INTEGRATION OF VISUAL AND OLFACTORY CUES BY HOST-SEEKING FOREST COLEOPTERA (SCOLYTIDAE, CERAMBYCIDAE)

by

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ABSTRACT

There has been a long standing preoccupation with how conifer-infesting beetles use olfactory cues to locate suitable breeding hosts, and avoid non-hosts. However, host-seeking insects should use whatever cues are accurate, and easily assessed, including visual cues. I investigated this understudied aspect of host selection, and asked how coniferophagous bark and woodboring beetles integrate visual and olfactory information. I analysed differences in spectral reflectance among the coniferous hosts of the Douglas-fir beetle, *Dendroctonus pseudotsugae*, the mountain pine beetle, *D. ponderosae*, the western balsam bark beetle, *Dryocoetes confusus*, the ambrosia beetles *Gnathotrichus sulcatus*, *Trypodendron lineatum*, *T. retusum*, and *T. rufitarsus* (Coleoptera: Scolytidae) and the large woodborers *Monochamus scutellatus*, *M. clamator*, *Xylotrechus longitarsis* (Coleoptera: Cerambycidae), as well as three prevalent non-host angiosperms: trembling aspen, *Populus tremuloides*, red alder, *Alnus rubra* and paper birch, *Betula papyrifera*. Trees did not differ in hue; however birch and aspen bark had higher reflectance than all other species, suggesting that this cue could be used during host selection. In experiments with white (non-host mimicking) and black (host) traps, bark and large woodboring beetles all avoided white, attractant-baited traps. In experiments combining white traps with non-host volatiles, bark beetles were repelled by these stimuli in an additive-redundant manner. Thus these species can integrate visual and olfactory information to avoid non-host angiosperms while flying. In an experiment that decoupled tree stimuli and attractive pheromones, the mountain pine beetle integrated olfactory and visual cues in a synergistic manner, with a host kairomone over-riding visual preference at close range. These results undermine the hypothesis that this species lands randomly on potential hosts, or uses purely visual characteristics to locate hosts after pheromone arrestment. Conversely, ambrosia beetles' demonstrated weaker visual preferences, possibly because they colonise hosts lying on the forest floor, which may lack accurate visual cues. However, *T. lineatum* demonstrated colour preference when host kairomones were released in addition to their pheromone, and non-host colour and odour were synergistically repellent in one case. These results demonstrate that a continuum of sensory integration operates during host selection, and that responses to visual stimuli can be contingent on olfactory input, and ecological context.

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1. INTRODUCTION

1.1 USE OF VISUAL CUES BY PHYTOPHAGOUS INSECTS

1.1.1 CHEMICAL *VS.* VISUAL CUES

Foraging animals assess their environment through a combination of sensory modes, including olfaction, vision, taste, and touch. However, predicting which cues, and consequently which of these sensory modes should be used by foragers, can be difficult. According to optimal foraging theory, animals searching for resources should attempt to minimise the costs associated with searching (Pyke et al. 1977), and should therefore avoid using sensory modes that are associated with costly (e.g. risky, time consuming) behaviours (e.g. landing on an unsuitable host to assess tactile cues). However, the resource information available to an animal may vary not only in how easy it is to acquire, but also in its accuracy. For example, to a phytophagous insect, a chemical emanating from an acceptable host plant may also be found in one or more non-hosts (Eisner and Grant 1981), and this overlap can lower the reliability of the cue. Animals are therefore expected to balance both relative accuracy and costs when interpreting and responding to multiple cues (Fawcett and Johnstone 2003).

These two factors arise from the inherent properties of the particular sensory mode. For example, olfactory cues are often transmitted in temporally and spatially discontinuous 'plumes' that demand that the forager move through an odour space to maintain contact with the signal (Prokopy 1986; Visser 1986; Bell 1990). However, this may mean moving through other, potentially confusing odour spaces. In addition, it is unclear how easily animals interpret olfactory information and form 'images', although this is theoretically possible (Hopfield 1991). Despite the inherent difficulties, many insects use olfactory cues to locate host plants for feeding, oviposition, and mating (Thorsteinson 1960; Dethier 1982; Visser'1986; Metcalf 1987; Bernays and Chapman 1993). Contact chemical or gustatory cues may also be important, and probably indicate host suitability with extreme accuracy (Thorsteinson 1960; Dethier 1982), but only after landing, a behaviour which may constitute some measure of host acceptance, and incur some cost.

The use of vision by foraging insects has received considerably less attention than olfaction, perhaps because of a general preconception that visual cues (form, colour, contrast) are "too variable and lack the identifiable uniqueness required to explain the obvious discriminatory power of insects" (Thorsteinson 1960). However, such a comparison is inherently anthropocentric: humans can rarely perceive host-associated odours at natural concentrations, and thus are relatively unaware of whether olfactory cues possess "identifiable uniqueness". For instance, many volatile alcohols and aldehydes in green leaves (green leaf volatiles) are ubiquitous among numerous angiosperms, yet many insects apparently use these chemicals as to find specific hosts (Visser 1986). Monoterpenes (e.g. α-pinene) are often characterised as volatiles of conifer bark and foliage, and appear to be used in host selection by conifer-feeding insects, but these cues are also common in the tissues of (non-host) angiosperm trees (Byers 2000; Huber et al. 2000a). Many information-bearing chemicals (semiochemicals) are probably the products of metabolic pathways common to many taxa (see Huber et al. 1999), and may be used by diverse insect groups, making the "identifiable uniqueness" of individual species odours questionable (Eisner and Grant 1981). However, insect selection may be based on relative quantities of compounds shared by potential hosts

(Pureswaran and Borden 2004; Pureswaran et al. 2004), or on compounds of relatively low variability within a host plant species'(Wright and Smith 2004).

Visual cues of host plants differ from olfactory cues in several ways. For instance, they may operate over a shorter distance than olfactory cues, but are also considerably less variable over both time and airspace. It is usually assumed that olfaction operates in long range host finding, while vision may mediate mid- to short-range host finding (Lanier 1983; Prokopy 1986; Finch and Collier 2000). The direction and dimensions of olfactory cues are almost always constrained by prevailing air currents, while visual cues, on the other hand, are "omnidirectional" (Prokopy 1986), and are constrained by prevailing light conditions. Overall, however, different environmental conditions may favour the use of different cues, and these may be perceived by different sensory systems. The ecological use of one or more of these cues, however, will also depend on how costly they are to assess and their relative uniqueness and reliability as host indicators. Because of these factors, foragers would benefit from an integrated response to cues from several modes when selecting hosts, yet such integration has received little empirical attention, as have responses to visual cues in general.

1.1.2 CHARACTERISTICS OF VISUAL INFORMATION

An insect's visual perception of an object depends on both the limitations of its own visual system, and the physical qualities of the object itself. The physical properties of a potential host object (e.g. leaf, stem, seed, fruit) comprise its form (its shape, or overall silhouette), its texture (roughness or other surface characteristics), and its spectral reflectance (the distribution of reflected 'light' radiation over a range of wavelengths) (Prokopy 1986; Endler 1993). The utility of form and shape cues to foraging insects is supported by studies showing that parasitoids can learn to associate shapes with rewards (e.g. Wäckers and Lewis 1999). Bumblebees, *Bombus terrestris* (L.), rely on shape cues to distinguish among flowers when light quality makes colour discrimination unreliable (Dyer and Chittka 2004). An object's spectral reflectance is usually quantified between 300-350 nanometers (ultraviolet, UV) and 700 nm (far red to infrared), and the shape and magnitude of this distribution determines several characteristics of colour, including the hue, chroma and intensity (Moericke 1969; Endler 1993). The *hue* of an object is often characterised as the dominant wavelength reflected from its surface; more specifically, it is the wavelength increment over which the transition from low to high intensity reflectance occurs. For example, an object is perceived as green when this transition is at ca. 500 nm, and there is a subsequent 'peak' in reflectance over ca. 520-530 nm. The *chroma* ('saturation', 'purity') depends on the magnitude and steepness of the transition. 'Pure' or high chroma red has a high, steep transition at ca. 630-650 nm. Pink is less pure, and its spectrum has a less defined transition (low chroma), while white has no transition at all (and no dominant wavelength), and is described as achromatic. Finally, *intensity* describes the magnitude of the light energy reflected over a given wavelength increment, which can be calculated by integrating the spectral curve over those wavelengths, or approximated by taking the maximum relative intensity (peak) at a given wavelength.

The appearance of the object depends on these factors, but also on the visual characteristics of the background, since the spectral difference between an object and its background defines the visual 'contrast'. The appearance also depends heavily on the quality of light in the environment. A green object, for example, is most visible when the available light is composed primarily of green (520-530 nm) wavelengths, and the quality and amount of available light varies with both environment (e.g. forest *vs.* open grassland), season, and time of day (Endler 1992, 1993).

The extent to which these physical characteristics (and thus the object itself) are perceived by an insect depends on the sensitivity of its visual system. Insect compound eyes (Chapman 1998) are composed of numerous types of ommatidial photoreceptors with characteristic pigments that absorb light over restricted wavelength intervals. Insects are usually and traditionally described as having two types of photoreceptors, one of which responds maximally to blue light (λ_{max} = ca. 400-470 nm), and the other to green light (λ_{max} = ca. 500-520 nm), and are thus said to possess dichromatic vision. Occasionally the same ommatidium may detect two colours (Mote and Goldsmith 1970). Some insects have been shown to possess a third receptor that absorbs maximally in the UV (λ_{max} = ca. 300-380 nm), however only a few taxa (e.g. certain anthophilous Lepidoptera) have a red photoreceptor (λ_{max} = ca. 570-670 nm), and are tetrachromatic (Briscoe and Chittka 2001). However, UV receptors have been found in every case in which investigators have actually sought them, and uv-blue-green trichromacy appears to be the ancestral trait of pterygote insects, thus trichromatic colour vision should probably be assumed unless contrary electrophysiological or behavioural evidence (e.g. Droska et al. 1983; Mazza et al. 2002) is provided (Briscoe and Chittka 2001; Kevan et al. 2001). Analysis of the biological significance of visual characteristics must take these factors into account. To a trichromatic insect, only surfaces that reflect all visual wavelengths equally (including UV) may be considered as ‘white’ from a human psychological perspective, while an object emitting only red wavelengths may be effectively ‘black’ to most insects. Any variation in long wavelength reflectance among host objects is of no ecological consequence to most foraging insects, as such variation is imperceivable.

1.1.3 VISUAL ECOLOGY

The study of how phytophagous insects respond to visual cues in their environment and the effect those responses have on species interactions has been described as 'visual ecology' (Prokopy 1986). Due to practical interest, much of the research in this area has focussed on the response of insects to trapping devices of differing hues. Many folivorous insects, e.g. the western flower thrips, *Frankliniella occidentalis* (Pergande) (Teulon et al. 1999), the psyllid *Heteropsylla cubana* Crawford (Lapis and Borden 1995), the apple maggot, *Rhagoletis pomonella* (Walsh) (Prokopy 1972; Aluja and Prokopy 1993) and the aphid *Hyalopterus pruni* (Geoffroy) (Moericke 1969) all prefer to land on yellow trapping surfaces over any other colour. It has been suggested that this is because yellow is reflected relatively abundantly from new leaves (Jolivet 1998), and constitutes an "overnormal" (Moericke 1969) or "supernormal" (Prokopy 1972; Prokopy and Owens 1983) foliage stimulus that is attractive to many insects (for studies of leaf spectral qualities see Billings and Morris 1951; Gates et al. 1965). Based on linear modeling of photoreceptor responses, Kelber (2001) suggested this common preference is mediated by opposing reactions to blue and green wavelengths. Coffee berry borers, *Hypothenemus hampeii* Ferr., prefer red over white funnel traps, a response perhaps linked to the colour of ripe coffee cherries (Mathieu et al. 1997), although it is unknown if this species can detect red light *per se*. Many species of insects that colonise trees with dark bark appear to orient to dark hues (e.g. red, brown, black). For example, lepidopterous male lilac borers, *Podosesia syringae* (Harris), appear to discriminate among colours, preferring black traps to any specific hue, and avoiding white traps (Timmons and Potter 1981). Similarly, the lesser peachtree borer, *Synanthedon pictipes* (Grote and Robinson), and the peachtree borer, *S.* exitiosa (Say) prefer red and black pheromone baited traps, respectively (Childers et al. 1979). The European striped ambrosia beetle, *Trypodendron lineatum* (Olivier), appears to prefer dark coloured flight barrier traps (Dubbell et al., 1985), and the coniferophagous root weevil *Hylobius pales* (Herbst) prefers brown and black pyramidal traps to white and yellow traps (Mizell and Tedders 1999).

In addition to hue, intensity also appears to play a role in host selection. Vernon and Gillespie (1990) found that reducing the intensity of hues attractive to the western flower thrips caused a linear decrease in attractiveness. Similarly, reducing the intensity of yellow caused a reduction in the attractiveness of yellow cards to *Heteropsylla cubana* (Lapis and Borden 1995). Saturation (chroma) may also be important. Adding both white, and UV-reflecting white paint to hues attractive to the western flower thrips (i.e. desaturating the strength of the hues) caused a decrease in attractiveness (Vernon and Gillespie 1990). Moericke (1969) found that two species of aphids preferred to alight on yellow cards, but when the yellow standard was mixed with UV-reflecting white lead paint (desaturating the strength of the yellow), each species had a different optimally preferred shade of yellow. However, responses to differences in saturation must be viewed with caution, since manipulating saturation involves increasing or decreasing the intensity of multiple wavelengths, any of which may have behavioural effects on an insect. For instance, Judd et al. (1988) concluded that the response of onion maggots, *Delia antiqua* (Meigen) to coloured sticky cards depended on the antagonistic interactions of several key wavelengths, including UV.

Ecological interpretations may be justifiably questioned in cases where the form, size and reflectance of the trapping device differ from that of the host object, but many studies have examined models of host objects (fruit, trees) or real hosts. For example, the leafhopper *Dalbulus maidis* (Delong & Wolcott) prefers to land on yellow, vertical models approximating maize stems over models of other colours (Todd et al. 1990a); the walnut fly, *Rhagoletis juglandis* Cresson, prefers green (uninfested) coloured models of walnuts to yellow and brown (ripe, infested) models (Henneman and Papaj 1999); cone colour significantly explained levels of infestation by the ponderosa pine cone beetle, *Conophthorus ponderosae* Hopkins in a seed orchard (Jenkins 1983); the mountain pine beetle, *Dendroctonus ponderosae* Hopkins prefers vertical, cylindrical mimics of its host conifers (Billings et al. 1976), with taller cylinders being more attractive (Borden et al. 1986); the apple maggot fly prefers black and red spherical mimics of apple fruits to green, yellow, white and silver-foil coloured mimics (Prokopy and Owens 1978); and the cabbage root fly, *Delia radicum* L. prefers models resembling host leaves to those resembling non-hosts (Prokopy et al. 1983). The latter two studies, in particular Prokopy et al. (1983), are exceptional in that great care was taken to quantify the spectral characteristics of the host objects, and used excellent form and reflectance models.

Few studies have sought to determine the complex integration of multimodal stimuli (in particular olfactory and visual stimuli) that must occur during host discrimination. Nectar feeding Lepidoptera use colour vision to locate flowers (e.g. Kelber et al. 2002) but often require both a visual cue and a scent cue to elicit proboscis insertion. However many of these studies (e.g. with *Manduca sexta* L., Raguso and Willis 2002), compare responses to the presence and absence of single stimuli, rather than among multiple stimuli in each sensory mode. Examination of this aspect of host discrimination involves isolation of certain ecologically relevant visual and semiochemical stimuli and testing responses to all possible combinations, so as to test whether responses to certain stimuli in one sensory mode depend on the presence of stimuli in the other sensory mode.

Some insects have been definitively shown to have more complex responses to visual and olfactory stimuli. Mathieu (1997) used a factorial design to show that visual responses of the coffee berry borer to red and white traps depended on the release rate of host-associated volatiles. The parasitoid wasp *Diachasmimorpha juglandis* (Muesebeck) uses olfactory cues to find walnut fruit infested with its host larvae, but does not discriminate between infested fruit and artificially damaged fruit, suggesting that this species could rely primarily on visual cues (which also quadruple olfactory responses) when available (Henneman et al. 2002). The haematophagous bug *Triatoma infestans* (Klug) appears to integrate visual and olfactory cues while aggregating, with visual preferences depending on the presence of a conspecific faecal cue (Reisenman et al. 2000). Male gypsy moths, *Lymantria dispar* L., use visual cues to find females when wind turbulence increases, presumably lowering the reliability of chemical cues (Cardé and Hagaman 1984), however when olfactory and visual cues are decoupled, moths follow the olfactory cues (Charlton and Cardé 1990). Bumblebees, *Bombus terrestris* L. rely on shape information when colour cues are unreliable (Dyer and Chittka 2004), and the honeybee *Apis mellifera mellifera* L. integrates scent cues when colours are similar, and thus uninformative (Giurfa et al. 1994). The latter studies also indicate that insects incorporate information about the reliability of a cue into orientation decisions.

The order in which stimuli are received by foraging insects may also affect the response. The mid- to short-range nature of visual relative to olfactory information, for example, may mean that visual cues do not elicit a response in the absence of chemical cues. The significance of this order also depends on whether one cue is sufficiently accurate alone (e.g. Fawcett and Johnstone 2003).

