.6517	0.2628	2.21	0.1185
	Error	63	0.0904			0.1191		

(Tables 3–5) reveal that MPB responses also exhibited the least number of significant interactions of colour and semiochemical factors, suggesting that visual preferences were consistent across semiochemical treatments. Given the redundant trend discussed above, this lack of interaction does not imply actual independence of visual and olfactory sensory systems. Also, compared with the DFB and the WBBB, the MPB is more aggressive at high population densities (as here), and colonises standing, living trees almost exclusively (Furniss & Carolin, 1977). Thus the MPB may have highly specialised behavioural responses to a more narrow range of attractive host profiles. Prokopy and Owens (1978) hypothesised that specialist foragers should have evolved specific orientation responses to host stimuli, particularly visual stimuli, and suggested that ‘visual specialists’ should be easily deterred by any deviation from their preferred host cues. Relative to the DFB and WBBB, which will

readily colonise freshly killed, fallen hosts that may lack accurate visual cues, the MPB may be more of a visual specialist, and this conclusion is supported by Strom *et al.* (2001), who suggested that the southern pine beetle was more of a visual specialist than the less aggressive western pine beetle.

Consistent with this hypothesis, visual responses by the DFB were more variable. Females did not discriminate between black and white traps in Experiment 2 (Fig. 1b), although there may have been insufficient numbers to detect a difference. In Experiment 3, there were insignificant reductions of male and female DFBs in white vs. black, baited traps; however, both sexes preferred black to white unbaited traps; however, females were repelled by white traps when they were also baited with a NHV, and there was a highly significant effect of colour for both sexes overall, with no interaction (Table 3). Finally males did not respond to colour in Experiment 5 (Table 3; Fig. 6b). The

Table 5. ANOVA of the response of three *Dryocoetes* species to visual and olfactory stimuli. * Insufficient *Dr. affaber* captured for analysis in Experiment 8.

Exp.	Source of variation	d.f.	<i>D. confusus</i>						<i>D. autographus</i>			<i>D. affaber</i> *		
			Males			Females			Mixed sexes			Mixed sexes		
			MS	F	P	MS	F	P	MS	F	P	MS	F	P
8	Colour	1	12.0700	4.40	0.0422	9.2116	5.41	0.0252	1.3165	17.06	0.0002			
	Semiochemical	1	85.8000	31.31	< 0.0001	105.2659	61.81	< 0.0001	4.4682	57.91	< 0.0001			
	Colour × Semio	1	8.3566	3.05	0.0885	5.0745	2.98	0.0920	0.1625	2.11	0.1545			
	Error	40	0.0824			0.0574			0.0772					
9	Colour	1	0.6354	8.85	0.0042	0.0359	1.15	0.2882	0.9318	10.18	0.0022	0.0617	2.64	0.1093
	Semiochemical	2	1.5505	21.59	< 0.0001	0.0990	3.17	0.0492	15.6448	170.88	< 0.0001	0.2287	9.79	0.0002
	Colour × Semio	2	0.1205	1.68	0.1951	0.0748	2.39	0.1000	0.3323	3.63	0.0324	0.0428	1.83	0.1684
	Error	61	0.0718	0.0313		0.0916			0.0234					

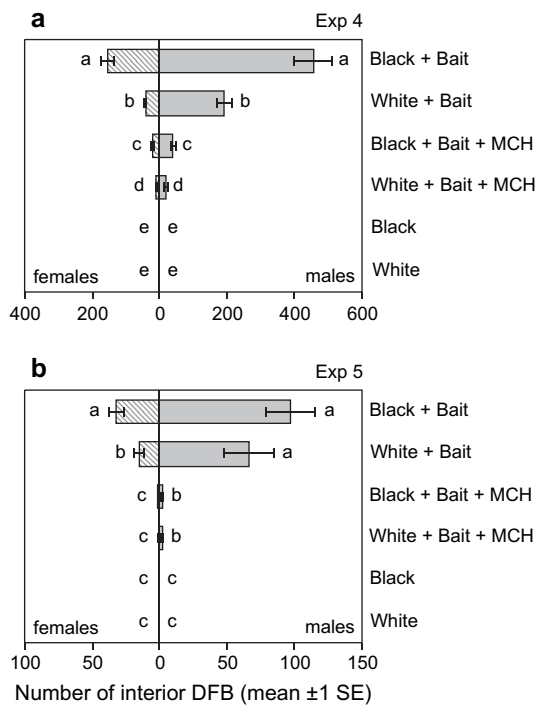


Fig. 6. Results of Experiments 4 and 5 for interior DFBs, demonstrating the effects of non-host visual and antiaggregation olfactory cues alone (a) and in combination with non-host volatiles (b,c). In the treatment combinations listed on the right, white and black denote trap colours, bait is a combination of aggregation pheromones and ethanol, MCH is the antiaggregation pheromone, and NHV denotes non-host volatile blends. Within an experiment and sex, means followed by the same letter are not significantly different (REGW test).

DFB is less aggressive than the MPB, and colonises fallen hosts readily (Atkins, 1966b; Humphreys, 1995). Forest floors are generally achromatic (lacking a hue), and fallen trees on the forest floor would present fewer, or less accurate visual cues than standing stems (Endler, 1993). The use of both classes of hosts may explain the slightly more variable response of this species, and perhaps the WBBB. In a similar fashion, several ambrosia beetles (which also prefer fallen hosts) do not demonstrate strong visual preferences (Campbell, 2004). Coastal and interior DFB beetles responded similarly (Figs 1 and 2), suggesting that observed differences in host use between interior and coastal habitats have not selected for differing integrated responses to visual and olfactory non-host cues.