1.2 STUDY SPECIES

Because of their economic importance, coniferophagous beetles have been the subject of a great deal of research on the mechanisms of host selection. As with many other species, this research has focussed almost exclusively on olfactory host selection mechanisms, providing a sound basis for investigating whether and how visual cues are important to this process. I investigated visual responses and visual-olfactory integration across a variety of ecological contexts by choosing three broad classes of beetles: bark beetles, ambrosia beetles (Coleoptera: Scolytidae) and large woodboring beetles (Coleoptera: Cerambycidae). I chose three bark beetles: the mountain pine beetle, the Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, and the western balsam bark beetle, *Dryocoetes confusus* Swaine; four ambrosia beetles: the *Trypodendron* spp. complex (*T. lineatum* [Olivier], *T. rufitarsus* [Kirby] and *T. retusum* [LeConte]), and *Gnathotrichus sulcatus* (LeConte); and three large woodborers: the pine sawyers *Monochamus scutellatus* (Say) and *M. clamator* (LeConte), and the zebra beetle *Xylotrechus longitarsis* (Casey).

1.2.1 BIOLOGY

Bark beetles

Bark beetles feed on the phloem tissue of trees for the majority of their life cycles. Some species can kill their host trees through this habit, causing devastating damage to large areas of timber (Hopkins 1892; Furniss and Carolin 1977). The mountain pine beetle (MPB) is monophagous on *Pinus*; however, in the area of this study it is essentially monophagous on lodgepole pine, *Pinus contorta* Dougl. var. *latifolia* Engelmann.

Beetles emerge in late July through September and disperse to find a new host, with "pioneer" females locating and selecting a suitable tree. Females initiate galleries beneath the outer bark, and emit a potent pheromone (primarily *trans*-verbenol) (Pitman 1968) that attracts both sexes, but primarily males, which release a second attractive pheromone, *exo*-brevicomin (which attracts primarily females) (Pitman 1971; Borden et al. 1987). These interact with host-produced monoterpenes (e.g. α-pinene, myrcene, terpinolene) (Billings et al. 1976; Conn et al. 1983; Borden et al. 1983, 1987; Miller and Borden 2000) to attract hundreds of additional beetles to the selected tree, where mating (ostensibly monogamous) takes place. This semiochemical-mediated "mass attack" facilitates beetles, together with symbiotic, pathogenic fungi (Whitney 1982) quickly overcoming the oleoresin defenses of the living host tree (Raffa and Berryman 1983; Byers 1995). Density-dependent larval competition (Reid 1963) has also caused the MPB to evolve an antiaggregation pheromone, verbenone, which is repellent to many *Dendroctonus* species (Borden et al. 1987; Hunt and Borden 1990), and regulates the aggregation (Geiszler et al. 1980). The females lay eggs along their vertically excavated galleries. The eggs hatch within days, and the larvae consume the phloem in horizontal tunnels as they develop, overwintering primarily as third and fourth instars, and completing their univoltine development and emerging the following summer (Reid 1962a,b).

The Douglas-fir beetle (DFB) has a similar life-cycle to the MPB, but beetles attack earlier in the spring and summer and overwinter as last instar larvae or adults (Atkins 1966a,b; Furniss and Carolin 1977). The DFB is essentially monophagous on coastal Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii* and interior Douglas-fir, *P. m.* var. *glauca* (Beissn.) Franco in each of these respective habitats, has an obligate diapause prior to spring emergence (Furniss and Carolin 1977), is generally considered less aggressive than the MPB, preferring fallen or extremely weakened trees (McMullen and Atkins 1962; Atkins 1966a; Humphreys 1995) and uses the chemicals 1-methyl-2-cyclohexenol (MCOL) (Lindgren et al. 1992), and frontalin (Pitman and Vité 1970) as its primary aggregation pheromones, and 3-methyl-2-cyclohexenone (MCH) as its primary antiaggregation pheromone (Rudinsky 1973), although several other compounds are also important pheromone components (Borden 1985).

The western balsam bark beetle (WBBB) is monophagous on 'interior' B.C. fir (*Abies lasiocarpa* [Hook.] Nutt, *A. bifolia* A. Murray and naturally occurring hybrids). It is polygamous, with pioneer males locating susceptible trees, and emitting primarily (+)-*exo*-brevicomin (Schurig et al. 1983) which attracts primarily females, three to four of which will mate with each male in a nuptial chamber, and bore radiating tunnels. Larvae mine out into the phloem, taking up to two years or less to reach adulthood, depending on local climate (Furniss and Carolin 1977; Garbutt 1992).

Ambrosia beetles – **Trypodendron** ***species and*** **G. sulcatus**

Ambrosia beetles are named for the fungal associates they consume as food. After mating, female *T. lineatum* bore directly into the sapwood of fallen, killed or highly moribund trees (Atkins 1966a; Shore 1998), and lay eggs in niches along galleries that run parallel to the growth rings. With each egg, they also inoculate the spores of various species of 'ambrosia fungi', which grow on the xylem tissue, are tended by parental grazing and serve as the sole larval and adult food source. Adults emerge in the late summer to find overwintering sites in forest litter and duff (Beaver 1989; Lindgren 1990). As with *Dendroctonus* bark beetles, the female are the primary host selecting sex, and emit the aggregation pheromone lineatin which attracts both sexes (Borden et al. 1979). The two coniferophagous *Trypodendron* species, *T. lineatum* and *T. rufitarsus*, are polyphagous, colonising numerous conifers, including lodgepole pine, Douglas-fir, interior firs, western hemlock, *Tsuga heterophylla* (Raf.) Sarg., interior spruce (*Picea engelmannii* Parry, *P. glauca* [Moench] Voss, and naturally occurring hybrids) (Pinaceae) and western redcedar, *Thuja plicata* Donn (Cupressaceae) (Lindgren 1990; Shore 1998). In coastal habitats, the preferred hosts are Douglas-fir and western hemlock (Johnson 1958), while in interior habitats, the preferred hosts are lodgepole pine and spruce (Shore 1998; pers. obs.). *Trypodendron retusum* is apparently monophagous on trembling aspen, *Populus tremuloides* Michx. (Bright 1983). *Gnathotrichus sulcatus* is similar in habits and host range to the coniferophagous *Trypodendron* species (Furniss and Carolin 1977), with the exceptions that the male is the first landing and primary host-selecting sex, the aggregation pheromone is a 65:35 blend of S-(+) and R-(–) sulcatol (Borden et al. 1976), and all life stages overwinter in the host (Prebble and Graham 1957).

Large woodborers

Adult females of the three large woodborers lay eggs in niches in the bark of freshly killed or moribund trees of almost all available conifer species (Furniss and Carolin 1977). The larvae first mine within the phloem, and then the xylem, relying on these tissues directly for their food source (Hanks 1999). They also consume bark beetle larvae (Dodds et al. 2001), and to that end, appear use the pheromones of co-infesting bark beetles as host-finding kairomones (Allison et al. 2001). These beetles do not appear to have evolved pheromones for host selection, but are readily attracted to the host kairomones ethanol (a putative indicator of a stressed plant [Kimmerer and Kozlowski 1982]) and α-pinene (Allison et al. 2004).'

1.2.2 HOST SELECTION – OLFACTION

There has been considerable research for over 80 years on how forest Coleoptera (and bark beetles in particular) locate hosts using olfactory cues (for reviews, see Moeck et al. 1981; Wood 1982a; Borden et al. 1986; Raffa et al. 1993). For those species with pheromones, there are two distinct phases of host selection: *primary*, which involves only a few beetles selecting a susceptible host tree, and *secondary*, which involves the majority of beetles as they respond to the pheromones produced by successful primary beetles (Borden 1982, 1985). There are two main hypotheses for how primary beetles locate hosts: 'primary attraction' using olfactory cues, and 'random landing' on many trees until a suitable host is found by chance (Moeck et al. 1981).

The hypothesis of primary attraction to host compounds has been supported recently for the DFB, which was attracted to proportional, synthetic blends of Douglas-fir foliage and bole monoterpenes, although results for the WBBB were less clear (Pureswaran and Borden 2004). On the other hand, a random landing strategy has been shown to be theoretically feasible (Byers 1996), and has been observed with the MPB (Hynum and Berryman 1980), which did not respond to proportional, synthetic blends of lodgepole pine volatiles (Pureswaran and Borden 2004). However, there is also limited evidence of primary attraction by this species (Syed and Graham 1987; Moeck and Simmons 1991), and several other bark beetles (Byers et al. 1985; Miller et al. 1986; Schroeder and Lindelöw 1989; Tunset et al. 1993; Brattli et al. 1998; Macías-Sámano et al. 1998).

The MPB, DFB and WBBB are attracted to host-produced compounds in conjunction with aggregation pheromones (secondary attraction). For instance several host-associated monoterpenes increase or even synergise the attractiveness of the MPB's pheromones, including α-pinene, terpinolene, β-phellandrene and particularly myrcene (Pitman 1969, 1971; Billings et al. 1976; Borden et al. 1987; Miller and Borden 2000). The DFB and WBBB are also attracted to several host compounds, including ethanol, when these are released in conjunction with its pheromones (Furniss and Schmitz 1971; Pitman et al. 1975; Stock and Borden 1983; Ross and Daterman 1995; SAC *unpublished data*). Implicit in discussions of primary and secondary attraction (e.g. Borden et al. 1986; Payne 1986; Gries et al. 1989; Byers 1996) is the assumption that beetles use some suite of visual cues, e.g. vertical stem silhouettes during random landing, or after pheromone arrestment. However the relationship of visual to semiochemical factors has not been extensively studied, particularly in terms of primary host finding.

In contrast to the bark beetles, evidence for primary host attraction by ambrosia and large woodboring beetles is less ambiguous. *Gnathotrichus sulcatus*, *T. lineatum*, as well as other ambrosia beetles are attracted to ethanol alone (an indicator of stressed or dying trees) (Graham 1968; Cade et al. 1970; Kerck 1972; Kelsey 1994; Kelsey and Joseph 1999) and to blends of α-pinene and ethanol, which also synergise the attractiveness of their pheromones (Vité and Bakke 1979; Borden et al. 1980). Thus, these species may rely more heavily than bark beetles on tree olfactory cues during host finding. Many large woodborers, including *M. scutellatus*, *X. undulatus* (Say) (Chénier and Philogène 1989), *M. titillator* (Fatzinger et al. 1987) and *M. alternatus* Hope (Sakai et al. 1992) are also attracted to tree-produced compounds (Allison et al. 2004), but also appear to locate hosts by responding to certain co-infesting bark beetle pheromones

(Billings and Cameron 1984; Allison et al. 2001, 2003). Similarly, there may also be pheromonal cross-attraction among host-seeking *Gnathotrichus* and *Trypodendron* ambrosia beetles (Borden and McLean 1979; Borden et al. 1981; SAC *unpublished data*).

Despite the differences in host location and use among these species, all inhabit conifers, and must be able to distinguish their host(s) from the variety of non-host, deciduous angiosperm species they also encounter. Recent studies have shown that many species of coniferophagous beetles can detect the volatile semiochemicals common to the bark and foliage of non-host angiosperm trees, and many species appear to use these as kairomones to avoid non-hosts while in flight. When added to attractant-baited traps, many non-host volatiles (NHVs) reduce catches of the MPB (Wilson et al. 1996; Borden et al. 1998; Huber and Borden 2003), the DFB (Huber and Borden 2001), the WBBB (Huber et al. 2000b; Huber and Borden 2003), and the ambrosia beetles *G. sulcatus* (Deglow and Borden 1998a), and *T. lineatum* (Borden et al. 1997). Numerous other North American and European bark beetles have also shown similar responses (e.g. Dickens et al. 1992; Schroeder 1992; Guerrero et al. 1997; Birgersson et al. 1998; Poland et al. 1998; Zhang et al. 1999). In general, when single NHVs are combined into blends, there is an additive or redundant effect on beetle avoidance, which may be adaptive in the avoidance of a wide variety of angiosperm taxa (Borden et al. 1998), particularly when there is overlap in the semiochemistry of hosts and non-hosts (Huber et al. 1999). Only one investigation (Zhang and Schlyter 2003) has tested for *non*-additivity (synergism) among NHVs, but problems with the experimental design and analysis preclude any conclusion of synergism from this study. Large woodborers do not appear to be repelled by non-host angiosperm volatiles, with the possible exception of conophthorin (Morewood et al. 2003).

1.2.3 HOST SELECTION – VISION

There has been comparatively little research on visual responses by Coleoptera. As with other insects, long range host location by bark beetles is thought to be mediated at by volatile semiochemicals, while "landing and short range orientation is [sic] guided by vision" (Lanier 1983). Two scolytids, *D. pseudotsugae* and *Ips paraconfusus* Lanier, have been shown to have at least two photoreceptors, one responding maximally to blue light (λ_{max} = 450 nm), and the other responding maximally to green light (λ_{max} = 510-530 nm) (Groberman and Borden 1982), although these and the other beetles in this study probably have a third photoreceptor that responds to UV light (Briscoe and Chittka 2001). Supporting this hypothesis, the white pine weevil, *Pissodes strobi* Peck, orients to UV, over non-UV reflecting white light (Droska et al. 1983). Lin and Wu (1992) found that four species of Coleoptera possess UV and green receptors, while one of these, *Coccinella septempunctata* L., also has a blue receptor. Marzke et al. (1973) found that eyes of two grain beetles responded maximally to green light. Pedestrian *D. pseudotsugae* and *T. lineatum* are also photopositive to blue and green light in laboratory bioassays (Groberman and Borden 1981) and beetles appear to be photopositive (Atkins 1966b; Shepherd 1966) during the dispersal flight that precedes host selection.

Most studies of visual responses by coniferophagous beetles have tested responses to traps of differing form, orientation or hue. None has examined the role of colour intensity or contrast in trap preference or host selection. With respect to form, bark and woodboring beetles appear to prefer traps that approximate tree boles. Lindgren et al. (1983) showed that multiple-funnel traps (baited) were as attractive to *T. lineatum* as tree-mimicking drainpipe and cylinder traps in some experiments, although flight barrier and wire mesh traps can also be effective for this species (Borden et al. 1982). Increasing the height of traps increases catches of *T. lineatum*, *T. rufitarsus* and *T. retusum* (Hoover et al. 2000; Lindgren et al. 2000), as well as the mountain pine beetle (Borden et al. 1986). The mountain pine beetle also prefers vertical to horizontal silhouettes (Billings et al. 1976; Schonherr 1977). Safranyik et al. (2003) found that the mountain pine beetle consistently preferred larger diameter cylindrical traps; catch ratios in large, medium and small traps were statistically indistinguishable from those predicted by trap diameter. These results collectively suggest a strong correlation between the responses of the mountain pine beetle to trapping devices, and the physical characteristics of its host. The Lindgren multiple-funnel trap (Lindgren 1983) is now widely used for experimentation with, and control of this and other coniferophagous beetles, in part because the tall, dark, vertical silhouette presented by the stacked funnels is strongly attractive to these beetles.

The handful of studies that have examined the role of colour (spectral) stimuli in host finding by bark and ambrosia beetles also indicate that coniferophagous beetles prefer the dark hues likely to be associated with their host material. The MPB (Schonherr 1977) and *T. lineatum* (Dubbell et al. 1985) were shown to prefer dark coloured sticky traps (black, brown and red) and avoid landing on lighter hues (yellow, white). Entwistle (1963) found that West African scolytids and platypodids (species not determined) prefer red sticky traps, but also black and brown, although it is unlikely that these beetles perceive red (Briscoe and Chittka 2001). Both the southern pine beetle, *Dendroctonus 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 traps, although it does not discriminate among other colours (black, brown, blue, gray, green or red) (Strom and

Goyer 2001). These authors did not relate these findings to host vs. nonhost discrimination, since they tested conspecific beetle and host tree semiochemicals.

There has also been some indication of sensory integration by foraging forest beetles, and even synergism between visual and olfactory cues. For example, Vité and Bakke (1979) found that tree-mimicking, cylindrical traps were only attractive to *T. lineatum* when they released α-pinene and ethanol, a finding corroborated by Borden et al. (1982) using cylindrical drainpipe pipes. Similarly, Lindgren et al. (1983) found that multiple-funnel traps were as attractive as barrier-type vane traps only when the bait included the host volatiles α-pinene and ethanol. These results conform with Kerck's (1972, 1978) conclusion that maximal responses by *Trypodendron domesticum* (Olivier), occur only when tree visual and olfactory stimuli are combined. Moreover, they imply that for some species, responses to tree stimuli in one sensory mode may depend on tree stimuli in other modes, although this hypothesis has never been explicitly tested. Studies by Strom et al. (1999, 2001) however, did not find a statistical interaction between visual and semiochemical stimuli, suggesting that southern and western pine beetles responded to cues in each sensory mode independently.

There are as yet no data on differences in visual responses among beetles at different attack phases or between primary host-seekers and secondary responders, although there is some corresponding olfactory evidence (e.g. Borden 1967; Zhang et al. 2000b; Wallin and Raffa 2000, 2002). Visual preferences in each of these contexts are often implicit. For instance, Gara et al. (1965) concluded that southern pine beetles in an expanding infestation land randomly on hosts and non-hosts, and suggested that vertical (but not horizontal) visual stem cues guide this process. Similarly, the so-called 'random' landing hypothesis (Hynum and Berryman 1980) also implies that beetles use visual cues such as an upright silhouette (but do not assess trees for chemical cues).

Almost all of the studies on host selection cited above have tested whether beetles utilise olfactory cues while flying, mostly by using traps that prevent taking off again. The fundamental, but often implicit assumption underlying tests of in-flight responses to host and non-host stimuli is that beetles actually benefit from behaviours that minimise the number of landings on unsuitable (e.g. non-host) trees. While this assumption has never been tested with these species in the field, it is reasonable if time spent landing reduces the time available for other activities such as finding mates (Pyke et al 1977), or increases the chance of predation or succumbing to environmental extremes. It is also indirectly supported by the growing body of data demonstrating in-flight avoidance of numerous beetle and non-host associated stimuli. The costs associated with assessing a potential tree for suitability (either in flight, or after landing) also have a bearing on what cues, and consequently which sensory modes, should be used by foraging beetles. Visual cues do not require casting through space to maintain contact with filamentous olfactory cues (Visser 1986; Bell 1990) and thus may be less costly to assess while flying. Conversely, if suitable and unsuitable trees are similar in terms of olfactory (Eisner and Grant 1981) or visual (Thorsteinson 1960) cues (i.e. low accuracy), then beetles should not use cues in those sensory modes.

1.2.4 FOREST LIGHT ENVIRONMENTS

The visual appearance of hosts and non-hosts depends not only on their spectral qualities and the forager's visual system (see §1.1.2 above), but also on the spectral characteristics of the light environment. In forests, these characteristics should be primarily influenced by canopy geometry (crown closure, gap size, tree height), the source of radiant light (sun, sky, vegetative reflection and refraction), the tree density (open woodland, dense forest) and species composition (broadleaf, coniferous) (Endler 1993). Most studies that have investigated this question suggest that temperate deciduous forests (oak, maple) are selective filters, with the light beneath the canopy dominated by green wavelengths, and also by far-red ($\lambda \geq 700$ nm), while coniferous forests are richer in blue wavelengths, but are less selective filters of skylight (Coombe 1957; Federer and Tanner 1966; Vézina and Boulter 1966; Freyman 1968). Conversely, in a comprehensive survey of forest light environments on three continents and in diverse ecosystems, Endler (1993) concluded that light environments do not vary with species composition or ecosystem, but rather with architecture. He found that *forest shade* (closed canopy) is relatively green to yellow shifted in spectral distribution, while *woodland shade* (more open canopy) is blue to grey due to the increasing light contributions from clouds and blue sky. He also found that clouds 'flatten' the ambient spectrum, because radiant light from clouds is grey to white rather than blue, and that forest backdrops are generally low chroma, and rich in long wavelengths (brown). It appears that early investigators did not account for architecture, and often studied young plantations (e.g. Federer and Tanner 1966) which may have more closely approximated 'woodlands' (*sensu* Endler 1993) rather than 'forests'.

Ecologically, spectral characters (colours) are most apparent when illuminated by matching light (a green object is most visible under green illumination) and when they constrast with a backdrop with different spectral characteristics (Endler 1992, 1993). Thus to a beetle foraging in a mature conifer, or mixed conifer and hardwood forest, conifers could be relatively apparent. To the human eye, conifer bark is usually dark brown or grey, which would appear quite dark in a light environment richest in green wavelengths. This apparency might diminish in a more open, woodland environment if the ambient spectrum was 'gray' (due to light contributions from clouds) or orange (due to direct contributions from the sun). The bark of non-host aspens and birches is white to grey to the human eye, and would reflect the green light abundant in closed forest canopies, and the blue light abundant in woodlands, perhaps making these species apparent in a variety of forest habitats. In both cases, however, these interpretations depend on the degree of contrast of the tree with the forest background as it appears to a beetle (something that has never been studied), and on the objective spectral characteristics of the bark itself (this study). For instance, dark, low chroma forest backdrops might not provide good contrast for conifer bark, but would provide excellent contrast for aspen and birch if they were sufficiently illuminated.

1.3 OBJECTIVES

Many recent studies support the hypothesis that coniferophagous beetles use olfactory cues to avoid non-host angiosperms while flying (e.g. Huber and Borden 2003). However, to the human eye, the bark of several species of these non-hosts differs in visual appearance from that of most conifers. I hypothesised that these differences constitute useful information to foraging beetles, and that beetles use this visual information during host finding. I predicted that flying beetles would avoid silhouettes that resembled non-host angiosperms, and integrate visual cues with non-host angiosperm olfactory cues when combined. To test these hypotheses, I set the following objectives, which were to:

1. survey the hosts of nine species of coniferophagous beetles and several predominant, sympatric, non-host angiosperms for quantitative differences in their bark reflectance spectra;

2. assay these beetles for their responses to putative host and non-host visual stimuli using traps;

3. combine non-host visual and semiochemical cues to determine how beetles integrate bimodal non-host information; and to

4. combine a non-host visual stimulus with beetle-produced, repellent semiochemicals to assess how beetles would integrate these cues.

2. METHODS

2.1 SPECTRAL REFLECTANCE OF TREE BARK

To compare the quality and intensity of reflectance of host and non-host tree bark, I sampled three host conifers: interior Douglas-fir, *Pseudotsuga menziesii* var. *glauca* (Beissn.) Franco[1], interior lodgepole pine *Pinus contorta* Dougl. var. *latifolia* Engelm., and 'interior' B.C. fir, *Abies lasiocarpa* (Hook.) Nutt, *A. bifolia* A. Murray and naturally occurring hybrids (Hunt 1993); and three prevalent angiosperms sympatric with these conifers (Meidinger and Pojar 1991): trembling aspen, *Populus tremuloides* Michx., paper birch, *Betula papyrifera* Marsh., and red alder, *Alnus rubra* Bong.. Sampling locations for the above trees in British Columbia (2003) were, respectively: Laluwissin Creek Forest Service Road (FSR), near Lytton (24 April); East Gate FSR, near Manning Park (12 April); Manning Park (6 August); near Aspen Grove (7 July); North Thompson River, along Highway 5 North, near Barrière (7 July); Burnaby Mountain, Burnaby (31 July). The bark of ponderosa pine, *Pinus ponderosae* Laws was also collected on 24 April, 2003 south of Laluwissin Creek Forest Service Road. For each species, I haphazardly selected eight trees which were at least 100 m apart and at least 25 cm diameter at breast height (130 cm), and removed a small square of bark from the north aspect of the bole at a height of 170-200 cm. Samples were wrapped in wax paper and stored at ca.6-15°C until analysed.

The quality of light (wavelength composition) reflected from the bark, as well as from the black and white funnel traps used in experiments (λ=300-670 nm in most cases), was measured relative to an internal magnesium oxide (MgO) standard on a Cary 17

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[1] Variety was not confirmed; however samples were taken from a location outside the range of the coastal variety, *P.m* var. *menziesii* (Mirb.) Franco (Farrar 1995).

reflectance recording spectrophotometer equipped with an integrating sphere. Scanning speed was 2 nm per second, and slit width was varied automatically to control for wavelength-dependent differences in the amount of incident light. The intensity of the reflected light was measured relative to the difference between black (cardboard) and white (MgO paste) external standards, to control for wavelength-dependent changes in instrument sensitivity. The output was converted to measurements in 10 nm increments; finer resolution was undesirable because of variation in the spectral bandwidth of incident light and bark sample heterogeneity.

For each 10 nm increment, I used analysis of variance (PROC GLM, SAS v8.02, 2003) followed by the Ryan-Einot-Gabriel-Welsch (REGW) multiple range test (SAS Institute 1990; Day and Quinn 1989) to test for differences in reflectance intensity among the tree species and the trap plastics made to approximate them. Two scolytids, *D. pseudotsugae* and *Ips paraconfusus*, have electroretinal sensitivity maxima at 450 and 510-530 nm (Groberman and Borden 1982). To evaluate differences among trees across wavelengths that are potentially visible to the beetles, I took data in the 400-580 nm range (to account for some physiological differences among beetle taxa) and used a multivariate analysis of variance (PROC GLM). As reflectances among wavelength intervals are expected to covary, Pillai's trace was used as the multivariate statistic, as it is considered more robust to multicollinearity (Zar 1999).

2.2 TRAPPING EXPERIMENTS

2.2.1 EXPERIMENTAL METHODOLOGY

I conducted field trapping experiments within established populations of bark beetles (*D.*

ponderosae, interior and coastal *D. pseudotsugae*, *Dr. confusus*), ambrosia beetles (interior *T. lineatum*, *T. rufitarsus* and *T. retusum*, coastal *T. lineatum*, and coastal *G. sulcatus*) and large woodborers (*M. scutellatus*, *M. clamator*, *X. longitarsis*, and any incidental species of round-headed borers [Coleoptera: Buprestidae] and wood wasps [Hymenoptera: Siricidae]). I tested both coastal and interior populations with two species that have geographically distinct host selection behaviours.

I used 12-funnel Lindgren traps (Phero Tech Inc., Delta, British Columbia), as these are thought to be perceived as tree boles by foraging beetles, and because these traps have become a standard method for field testing beetle responses to semiochemicals (Lindgren 1983; Lindgren et al. 1983). I used black and white traps to mimic ‘conifer’ and ‘non-host angiosperm’ boles, respectively. To evaluate the relative roles of both vision and olfaction in foraging responses, experiments had a full factorial structure, with two levels of a visual factor (white or black traps) and two or three levels of a semiochemical factor. Semiochemical treatments always contained a bait of attractive pheromones and/or kairomones, so that captured insects would be host-seeking, and visual responses would be interpretable in that context. Treatment combinations were randomized within complete, linear blocks set up along logging roads, trails and cut-block margins, except for Experiments 17 and 21, which were set up within a thinned Douglas-fir and western hemlock stand. Experiment 23 with large woodborers was set up beside log decks within a sawmill sorting yard.

In all experiments, semiochemicals were hung within the middle funnels of the traps. Individual traps were 15 m apart to minimise the effects of adjacent treatments, while clusters of traps were 20 m apart. A small block of dichlorvos impregnated plastic (Vapona No-pest® strip, Monsanto Canada Ltd., Mississauga, Ontario) was placed in each collecting cup to minimise escape and predation. Insects were collected and frozen until counted. Beetles were speciated following Bright (1976) and Wood (1982); sex ratios were estimated by subsampling N=50 (Lyon 1958; Jantz and Johnsey 1964; Bright 1976; Wood 1982). Experimental details (species, locations, dates, treatment combinations and sample sizes) are given in Table 1 and semiochemical information is provided in Table 2. Unequal sample sizes resulted when traps had blown down, or had been damaged by cattle or bears.

As detailed in Table 1, all species were assayed with an initial experiment which tested the prediction that beetles would prefer white, baited traps less than black, baited traps. Black and white unbaited traps were included as controls to give four treatments. The attractive baits were a combination of pheromones and/or host (or host-indicating) kairomones. For coastal *T. lineatum*, I performed two such experiments (with two different baits) so I could compare responses of this beetle with its interior counterpart and coastal *G. sulcatus*.

A second series of experiments tested the predictions that beetles would avoid attractant-baited traps that also had either a non-host angiosperm volatile stimulus (NHV) or a non-host angiosperm visual stimulus (white colour), and that this avoidance would be greatest when both of these putative deterrents were present. The six treatments included: black and white attractant baited traps, black and white unbaited control traps, and black and white traps with both an attractive bait and known NHV repellents. For these experiments, I chose NHVs that have been shown to have low to moderate behavioural activity (Wilson et al. 1996; Borden et al. 1998; Deglow and Borden 1998; Huber and Borden 2001; S. Kühnholz and J. Borden *unpublished data*) so that they would be unlikely to overwhelm a visual-olfactory stimulus interaction. For the same reason, two

TABLE 1. DESCRIPTION OF ALL EXPERIMENTS (TREATMENTS, FINAL SAMPLE SIZES AND DATES) LISTED BY PRIMARY TARGET INSECT AND STUDY SITE

Experiment number and treatments*		*N*	Dates	Experiment number and treatments		*N*	Dates
Interior Douglas-fir beetle (Laluwissin Creek Forest Service Road, near Lytton, B.C.)							
1	Black	14	29 May-4 Jun, 2001	**2**	Black	13	1-11 Jun, 2001
	Black+Bait	14			Black+Bait	14	
	White	12			Black+Bait+NHV1	13	
	White+Bait	14			White	14	
					White+Bait	13	
					White+Bait+NHV1	13	
3	Black	15	8 replicates: 18 Jun-6 Jul; 8 replicates: 6 Jul-11 Aug, 2002	**4**	Black	14	11-22 Jun, 2001
	Black+Bait	16			Black+Bait	15	
	Black+Bait+NHV2	16			Black+Bait+MCH	14	
	White	16			White	15	
	White+Bait	16			White+Bait	15	
	White+Bait+NHV2	15			White+Bait+MCH	15	
5	Black	14	3-6 Jul, 2001				
	Black+Bait	15					
	Black+Bait+NHV1+MCH	15					
	White	15					
	White+Bait	16					
	White+Bait+NHV1+MCH	14					
Coastal Douglas-fir beetle (Malcolm Knapp University of B.C. Research Forest, Maple Ridge, B.C.)							
6	Black	21	15 replicates: 17 Apr-13 May; 6 replicates: 29 Apr-13 May, 2002	**7**	Black	14	13 May-3 June, 2002
	Black+Bait	21			Black+Bait	15	
	White	20			Black+Bait+NHV2	15	
	White+Bait	21			White	15	
					White+Bait	15	
					White+Bait+NHV2	15	

Western Balsam bark beetle (Buchanan Forest Service Road, Buck Mountain, near Kelowna, B.C.)

8	Black	14	22 Jun-14 Jul, 2002		**9**	Black	13	14 Jul-15 Aug, 2002
	Black+Bait	15				Black+Bait	13	
	White	14				Black+Bait+HV	14	
	White+Bait	15				White	14	
						White+Bait	14	
						White+Bait+HV	12	

Mountain pine beetle (Opax Mountain, near Kamloops, B.C.)

10	Black	13	18 Jul-15 Aug, 2001		**11**	Black	14	18 Jul-8 Aug, 2001
	Black+Bait	14				Black+Bait	14	
	White	14				Black+Bait+NHV2	14	
	White+Bait	14				White	12	
						White+Bait	14	
						White+Bait+NHV2	13	
12	Black	15	29 Aug-10 Sept, 2001		**13**	Black	14	15-21Aug, 2001
	Black+Bait	16				Black+Bait	15	
	Black+Bait+NHV3	13				Black+Bait+Verb	15	
	White	15				White	15	
	White+Bait	16				White+Bait	15	
	White+Bait+NHV3	14				White+Bait+Verb	15	
14	Black	14	8-15 Aug, 2001		**15**	Baited clusters of black and white traps (2 each)	6	9 Sept-8 Oct, 2001
	Black+Bait	14						
	Black+Bait+NHV2+Verb	13						
	White	14						
	White+Bait	13						
	White+Bait+NHV2+Verb	14						
16[¥]	Myrcene on black	16	7 replicates: 22-29 Aug; 9 replicates: 29 Aug-4 Oct, 2002	(clusters of traps)				
	Myrcene on white	16						
	Myrcene on both	16						
	No myrcene	16						

Coastal Trypodendron lineatum (Malcolm Knapp University of B.C. Research Forest, Maple Ridge, B.C)

17	Black	15	24 Apr-2 May, 2001	**18**	Black	11	8 replicates: 17 Jun-13 Jul; 3 replicates: 17 Jun-27 Aug, 2002
	Black+Bait1	15			Black+Bait2	11	
	White	15			White	11	
	White+Bait1	15			White+Bait2	11	
19	Black	13	24 Apr-2 May, 2001				
	Black+Bait	13					
	Black+Bait+NHV4	15					
	White	15					
	White+Bait	12					
	White+Bait+NHV4	13					

Interior Trypodendron species, T. lineatum, T. rufitarsus and T. retusum (Deep Gulch Forest Service Road, near Princeton, B.C.)

20	Black	8	5 replicates: 3-9 May; 3 replicates: 9-16 May, 2001
	Black+Bait2	8	
	Black+Bait2+NHV4	8	
	White	8	
	White+Bait2	8	
	White+Bait2+NHV4	8	

Coastal Gnathotrichus sulcatus (Malcolm Knapp University of B.C. Research Forest, Maple Ridge, B.C)

21	Black	15	2-11 May, 2001	**22**	Black	15	2-11 May, 2001
	Black+Bait	15			Black+Bait	15	
	White	15			Black+Bait+NHV5	15	
	White+Bait	15			White	15	
					White+Bait	14	
					White+Bait+NHV5	14	

Large woodboring insects (Weyerhaeuser sawmill, Vavenby, B.C.)

23	Black	15	28 Aug-29 Oct, 2001
	Black+Bait	15	
	White	16	
	White+Bait	15	

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* Colour refers to trap colour, followed by abbreviations for semiochemical treatments. NHV1 (non-host volatile blend 1) = benzyl alcohol + guaiacol; NHV2 = benzyl alcohol + hexanol; NHV3 = guaiacol; NHV4 = salicylaldehyde; 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.

[¥] Experiment 16 conducted along Sunday Summit Forest Service Road, near Princeton, B.C.

TABLE 2. OPTICAL NATURE, PURITY, RELEASE DEVICES AND RATES FOR SEMIOCHEMICALS USED IN ALL EXPERIMENTS.