Visual responses often appeared to be contingent on the olfactory context, e.g. there were often similar catches in black and white traps in the absence of olfactory stimuli. Semiochemical attraction, however, occurs at a greater distance than that at which visual perception is possible (Prokopy, 1986), and there was also evidence that the MPB and DFB visually discriminated between black and white unbaited traps. In Experiment 8, *Dr. autographus* did not discriminate between *exo*-brevicom-baited black and white traps, but did prefer black over white traps when the traps also released host volatiles (Fig. 5b). A

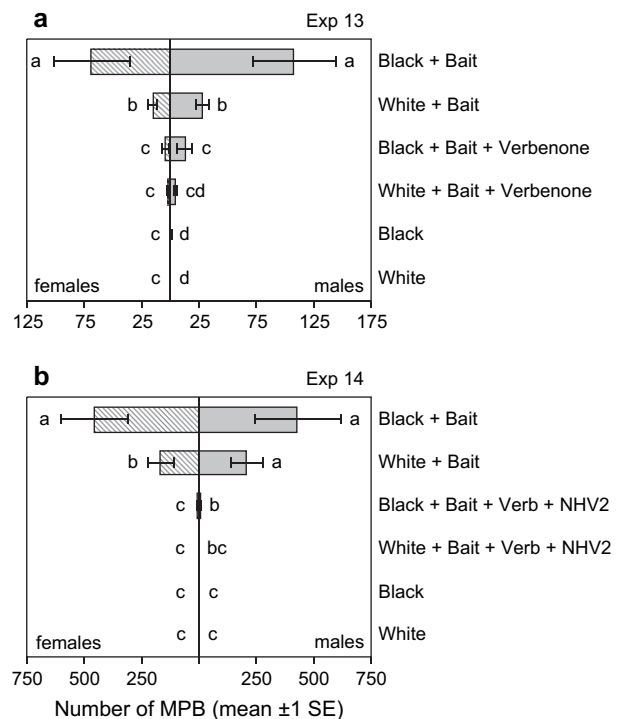


Fig. 7. Results of Experiments 13 and 14 for the MPB, demonstrating the effects of non-host visual and antiaggregation olfactory cues alone (a) and in combination with non-host volatiles (b). In the treatment combinations listed on the right, white and black denote trap colours, bait is a combination of aggregation pheromones and myrcene, verbenone (Verb) is the antiaggregation pheromone, and NHV denotes non-host volatile blends. Within an experiment and sex, means followed by the same letter are not significantly different (REGW test).

similar trend was observed for *Dr. affaber* (Fig. 5c). These results are further evidence for integration of visual and olfactory cues of hosts and non-hosts by bark beetles, and in fact suggest that synergism of olfactory and visual information during host-selection can mediate landing decisions (Campbell, 2004). This hypothesis was supported in a subsequent experiment, in which the MPB was shown to integrate olfactory and visual host stimuli but prioritise a host semiochemical, even at close range and when the attractive pheromone was decoupled from the 'tree' stimuli (Campbell & Borden, 2006).

It could be argued that avoidance of white traps is not an indication that beetles avoid non-host trembling aspen and paper birch on the basis of vision, but is because they do not perceive white traps to the same extent as the black traps. This is unlikely for three reasons. First, one of the study species, *D. pseudotsugae*, and another scolytid, *Ips paraconfusus* have electrophysiological sensitivity maxima for blue and green wavelengths (Groberman & Borden, 1982), which are reflected abundantly from white, but not black, traps. Second, the DFB and the striped ambrosia beetle, *T. lineatum*, both oriented toward sources of blue and green light in laboratory bioassays of walking beetles (Groberman & Borden, 1981), yet exhibited contrasting behaviours in field experiments (Figs 1 and 2;

Campbell, 2004). Finally, even when black traps were preferred to white traps, there were often moderate numbers of beetles caught in white traps, indicating that some beetles chose to land there.

One might also question the similarity of white traps to trembling aspen and paper birch bark, as white traps had higher reflectance than either species at wavelengths longer than 400 nm (Campbell & Borden, 2005). It is possible that this difference arose in part because the spectrophotometer was sensitive to small aberrations in the bark surface, e.g. birch bark lenticels, that reduced the overall reflectance intensity recorded by the light detector at close range, but which would not be resolvable at a greater distance by a flying beetle. In addition, Strom and Goyer (2001) caught low, but similar numbers of southern pine beetles in both white and yellow traps. To a green photoreceptor responding maximally at 530 nm, the yellow paint used in that study would have a relative intensity of ≈ 0.43 , while paper birch and trembling aspen have reflectance intensities of 0.57 and 0.34 at that wavelength respectively (Campbell & Borden, 2005). The similar catches in both yellow and white traps (Strom & Goyer, 2001), and the fact that these yellow traps had a peak reflectance intensity closely approximating that of the principal non-host angiosperms examined in our study, support the ecological relevance of our experimental stimuli.

In conclusion, the results of these experiments demonstrate that all three bark beetles could avoid certain non-host angiosperms using visual cues. The additive-redundant, and occasionally synergistic responses to visual and olfactory stimuli further suggest that beetles also integrate cues of both hosts and non-hosts across sensory modes when making crucial host-selection decisions. Our results underscore the need to consider responses to ecologically relevant cues of both hosts and non-hosts in multiple sensory modes when evaluating host discrimination behaviour.

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