Semiochemical[a]	Optical Nature %(+ : -), where present	Chemical Purity (%)	Release device[b]	Release Rate[c] (mg/24hr)	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					
exo-brevicomin	50:50	98	1.5 mL PP tube in PE pouch	3	25
Mountain pine beetle Bait					
trans-verbenol		90 *trans*, 7 *cis*	PE bubblecap	1.2	20
exo-brevicomin	50:50	98	PVC flexlure	0.2	20
myrcene		90	PE bottle	250	20
Trypodendron Bait 1					
lineatin	50:50	99	PVC flexlure	0.075	30
α-pinene	25:75	95	PE bottle	250	20
ethanol		95	PVC pouch	30-50	20
Trypodendron Bait 2					
lineatin	50:50	99	PVC flexlure	0.075	30
G. sulcatus Bait					
sulcatol	50:50	99	PE bubblecap	5.5	25
α-pinene	25:75	95	PE bottle	250	20
ethanol		95	PVC pouch	30-50	20
Large Woodborer Bait					
ipsenol	50:50	99	PVC bubblecap	0.25	25
ipsdienol	50:50	99	PVC bubblecap	0.16	25
α-pinene	25:75	95	PE bottle	250	20
ethanol		95	PVC pouch	30-50	20
Antiaggregation pheromones and non-host volatiles					
MCH (regular)		98	PE bubblecap	4	20
MCH (low)		98	glass microcapillary tube (open)[d]	0.307	23
verbenone	20:80	99	PE bubblecap	0.68	25
guaiacol		99	PE bubblecap	5	20
hexanol		99	PE bubblecap	4	20
salicylaldehyde		97	PE bubblecap	5	20
benzyl alcohol		99	PE bubblecap	5	20

TABLE 2 *CONTINUED.*

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[a] 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*-brevicomin, *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; lineatin, 3,3,7-trimethyl-2,9-dioxatricyclo[3.3.1.0]nonane; α-pinene, 2,6,6-trimethylbicyclo[3.1.1]hept-2-ene; sulcatol, 6-methyl-5-hepten-2-ol; ipsenol, 2-methyl-6-methylene-7-octen-4-ol; ipsdienol, 2-methyl-6-methylene-2,7-octadiene-4-ol; MCH, 3-methyl-2-cyclohexen-1-one; (*S*)-(-)-verbenone, (*S*)-(-)-4,6,6-trimethylbicyclo[3.1.1]hept-3-en-2-one; guaiacol, 2-methoxyphen-1-ol; hexanol, hexan-1-ol; salicylaldehyde, 2-hydroxybenzaldehyde.

[b] Release device materials: PE, polyethylene; PVC, polyvinyl chloride; PP, polypropylene. All release devices were sealed except that for MCH (low).

[c] Release rates determined by Phero Tech Inc., except for MCH (low) and verbenone, determined at S.F.U.

[d] Open glass tube was mounted inside an open, 400μL PE tube.

host volatiles were added for the western balsam bark beetle, because it does not respond aggressively to traps baited only with its pheromone *exo*-brevicomin. For the mountain pine and Douglas-fir beetles, I also tested the effects of repellent antiaggregation pheromones and the putative non-host visual stimulus, as well as the combined effects of NHVs, anti-aggregation pheromones and the non-host visual stimulus.

Mountain pine beetle trap cluster experiments

Trapping experiments like those just described often assume that beetles respond in an additive manner to different positive and negative stimuli, and interpreting these experiments assumes that this additivity is ecologically meaningful. However, the results of some of these experiments suggested that some species respond in a *non*-additive manner: that is, stimuli in one sensory mode elicit different behaviours depending on the stimuli in the other sensory mode. To investigate integration of stimuli in a more realistic setting, I removed the attractive pheromone from the target trap silhouettes, and tested responses of the mountain pine beetle to visual stimuli and a tree volatile in two experiments.

In Experiment 15, I erected a pole baited with three release devices of each of the MPB bait components (the aggregation pheromones *exo*-brevicomin and *trans*-verbenol, and the host kairomone myrcene) at a height of 1.5-1.8 m. Two black and two white traps (alternating) were then evenly spaced in a 2 m radius circle around the central pole, to create a 'cluster' of four traps. The position and colour of the first trap were determined randomly using a compass and coin toss, respectively.

Experiment 16 examined the relative roles of silhouette colour and a key host semiochemical (myrcene) in eliciting landing rates by beetles that had responded to aggregation pheromones (*exo*-brevicomin and *trans*-verbenol). Two release devices of each aggregation pheromone were hung from a central pole at 1.5-1.8 m, and four traps were arranged in a 2.5 m radius circle. Trap 1 was black, and its position was determined by random compass bearing. Four semiochemical treatments were assigned to clusters in a randomized, complete blocks design: 1) a myrcene release device on each black trap in a cluster, 2) myrcene on each white trap, 3) myrcene on all four traps and 4) no host volatile (control). All blocks were independently randomized.

2.2.2 STATISTICAL ANALYSES

To improve normality and heteroscedasticity, all catches were $\log_{10}$ transformed, except in Experiment 15, where catch proportions were arcsine square root transformed (Zar 1999). In all cases, this reduced the difference between the largest and smallest treatment standard deviations to less than four-fold, which is considered appropriate for analysis of variance (Schwarz 2003 *personal communication*). Except for Experiments 15 and 16, the responses of male and female beetles to the different stimuli were compared by ANOVA (PROC GLM) for two fixed effects (colour and semiochemical). In unbalanced experiments, standard treatment means were similar to least squares means, and were compared by the REGW multiple-range test. Although the absence of a significant ANOVA interaction could have permitted within-factor tests of means, the same REGW procedure was used to allow qualitative comparisons between sexes, and among experiments both within and across species. Experiments with replicates at different times (but the same trap locations) were tested for a treatment × time interaction. This was absent in all cases except Experiment 20 for male *T. rufitarsus*, where catches were too low and variable to draw any conclusions. In Experiment 16, two of the 16 blocks were located on East Gate Forest Service Road, near Princeton, B.C. Because of low catches in these replicates, I could not adequately test for a treatment × location interaction; however, removal of these replicates did not affect the results, and all 16 replicates were analysed together.

Due to low sample sizes and the loss of several traps in Experiment 15, I averaged the proportions of beetles caught in each trap colour and cluster in this experiment, and calculated 95% confidence limits for the difference between black and white traps. The effect of colour was also analysed using ANOVA of catch proportions. For each cluster in Experiment 16, catches in the two traps of each colour were averaged for all analyses. I tested the main effect of semiochemical treatment by ANOVA of the cluster totals (log transformed). To test for differences in discrimination among semiochemical treatments, I used an ANOVA of the mean proportional difference between trap colours (black – white). In both cases, the four treatment means were then tested by the REGW test. Within each semiochemical treatment group, I used an ANOVA to test for differences between 'black' and 'white' traps.

All analyses considered block as a random effect, used Type III sums of squares, and experimentwise $\alpha = 0.05$.

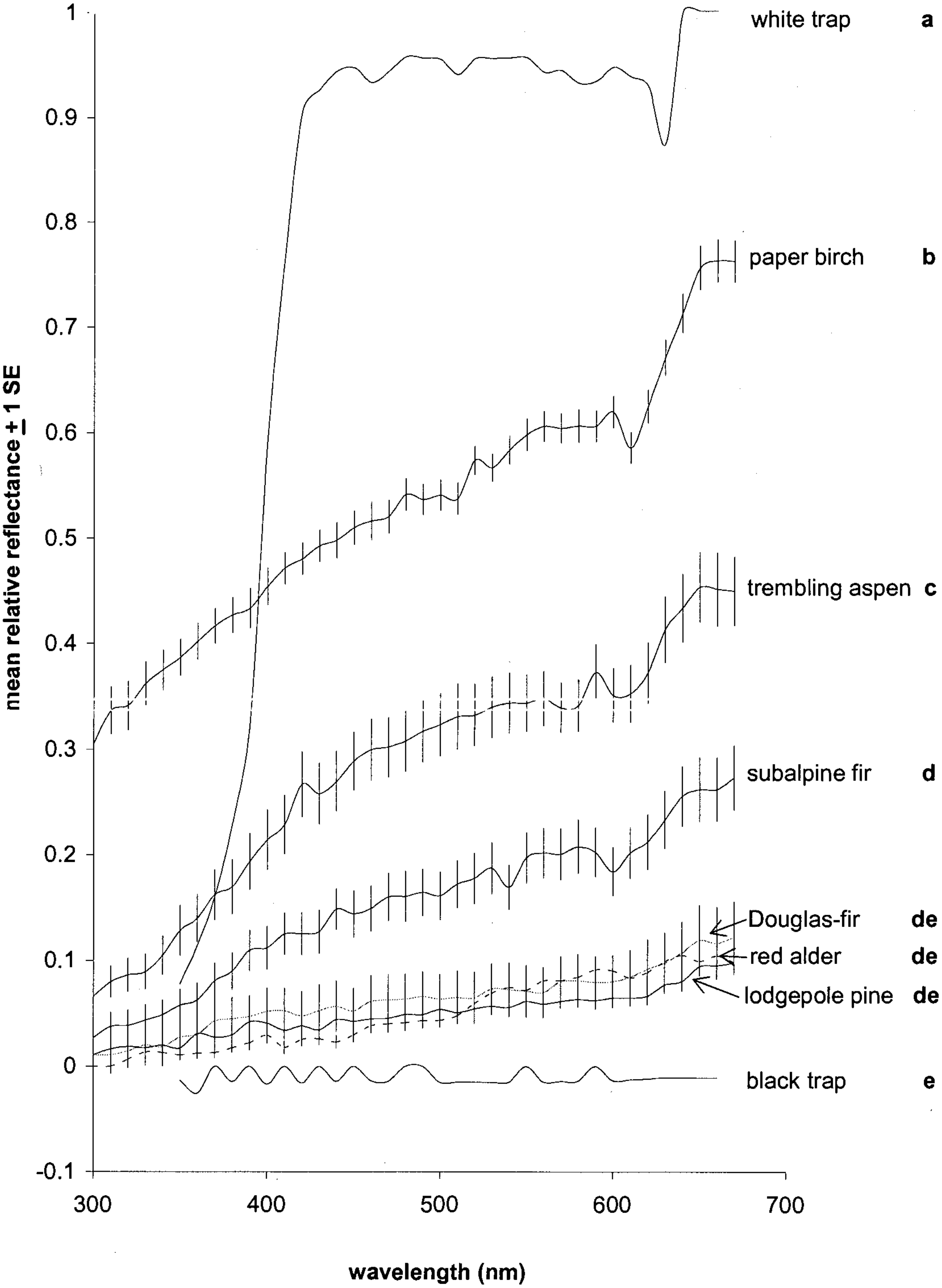
3. RESULTS

3.1 SPECTRAL REFLECTANCE OF TREE BARK

There were few qualitative differences in reflectance among tree species, and between tree bark and trap plastics; all surfaces were generally achromatic (Figure 1). However, species and traps differed quantitatively ($P<0.0001$ for all wavelengths) in reflectance intensity. Of the trees, paper birch had the highest reflectance over most wavelengths, followed by trembling aspen, subalpine fir, Douglas-fir, red alder and lodgepole pine. For most wavelengths within the hypothesised range of scolytid vision, the latter four species were not different from each other, and the latter three were not different from the black trap (Figure 1). Considering all potentially visible wavelengths together (400-580 nm), species also differed significantly from one another (MANOVA for trees only: Pillai's trace=3.7938; $F_{95,140}=4.64$; $P<0.0001$). Significant differences among species means for this analysis were the same as above, except that subalpine fir reflectance was significantly higher than Douglas-fir, red alder and lodgepole pine.

Paper birch and trembling aspen reflected more intensely than the white trap for $\lambda<400$ nm, and $\lambda<370$ nm, respectively. Only paper birch, however, reflected light into the short blue/UV wavelengths, or 300-400 nm. No species had bark that reflected as intensely as the white trap across the probable sensitivity maxima of scolytids (400 and 510-530 nm).

FIGURE 1. Reflectance spectra of hosts, non-hosts, and experimental traps. Traces comprise means of the proportional reflectance ± 1 SE for 10 nm increments from 300-670 nm. Spectra followed by the same letter are not significantly different across most increments for λ=400-580 by the REGW multiple-range test.


mean relative reflectance ± 1 SE
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
300
400
500
600
700
wavelength (nm)
white trap a
paper birch b
trembling aspen c
subalpine fir d
Douglas-fir de
red alder de
lodgepole pine de
black trap e

3.2 TRAPPING EXPERIMENTS

In describing lower catches in a particular treatment, use of the terms 'repelled', 'avoided', 'disrupted' and 'deterred' is always relative to black, attractant-baited control traps unless otherwise stated.

3.2.1 BARK BEETLES

Effect of a non-host angiosperm visual cue

All three bark beetle species avoided white, baited traps as compared to black, baited traps (Experiments 1, 6, 8, 10; Figures 2-5; Tables 3-6). For interior and coastal DFBs (Experiments 1 and 6), there was a significant interaction of colour × semiochemical treatment for both sexes, with more beetles caught in black over white traps only when the traps were baited (Figures 2, 3; Tables 3, 4). There was no such interaction in the case of the MPB (Experiment 10), with significantly more beetles caught in black as opposed to white traps even when these were unbaited (Figure 4; Table 5). Similarly, for the WBBB (Experiment 8), there was a 65% reduction in white as opposed to black baited traps for both sexes; however this reduction was only significant for females (Figure 5; Table 6). The fir-colonising *Dryocoetes autographus* (Patzeburg) and *Dr. affaber* (Mannerheim) were also caught in Experiment 8. Analysis of mixed sexes of *Dr. autographus* (Figure 6; Table 7) indicated a strong avoidance of white, baited traps, although there were insufficient numbers of *Dr. affaber* for analysis.

Effects of visual and semiochemical cues of hosts and non-hosts

Both the DFB and MPB demonstrated avoidance of both non-host visual and non-host semiochemical stimuli (Experiments 2, 3, 7, 11, 12). In Experiment 2 (Figure 2; Table 3),

FIGURE 2. Results of Experiments 1-3 for interior Douglas-fir beetles (DFB). In the treatment combinations listed on the right, colour denotes trap colour, 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 by the REGW multiple-range test.

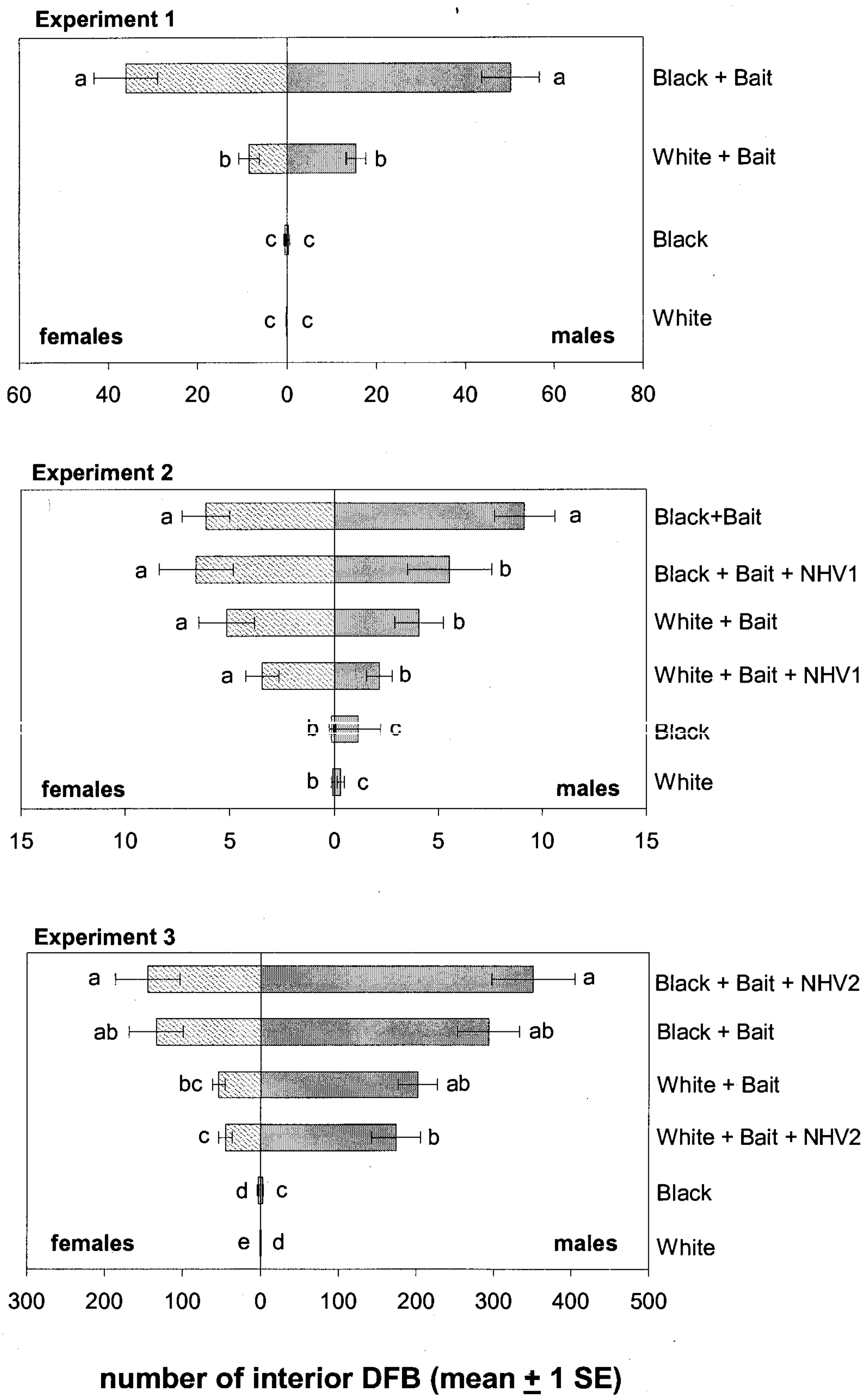

Experiment 1
a
a
Black + Bait
b
b
White + Bait
c
c
Black
c
c
White
females
males
60
40
20
0
20
40
60
80
Experiment 2
a
a
Black+Bait
a
b
Black + Bait + NHV1
a
b
White + Bait
a
b
White + Bait + NHV1
b
c
Black
b
c
White
females
males
15
10
5
0
5
10
15
Experiment 3
a
a
Black + Bait + NHV2
ab
ab
Black + Bait
bc
ab
White + Bait
c
b
White + Bait + NHV2
d
c
Black
e
d
White
females
males
300
200
100
0
100
200
300
400
500
number of interior DFB (mean ± 1 SE)

TABLE 3. Analysis of variance of the response of *D. pseudotsugae* to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and two or three levels of a semiochemical stimulus. In Experiment 1, the semiochemical stimulus was either an attractive bait or no bait, and in Experiments 2 and 3, a bait + non-host volatile (NHV1 and NHV2, respectively) level was included.

			MALES			FEMALES		
Exp.	Source of Variation	df	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 *x* 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 *x* 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 *x* Semio	2	0.0484	0.72	0.4905	0.0009	0.01	0.9918
	Error	73	0.0673			0.1154		

FIGURE 3. Results of Experiments 6 and 7 for coastal Douglas-fir beetles (DFB). In the treatment combinations listed on the right, colour denotes trap colour, 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 by the REGW multiple-range test.

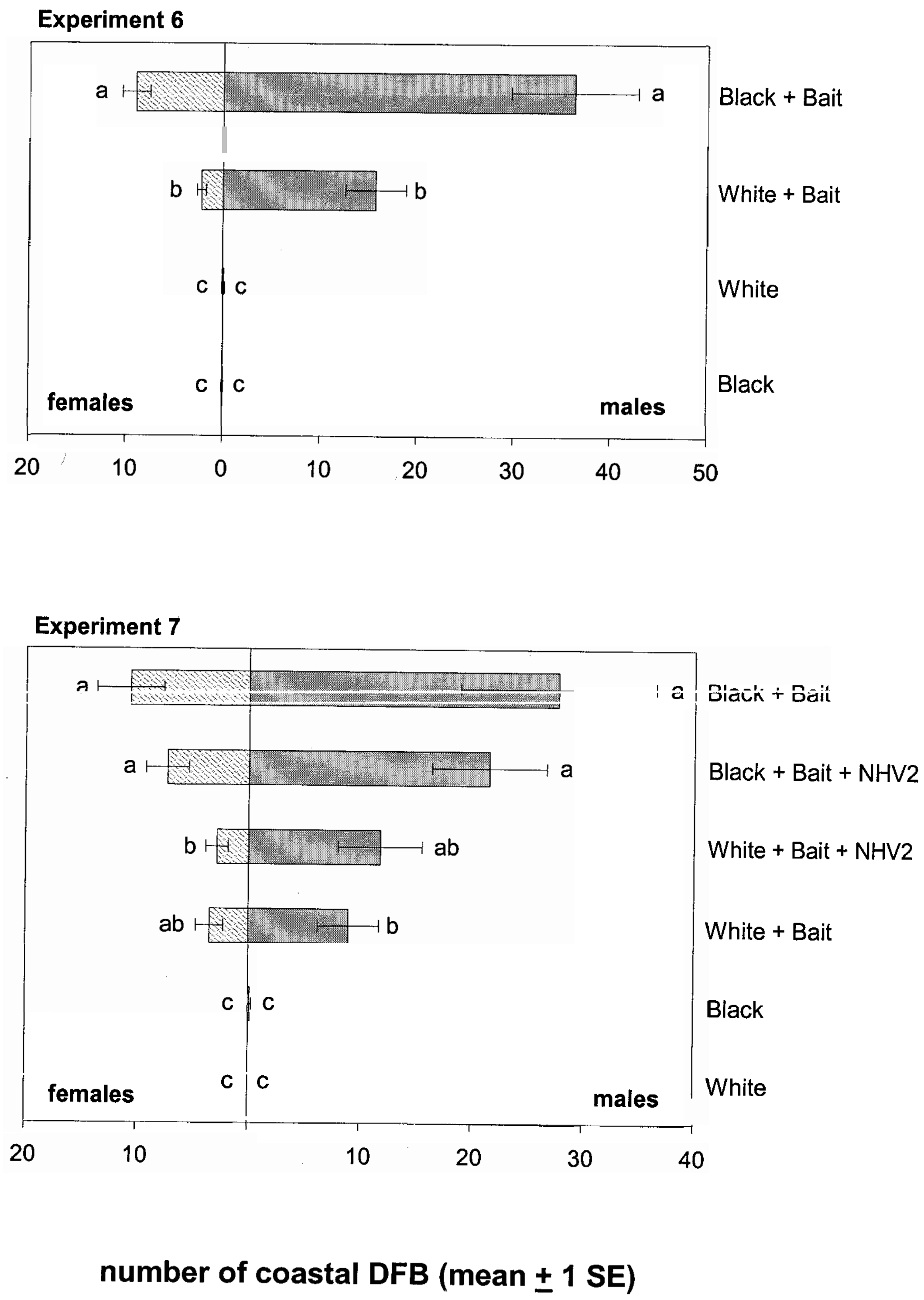

Experiment 6
a
a
Black + Bait
b
b
White + Bait
c
c
White
c
c
Black
females
males
20
10
0
10
20
30
40
50
Experiment 7
a
a
Black + Bait
a
a
Black + Bait + NHV2
b
ab
White + Bait + NHV2
ab
b
White + Bait
c
c
Black
c
c
White
females
males
20
10
10
20
30
40
number of coastal DFB (mean ± 1 SE)

TABLE 4. Analysis of variance of the response of *D. pseudotsugae* to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and two or three levels of a semiochemical stimulus. In Experiment 6, the semiochemical stimulus was either an attractive bait or no bait, and in Experiment 7, a bait + non-host volatile (NHV2) level was included.

			MALES			FEMALES		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
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 *x* 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 *x* Semio	2	0.2175	1.89	0.1592	0.2048	2.25	0.1126
	Error	69	0.1152			0.0909		

FIGURE 4. Results of Experiments 10-12 for the mountain pine beetle (MPB). In the treatment combinations listed on the right, colour denotes trap colour, bait is a combination of aggregation pheromones and myrcene, and NHV denotes the non-host volatile blend. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.

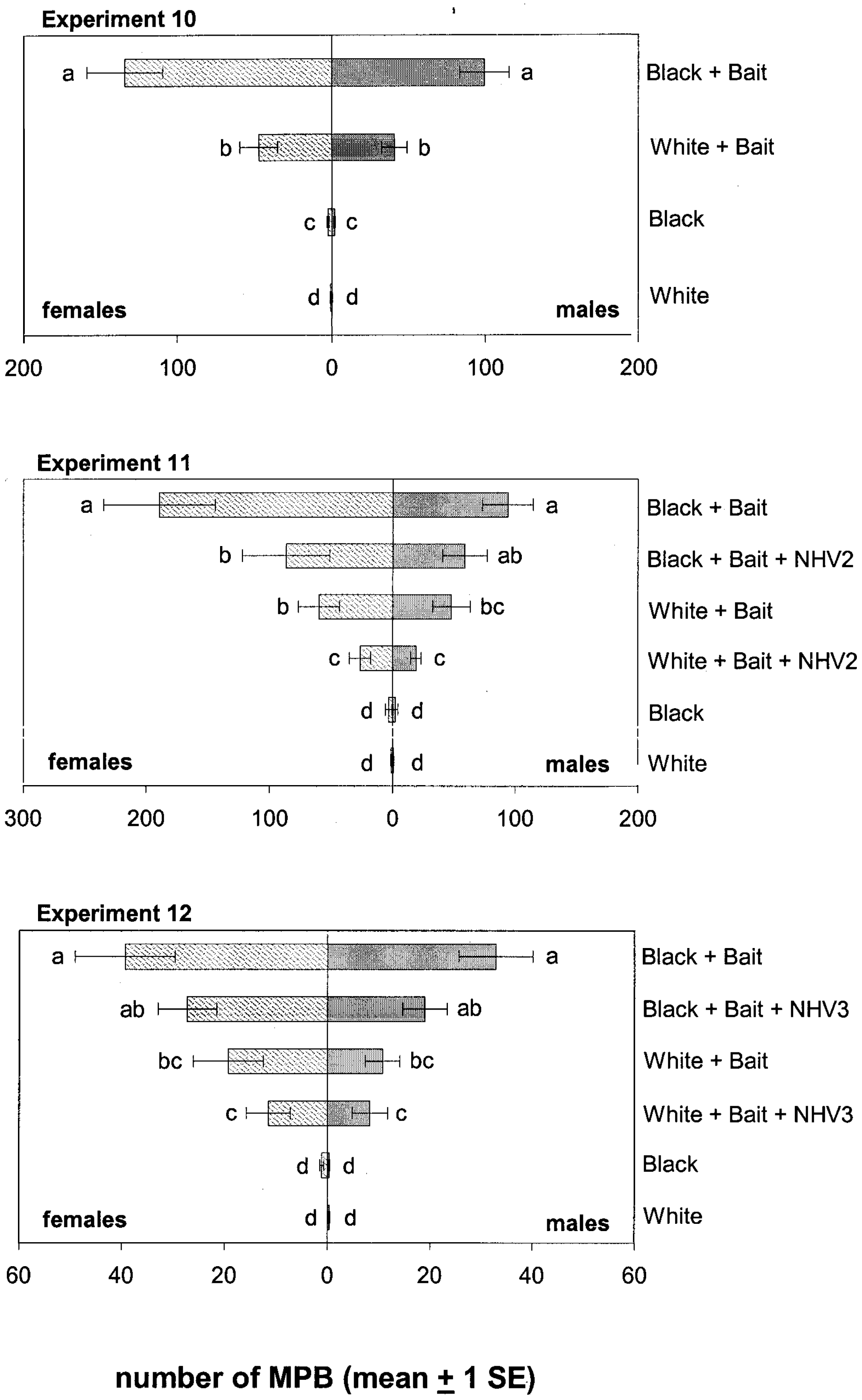

Experiment 10
a
a
Black + Bait
b
b
White + Bait
c
c
Black
d
d
White
females
males
200
100
0
100
200
Experiment 11
a
a
Black + Bait
b
ab
Black + Bait + NHV2
b
bc
White + Bait
c
c
White + Bait + NHV2
d
d
Black
d
d
White
females
males
300
200
100
0
100
200
Experiment 12
a
a
Black + Bait
ab
ab
Black + Bait + NHV3
bc
bc
White + Bait
c
c
White + Bait + NHV3
d
d
Black
d
d
White
females
males
60
40
20
0
20
40
60
number of MPB (mean ± 1 SE)

TABLE 5. Analysis of variance of the response of *D. ponderosae* to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and two or three levels of a semiochemical stimulus. In Experiment 10, the semiochemical stimulus was either an attractive bait or no bait, and in Experiments 11 and 12, a bait + non-host volatile (NHV2 and NHV3, respectively) level was included.

			MALES			FEMALES		
Exp.	Source of Variation	df	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 *x* 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 *x* 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 *x* Semio	2	0.5267	5.63	0.0055	0.0507	0.56	0.575
	Error	68	0.0936			0.0909		

FIGURE 5. Results of Experiments 8 and 9 for the western balsam bark beetle (WBBB). In the treatment combinations listed on the right, colour denotes trap colour, bait is the aggregation pheromone, and HV denotes the host volatile blend. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.

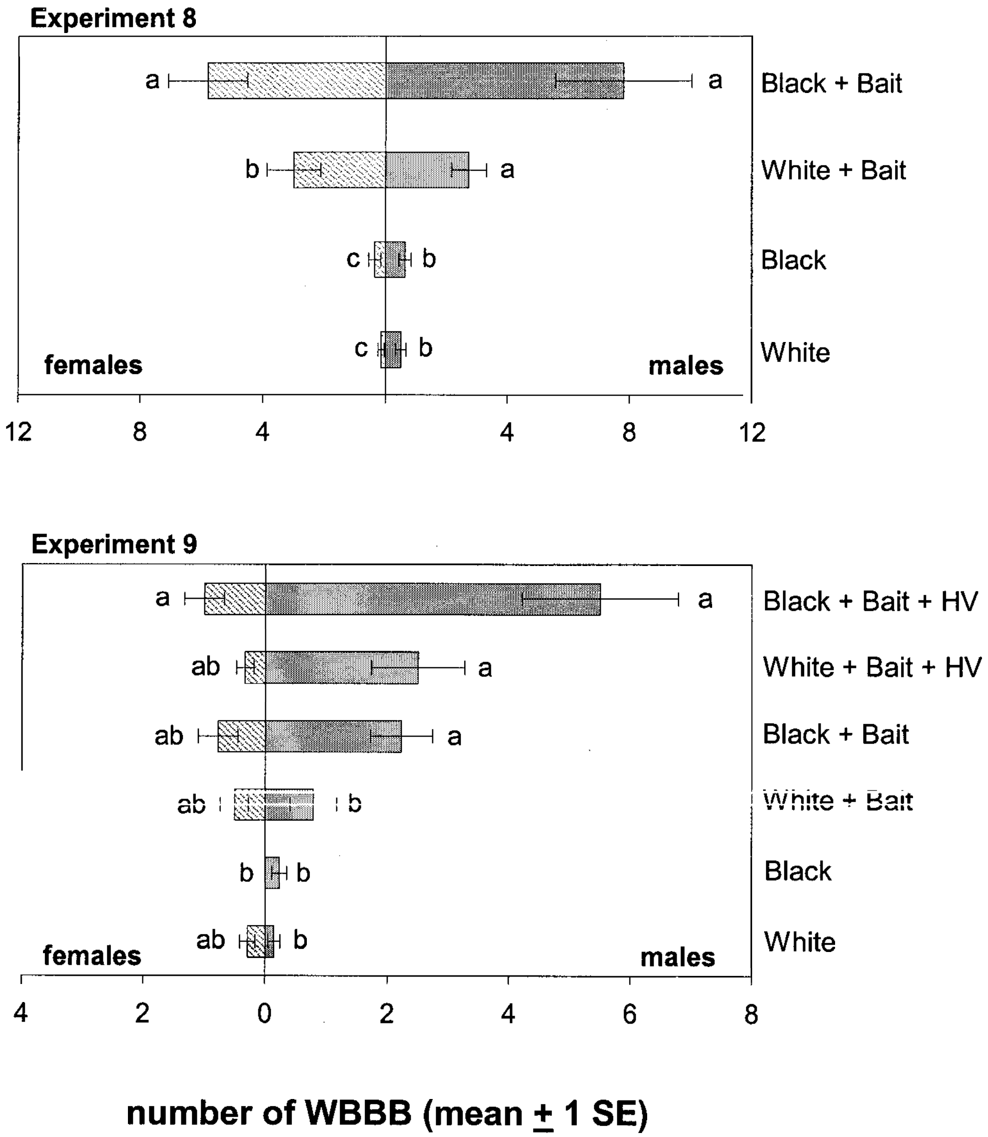

Experiment 8
a
a
Black + Bait
b
a
White + Bait
c
b
Black
c
b
White
females
males
12
8
4
4
8
12
Experiment 9
a
a
Black + Bait + HV
ab
a
White + Bait + HV
ab
a
Black + Bait
ab
b
White + Bait
b
b
Black
ab
b
White
females
males
4
2
0
2
4
6
8
number of WBBB (mean ± 1 SE)

TABLE 6. Analysis of variance of the response of *Dryocoetes confusus* to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and two or three levels of a semiochemical stimulus. In Experiment 8, the semiochemical stimulus was either an attractive bait or no bait, and in Experiment 9, a bait + host volatile (HV) level was included.

			MALES			FEMALES		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
8	Colour	1	12.0700	4.40	0.0422	9.2116	5.41	0.0252
	Semiochemical	1	85.8000	31.31	<0.0001	105.2659	61.81	<0.0001
	Colour *x* Semio	1	8.3566	3.05	0.0885	5.0745	2.98	0.0920
	Error	40	0.0824			0.0574		
9	Colour	1	0.6354	8.85	0.0042	0.0359	1.15	0.2882
	Semiochemical	2	1.5505	21.59	<0.0001	0.0990	3.17	0.0492
	Colour *x* Semio	2	0.1205	1.68	0.1951	0.0748	2.39	0.1000
	Error	61	0.0718			0.0313		

FIGURE 6. Catches of mixed sexes of *Dryocoetes autographus* and *Dr. affaber* in Experiments 8 and 9. In the treatment combinations listed on the right, colour denotes trap colour, bait is the aggregation pheromone, and HV denotes the host volatile blend. Within an experiment and species, means followed by the same letter are not significantly different by the REGW multiple-range test.

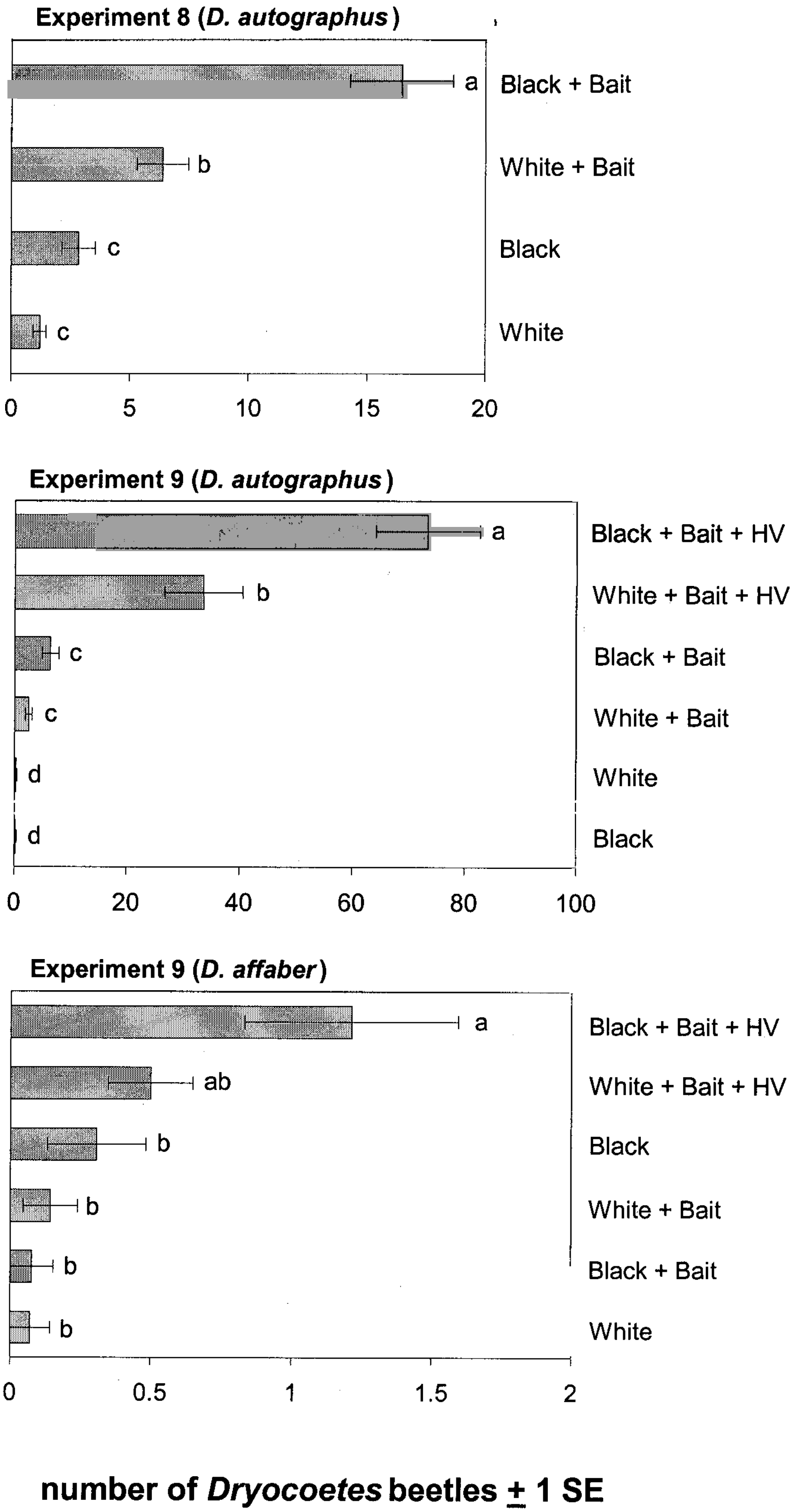
Experiment 8 (*D. autographus*)
a
Black + Bait
b
White + Bait
c
Black
c
White
0
5
10
15
20
Experiment 9 (*D. autographus*)
a
Black + Bait + HV
b
White + Bait + HV
c
Black + Bait
c
White + Bait
d
White
d
Black
0
20
40
60
80
100
Experiment 9 (*D. affaber*)
a
Black + Bait + HV
ab
White + Bait + HV
b
Black
b
White + Bait
b
Black + Bait
b
White
0
0.5
1
1.5
2
number of *Dryocoetes* beetles ± 1 SE

TABLE 7. Analysis of variance of the response of mixed sexes of *Dryocoetes* species to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and two or three levels of a semiochemical stimulus. In Experiment 8, the semiochemical stimulus was either an attractive bait or no bait, and in Experiment 9, a bait + host volatile (HV) level was included. *Catches in Experiment 8 were too low for analysis.

			D. autographus			*D. affaber**		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
8	Colour	1	1.3165	17.06	0.0002			
	Semiochemical	1	4.4682	57.91	<0.0001			
	Colour *x* Semio	1	0.1625	2.11	0.1545			
	Error	40	0.0772					
9	Colour	1	0.9318	10.18	0.0022	0.0617	2.64	0.1093
	Semiochemical	2	15.6448	170.88	<0.0001	0.2287	9.79	0.0002
	Colour *x* Semio	2	0.3323	3.63	0.0324	0.0428	1.83	0.1684
	Error	61	0.0916			0.0234		

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. These two stimuli combined had a mild additive and/or redundant effect on catches, contributing to a significant semiochemical × colour interaction. There were no significant reductions in female catches in this experiment. However, in Experiment 3, black traps caught significantly more beetles than white traps (Table 3), and females were significantly disrupted by the combination of white traps and the NHVs; there was an additive/redundant effect of combining both types of stimuli (Figure 2). In unbaited traps, significantly more beetles of both sexes were also caught in black over white traps. More male and female coastal DFBs were caught in black than in white traps in Experiment 7 (significant effect of colour, and no interaction; Table 4). 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 white trap stimulus significantly reduced catches relative to the black, baited controls (Figure 3).

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 (Figure 4; Table 5). 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 (Figure 4). There were no differences between unbaited traps for either sex, contributing to significant interactions of semiochemical × visual treatments (Table 5). In Experiment 12, white traps deterred both sexes, but the NHV guaiacol did not significantly disrupt responses to baited traps of either colour. Female colour preference was similar in each semiochemical treatment, although there was a significant interaction for males in this experiment (Table 5; Figure 4).

The DFB (Experiment 4; Figure 7; Table 8) and the MPB (Experiment 13; Figure 8; Table 9) both strongly avoided the black, attractant baited traps that also released their antiaggregation pheromone. They also avoided white, baited traps in these experiments, and avoidance by the DFB was strongest when the two stimuli were combined. In the presence of the potent antiaggregation pheromones, colour became redundant in deterring beetles. With female MPBs, verbenone always reduced catches to levels not significantly different from those in the unbaited control traps. There was a significant interaction with the DFB, but not the mountain pine beetle in these experiments (Tables 8, 9).

Similarly, in Experiment 5 (Figure 7), female (but not male) DFBs were deterred by white traps. The addition of MCH + NHV1 reduced catches of both sexes significantly, with female catches being as low as those in the unbaited traps. As in Experiment 4, the white trap stimulus was redundant with the addition of the MCH + NHV1 blend, contributing to a significant interaction for females (Table 8). As with the DFB in Experiment 5, the addition of verbenone + NHV2 in Experiment 14 reduced catches of female mountain pine beetles to levels not significantly different from those in the unbaited control traps (Figure 8), and while there was an effect of colour overall (both sexes, no interaction; Table 9), the repellency of the white stimulus was again redundant in combination with the powerful antiaggregation + NHV blend.

Over twice as many male WBBB were caught in traps with *exo*-brevicomin, α-pinene and ethanol than in traps baited with *exo*-brevicomin alone, although this increase was significant in white, but not in black traps (Experiment 9; Figure 5). There was also

FIGURE 7. Results of Experiments 4 and 5 for interior Douglas-fir beetles (DFB). In the treatment combinations listed on the right, colour denotes trap colour, bait is a combination of aggregation pheromones and ethanol, MCH is the antiaggregation pheromone, and NHV denotes the non-host volatile blend. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.

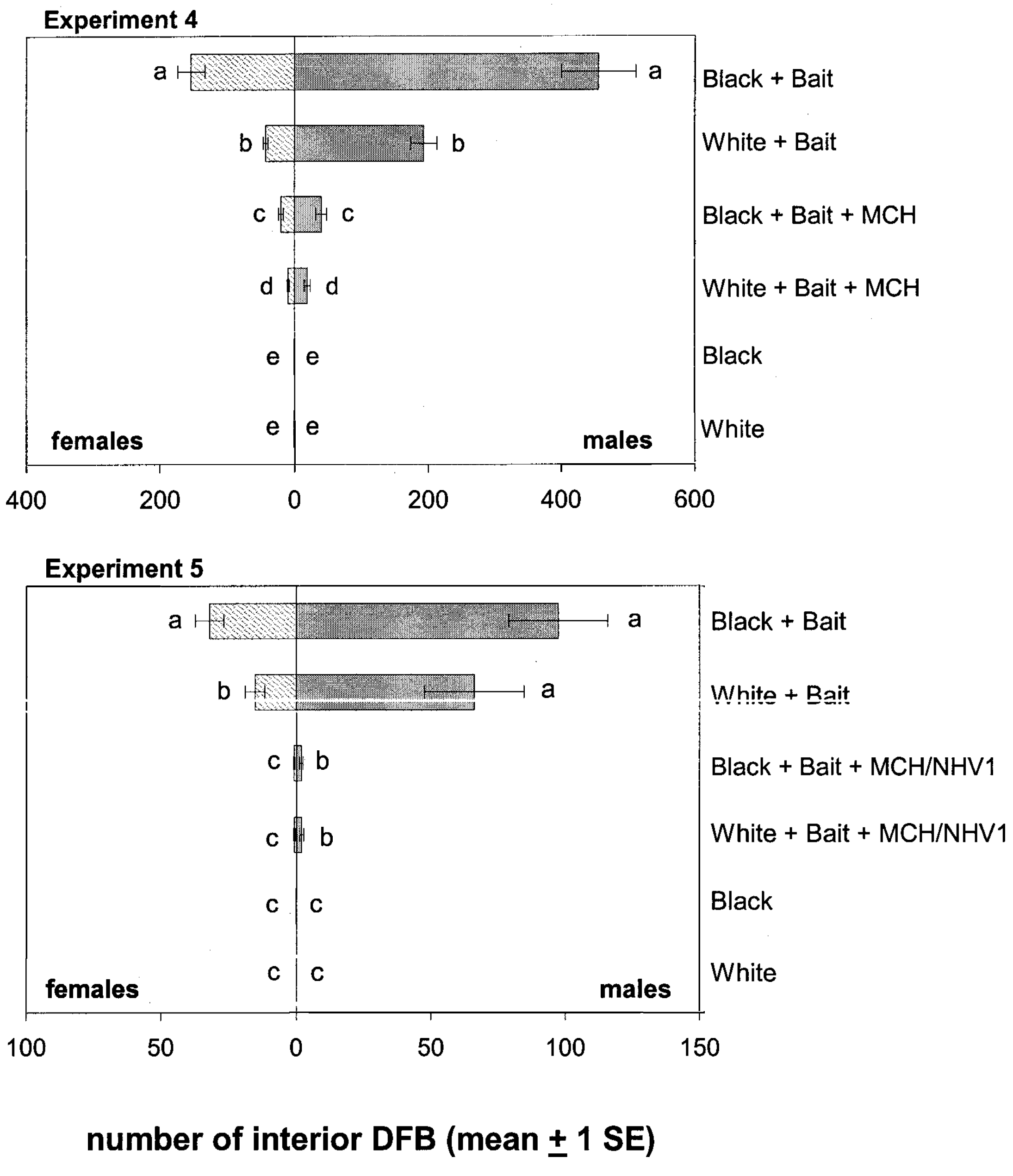

Experiment 4
a
a
Black + Bait
b
b
White + Bait
c
c
Black + Bait + MCH
d
d
White + Bait + MCH
e
e
Black
e
e
White
females
males
400
200
0
200
400
600
Experiment 5
a
a
Black + Bait
b
a
White + Bait
c
b
Black + Bait + MCH/NHV1
c
b
White + Bait + MCH/NHV1
c
c
Black
c
c
White
females
males
100
50
0
50
100
150
number of interior DFB (mean ± 1 SE)

TABLE 8. Analysis of variance of the response of *D. pseudotsugae* to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and three levels of a semiochemical stimulus: no bait, attractive bait, and either bait + MCH (Experiment 4) or bait + MCH + a non-host volatile (NHV1) (Experiment 5).

			MALES			FEMALES		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
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 *x* 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 *x* Semio	2	0.1576	1.57	0.2164	0.2559	4.27	0.0178
	Error	69	0.1007			0.0599		

FIGURE 8. Results of Experiments 13-15 for the mountain pine beetle (MPB). In the treatment combinations listed on the right, colour denotes trap colour, bait is a combination of aggregation pheromones and myrcene, verbenone is the antiaggregation pheromone, and NHV denotes the non-host volatile blend. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.

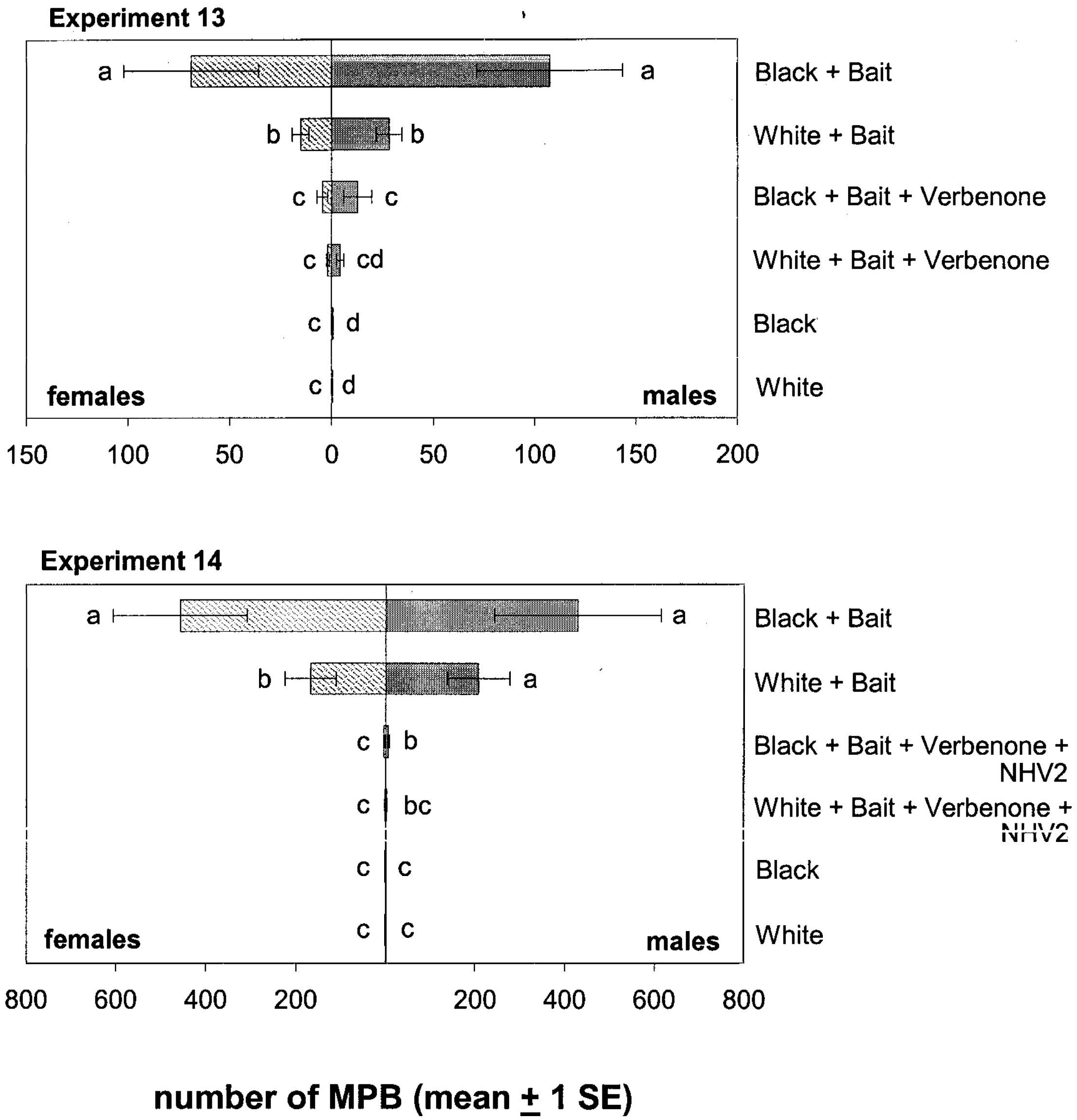

Experiment 13
a
a
Black + Bait
b
b
White + Bait
c
c
Black + Bait + Verbenone
c
cd
White + Bait + Verbenone
c
d
Black
c
d
White
females
males
150
100
50
0
50
100
150
200
Experiment 14
a
a
Black + Bait
b
a
White + Bait
c
b
Black + Bait + Verbenone + NHV2
c
bc
White + Bait + Verbenone + NHV2
c
c
Black
c
c
White
females
males
800
600
400
200
200
400
600
800
number of MPB (mean ± 1 SE)

TABLE 9. Analysis of variance of the response of *D. ponderosae* to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and three levels of a semiochemical stimulus: attractive bait, no bait, and either bait + verbenone (Experiment 13), or a bait + verbenone + non-host volatile (NHV2) (Experiment 14).

			MALES			FEMALES		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
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 *x* 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 *x* Semio	2	0.0390	0.43	0.6517	0.2628	2.21	0.1185
	Error	63	0.0904			0.1191		

a significant main effect of colour, and no interaction, indicating that males preferred black over white traps across all semiochemical treatments (Table 6). Few female beetles were caught, and 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 6). In this experiment, *Dr. autographus* (mixed sexes) did not discriminate between black and white traps baited with only *exo*-brevicomin, but did prefer black over white traps when these were baited with both *exo*-brevicomin and host volatiles (Figure 6), leading to a significant visual × semiochemical interaction (Table 7). The host semiochemicals attracted greater numbers of beetles to traps of both colours relative to all other treatments. Similarly, with *Dr. affaber* (Experiment 9), the difference between black and white traps was greater (over 2-fold) 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 blend caught significantly more beetles than the unbaited traps (Figure 6).

Mountain pine beetle cluster experiments

In Experiment 15, the average proportion of females caught in black and white traps was 37% and 14%, respectively. The 95% confidence interval for the mean difference between black and white was 9.2 – 37.6 % ($F_{1,10} = 13.49$, $P = 0.0043$). Male colour preference was weaker: the average percentage of males caught in black and white traps was 32% and 20%, respectively, and the 95% confidence interval for the difference in colour was 1.7 – 22.1% ($F_{1,10} = 6.40$, $P = 0.0298$).

In Experiment 16 (Figure 9; Table 10A), catches were highest in clusters with myrcene on both colours (all 4 traps), followed by clusters with myrcene on only one trap

FIGURE 9. Catches of the mountain pine beetle (MPB) in pheromone-baited clusters of traps in Experiment 16. Dark and white bars are catches in black and white traps, respectively, in the four semiochemical treatments (listed along the abscissa). For each sex, semiochemical treatments with the same letter are not significantly different by the REGW multiple-range test (means of cluster totals). Within each treatment group, * denotes significant ANOVA differences between colours for both sexes; *NS*: not significant.

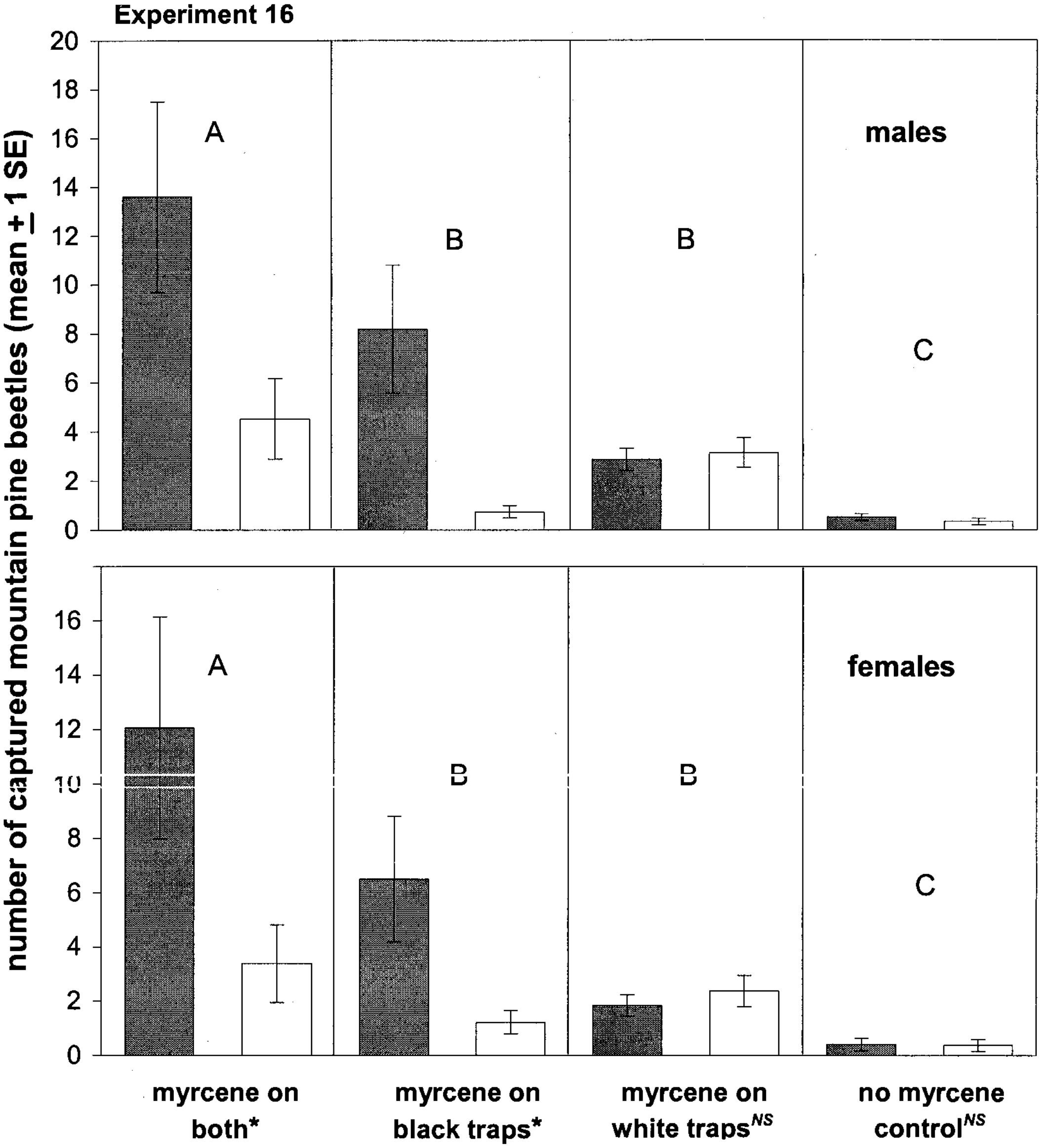

Experiment 16
number of captured mountain pine beetles (mean ± 1 SE)
20
18
16
14
12
10
8
6
4
2
0
A
B
B
C
males
16
14
12
10
8
6
4
2
0
A
B
B
C
females
myrcene on both*
myrcene on black traps*
myrcene on white traps^{NS}
no myrcene control^{NS}

TABLE 10. Analysis of variance of the response of *D. ponderosae* in Experiment 16. *(A)* Effect of semiochemical treatment (myrcene) on catch totals in each cluster, and on the percent difference between black and white traps. *(B)* Effect of trap colour on catches (for each semiochemical treatment).

(A) EFFECT OF SEMIOCHEMICAL

		MALES			FEMALES		
Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
Cluster totals							
Semiochemical	3	2.0094	27.52	<0.0001	1.8765	21.90	<0.0001
Error	45	0.0730			0.0857		
% Difference							
Semiochemical	3	0.6345	17.06	<0.0001	0.6409	18.41	<0.0001
Error	45	0.0372			0.0348		

(B) EFFECT OF TRAP COLOUR

		MALES			FEMALES		
Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
Myrcene on both							
Colour	1	1.3564	35.35	<0.0001	1.8167	44.69	<0.0001
Error	15	0.0384			0.0407		
Myrcene on black traps							
Colour	1	2.2192	43.03	<0.0001	1.1491	40.81	<0.0001
Error	15	0.0516			0.0282		
Myrcene on white traps							
Colour	1	0.0003	0.01	0.9116	0.0404	2.17	0.1612
Error	15	0.0258			0.0186		
No myrcene (control)							
Colour	1	0.0202	2.12	0.1656	0.0012	0.13	0.7200
Error	15	0.0095			0.0093		

colour, (myrcene on black only, myrcene on white only) and very few beetles were caught in clusters without myrcene (Figure 9). The mean proportional difference of black minus white traps differed among treatments (Table 10A; Figure 10). Male discrimination was greatest in clusters with myrcene on black traps only, followed by clusters with myrcene on all four traps. Female discrimination was greatest in clusters with myrcene on both colours, and myrcene on black traps (Figure 10). For both sexes, differences between black and white traps were only significant in these two treatments; trap catches were not different between colours in clusters with myrcene on white traps, and clusters without myrcene (Table 10B; Figure 9).

3.2.2 AMBROSIA BEETLES

Effect of a non-host angiosperm visual cue

In contrast to the bark beetles, ambrosia beetles did not respond consistently to a visual non-host angiosperm stimulus. Coastal *T. lineatum* (Experiment 17; Figure 11) males, but not females, preferred black more often than white baited traps when the attractive bait included both the pheromone lineatin and a host volatile blend (marginal overall effect of colour, Table 11). However, without the host volatiles (Experiment 18), neither sex discriminated between colours (Figure 11). In Experiment 21, neither sex of *G. sulcatus* discriminated between trap colours (Figure 12; Table 12).

Effects of visual and semiochemical stimuli

In Experiment 19 (Figure 11), coastal *T. lineatum* avoided traps with the non-host volatile salicylaldehyde; however there were no differences between catches in black and white traps for any semiochemical treatment, with the exception that males preferred black,

FIGURE 10. Differences in visual 'preference' among semiochemical treatments in Experiment 16 for the mountain pine beetle (MPB). Treatments are listed along the abscissa. For each sex, bars with the same letter are not significantly different by the REGW multiple-range test.

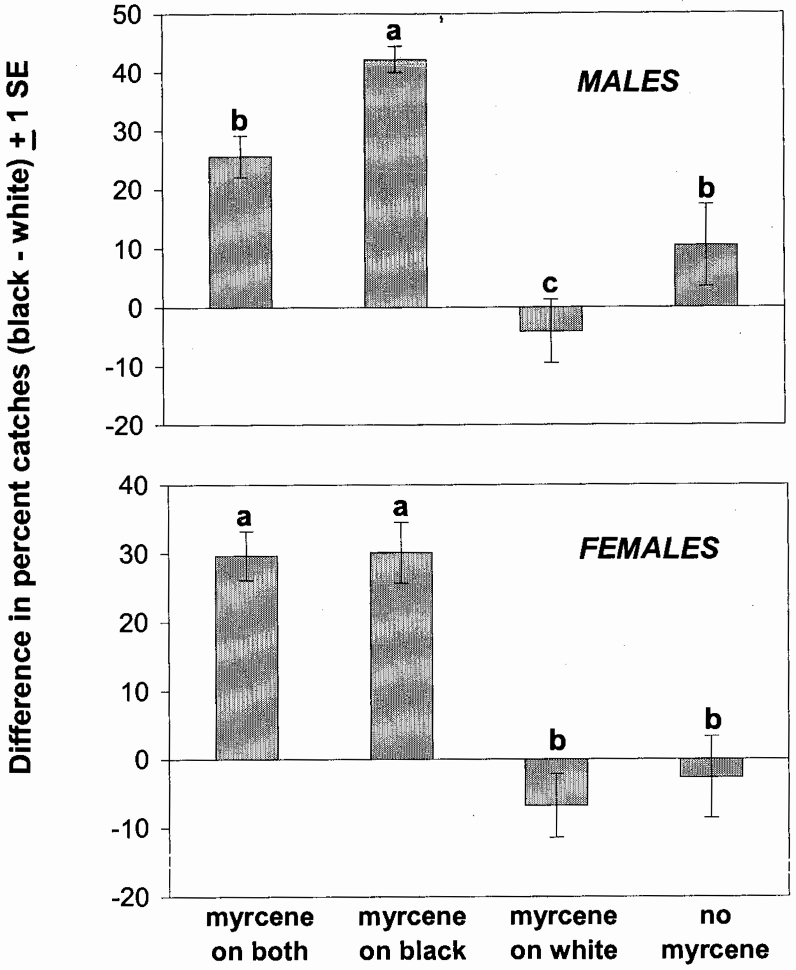

Difference in percent catches (black - white) ± 1 SE
50
40
30
20
10
0
-10
-20
MALES
b
a
c
b
40
30
20
10
0
-10
-20
FEMALES
a
a
b
b
myrcene on both
myrcene on black
myrcene on white
no myrcene

FIGURE 11. Results of Experiments 18-20 for coastal *Trypodendron lineatum*. In the treatment combinations listed on the right, colour denotes trap colour, bait1 is a combination of the aggregation pheromone lineatin, α-pinene and ethanol, bait2 is lineatin alone, and NHV denotes the non-host volatile blend. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.

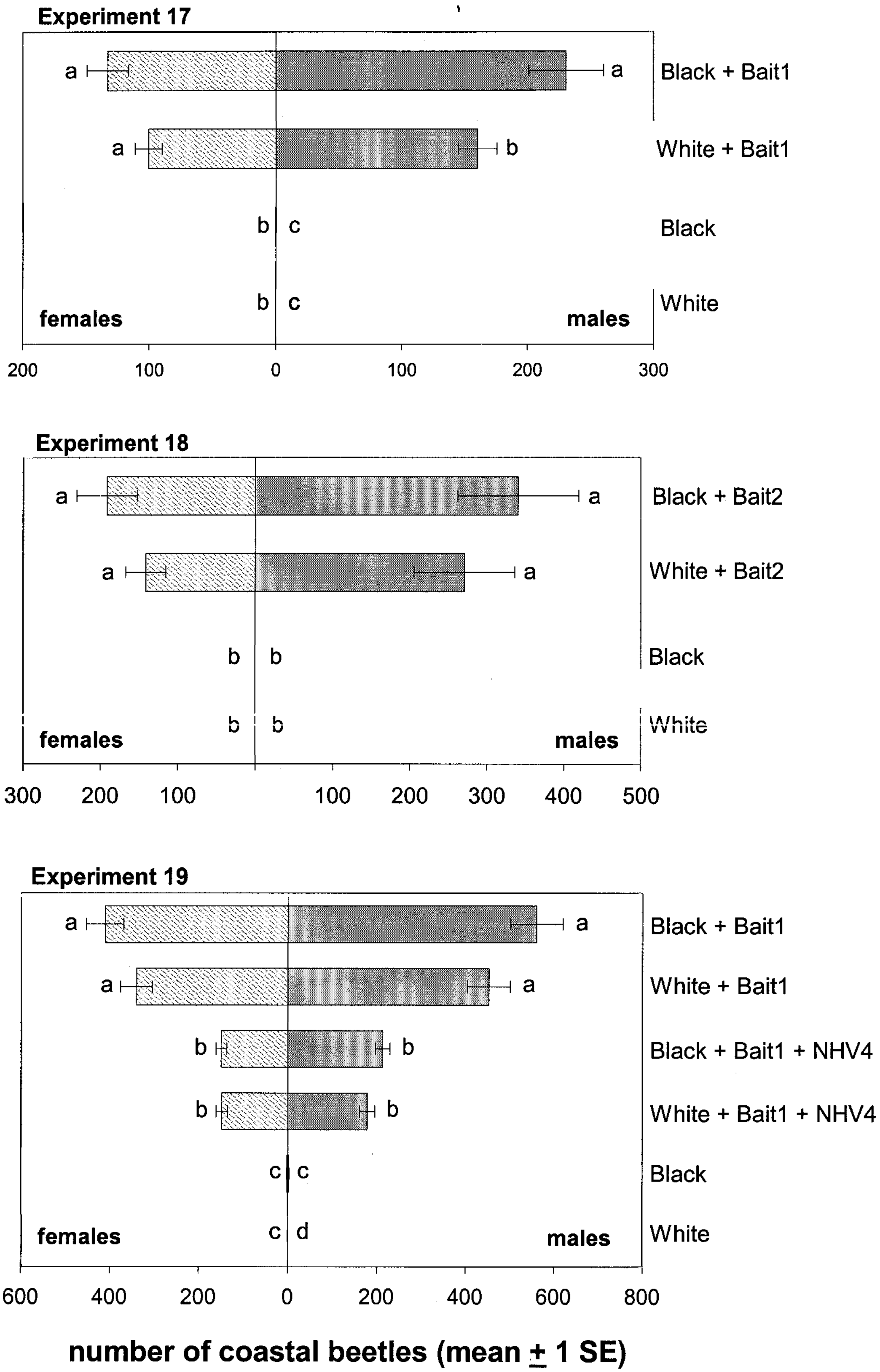
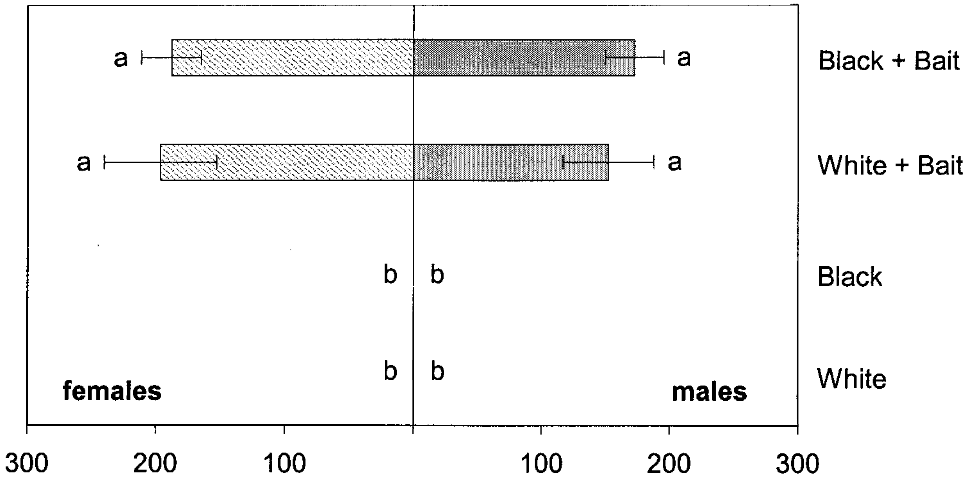

Experiment 17
a
a
Black + Bait1
a
b
White + Bait1
b
c
Black
b
c
White
females
males
200
100
0
100
200
300
Experiment 18
a
a
Black + Bait2
a
a
White + Bait2
b
b
Black
b
b
White
females
males
300
200
100
100
200
300
400
500
Experiment 19
a
a
Black + Bait1
a
a
White + Bait1
b
b
Black + Bait1 + NHV4
b
b
White + Bait1 + NHV4
c
c
Black
c
d
White
females
males
600
400
200
0
200
400
600
800
number of coastal beetles (mean ± 1 SE)

TABLE 11. Analysis of variance of the response of coastal *T. lineatum* to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and two or three levels of a semiochemical stimulus. In Experiments 17 and 18, the semiochemical stimulus was either an attractive bait or no bait, and in Experiment 19 a bait + non-host volatile (NHV4) level was included.

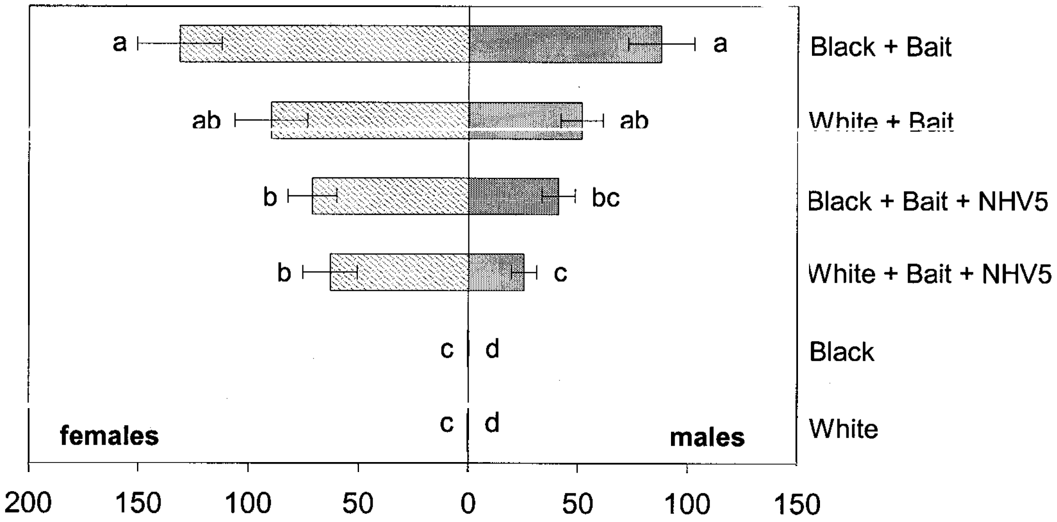
			MALES			FEMALES		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
17	Colour	1	0.0881	4.05	0.0505	0.0491	2.41	0.1277
	Semiochemical	1	73.8650	3397.8	<0.0001	60.3062	2968.9	<0.0001
	Colour *x* Semio	1	0.0480	2.21	0.1447	0.0207	1.02	0.3189
	Error	42	0.0217			0.0203		
18	Colour	1	0.0459	0.93	0.3417	0.0145	0.39	0.5355
	Semiochemical	1	61.1780	1245.0	<0.0001	47.1028	1277.4	<0.0001
	Colour *x* Semio	1	0.0459	0.93	0.3417	0.0698	1.89	0.1790
	Error	30	0.0491			0.0369		
19	Colour	1	0.2934	8.07	0.0061	0.1652	2.77	0.1010
	Semiochemical	2	45.7424	1258.8	<0.0001	39.4889	663.09	<0.0001
	Colour *x* Semio	2	0.0403	1.11	0.3362	0.0708	1.19	0.3114
	Error	60	0.0363			0.0596		

FIGURE 12. Results of Experiments 21 and 22 for coastal *Gnathotrichus sulcatus*. In the treatment combinations listed on the right, colour denotes trap colour, bait is a combination of the aggregation pheromone sulcatol, α-pinene and ethanol, and NHV denotes the non-host volatile blend. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.

Experiment 21



Experiment 22



number of beetles (mean ± 1 SE)

TABLE 12. Analysis of variance of the response of *Gnathotrichus sulcatus* to visual and semiochemical stimuli. Each experiment combined two levels of a colour stimulus (black or white traps), and two or three levels of a semiochemical stimulus. In Experiment 21, the semiochemical stimulus was either an attractive bait or no bait, and in Experiment 22, a bait + non-host volatile (NHV5) level was included.

			MALES			FEMALES		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
21	Colour	1	0.0605	2.25	0.1413	0.0000	0.00	0.9885
	Semiochemical	1	67.6593	2513.1	<0.0001	72.6446	2749.7	<0.0001
	Colour *x* Semio	1	0.0082	0.3	0.5839	0.0064	0.24	0.6248
	Error	42	0.0269			0.0264		
22	Colour	1	0.6682	10.15	0.0022	0.2861	5.62	0.0205
	Semiochemical	2	23.5992	358.53	<0.0001	31.6974	623.17	<0.0001
	Colour *x* Semio	2	0.1006	1.53	0.2243	0.0335	0.66	0.5204
	Error	68	0.0658			0.0509		

unbaited traps to white, unbaited traps (Figure 11), and preferred black traps overall (Table 11). In an interior population of three *Trypodendron* species (Experiment 20; Figure 13; Table 13), trembling aspen-colonising, male *T. retusum* did not discriminate between colours, or between traps with lineatin and the host volatile salicylaldehyde and traps with lineatin alone. Females also did not discriminate between colours, and only traps with both lineatin and salicylaldehyde caught more beetles than unbaited traps (both colours). For the coniferophagous *T. rufitarsus*, traps baited with the NHV salicylaldehyde caught no more beetles of either sex than unbaited traps, but this species also did not demonstrate colour preference. Male and female *T. lineatum* were also significantly deterred by the NHV. In addition, females avoided white traps, but only when the semiochemical treatment included the NHV salicylaldehyde, leading to a significant interaction between visual and semiochemical factors. Males demonstrated a similar, though weaker interaction (Table 13).

In Experiment 22, *G. sulcatus* of both sexes avoided traps with the NHV hexanol, but did not discriminate between colours for any particular semiochemical treatment (Figure 12). However, there was a significant preference for black traps when averaged over all semiochemical levels, and there was a weak additive and/or redundant effect of combining the two types of stimuli (Figure 12).

3.2.3 LARGE WOODBORING INSECTS

In Experiment 24 (Figure 14) both sexes of all three species of cerambycid beetle were significantly deterred by white traps. For *X. longitarsus* and *M. clamator*, numbers of beetles in white, baited traps were not significantly different from those in unbaited traps. Colour preference was exhibited only in baited traps for these three species, although the

FIGURE 13. Results of Experiment 21 for the sympatric, interior ambrosia beetles *Trypodendron retusum*, *T. rufitarsus* and *T. lineatum*. In the treatment combinations listed on the right, colour denotes trap colour, bait2 is the aggregation pheromone, and NHV denotes the non-host volatile blend. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.

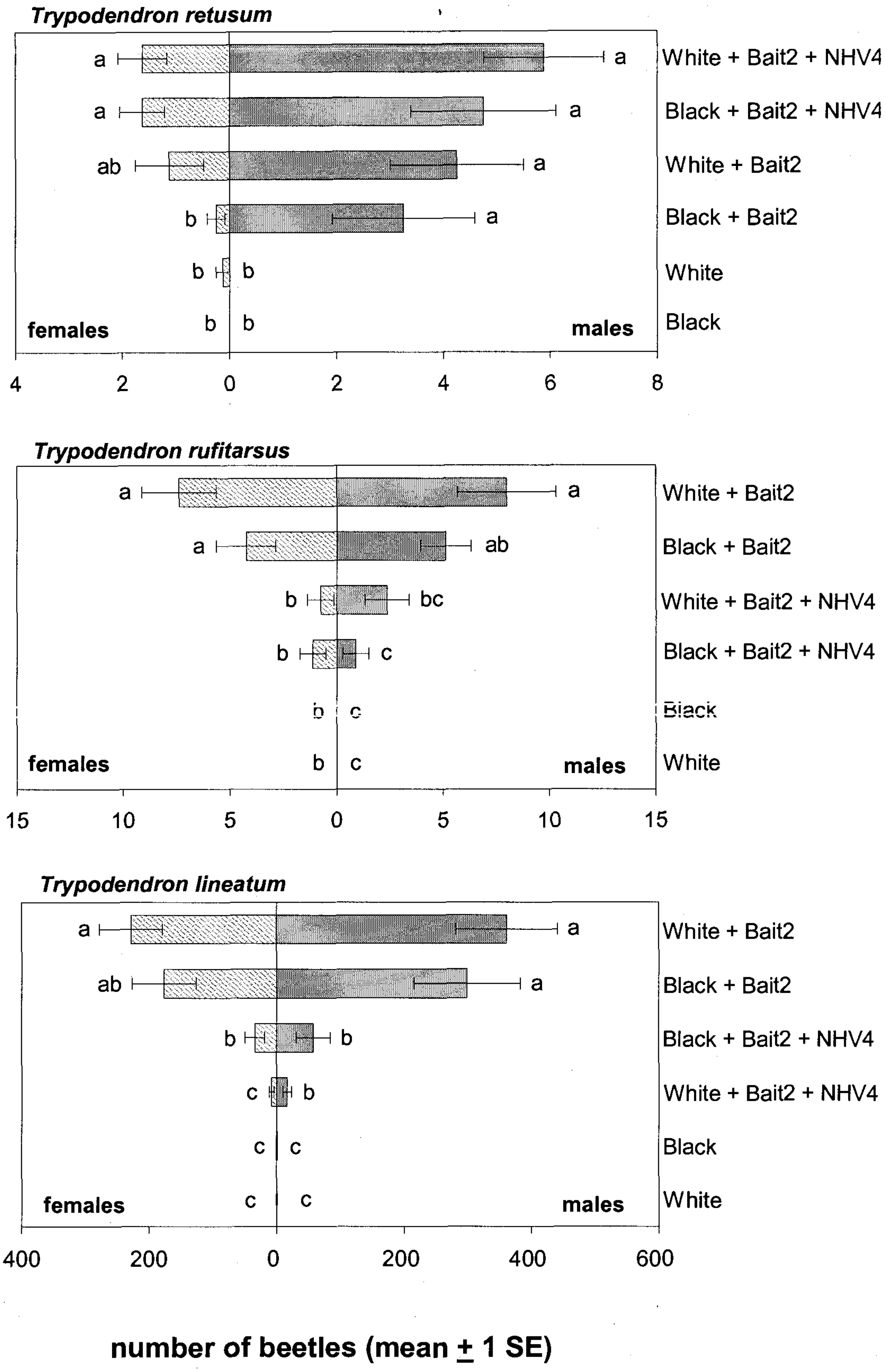

Trypodendron retusum
a
a
White + Bait2 + NHV4
a
a
Black + Bait2 + NHV4
ab
a
White + Bait2
b
a
Black + Bait2
b
b
White
b
b
Black
females
males
4
2
0
2
4
6
8
Trypodendron rufitarsus
a
a
White + Bait2
a
ab
Black + Bait2
b
bc
White + Bait2 + NHV4
b
c
Black + Bait2 + NHV4
b
c
Black
b
c
White
females
males
15
10
5
0
5
10
15
Trypodendron lineatum
a
a
White + Bait2
ab
a
Black + Bait2
b
b
Black + Bait2 + NHV4
c
b
White + Bait2 + NHV4
c
c
Black
c
c
White
females
males
400
200
0
200
400
600
number of beetles (mean ± 1 SE)

TABLE 13. Analysis of variance of the response of three interior *Trypodendron* spp. to visual and semiochemical stimuli. Experiment 20 combined two levels of a colour stimulus (black or white traps), and three levels of a semiochemical stimulus: attractive bait; bait + non-host volatile (NHV4); unbaited.

			MALES			FEMALES		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
					T. retusum			
20	Colour	1	0.0986	1.23	0.2752	0.0343	0.90	0.3488
	Semiochemical	2	2.1798	27.15	<0.0001	0.5056	13.29	<0.0001
	Colour *x* Semio	2	0.0293	0.36	0.6969	0.0263	0.69	0.5078
	Error	35	0.0803			0.0380		
					T. rufitarsus			
	Colour	1	0.1587	1.96	0.1707	0.0358	0.54	0.4659
	Semiochemical	2	2.4261	29.90	<0.0001	2.1651	32.88	<0.0001
	Colour *x* Semio	2	0.0420	0.52	0.6002	0.1374	2.09	0.1393
	Error	35	0.0811			0.0658		
					T. lineatum			
	Colour	1	0.2031	0.97	0.332	0.0932	0.41	0.5277
	Semiochemical	2	18.6922	89.06	<0.0001	15.4703	67.53	<0.0001
	Colour *x* Semio	2	0.6551	3.12	0.0566	0.9451	4.13	0.0246
	Error	35	0.2099			0.2291		

FIGURE 14. Results of Experiment 24 for the large woodboring beetles *Xylotrechus longitarsus*, *Monochamus clamator* and *M. scutellatus*. In the treatment combinations listed on the right, colour denotes trap colour, and the bait is a combination of α-pinene, ethanol and the bark beetle pheromones ispdienol and ipsenol. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.

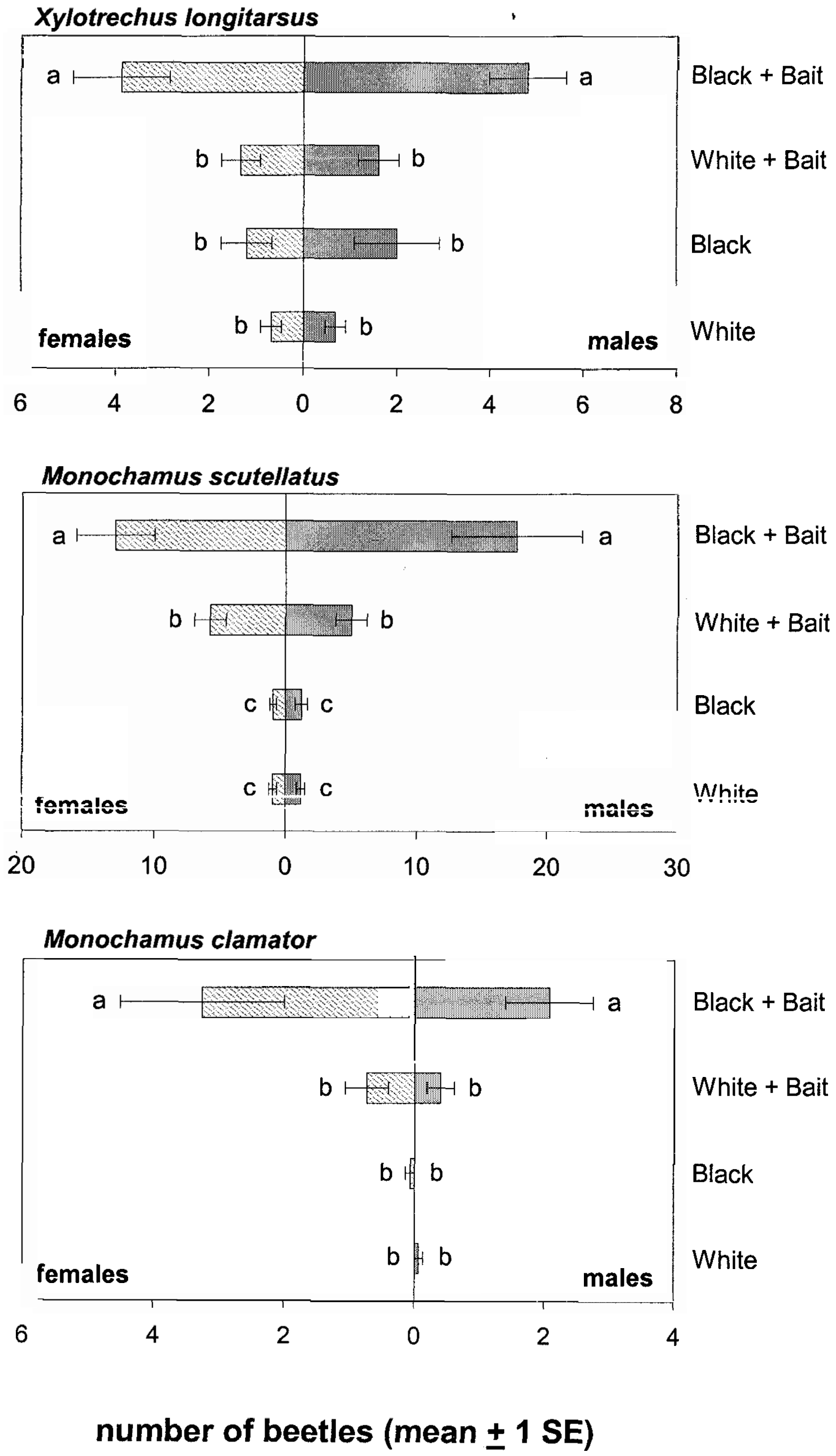
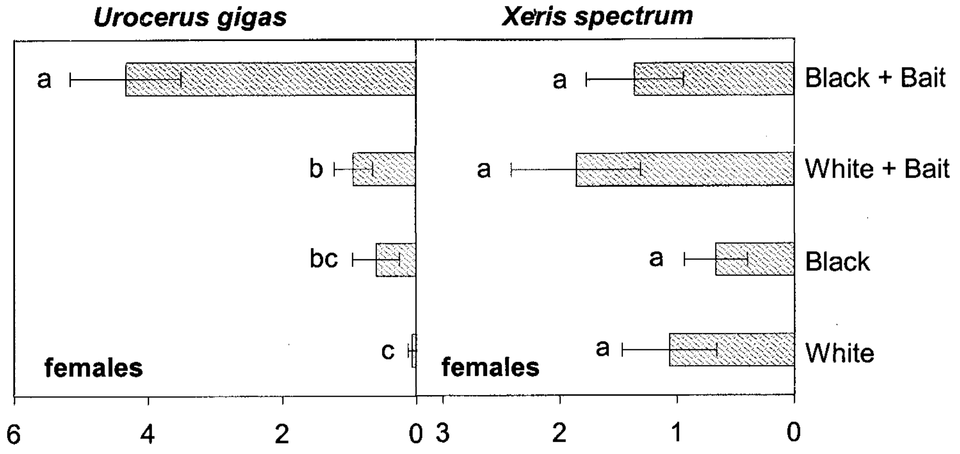

Xylotrechus longitarsus
a
a
b
b
b
b
b
b
Black + Bait
White + Bait
Black
White
females
males
6
4
2
0
2
4
6
8
Monochamus scutellatus
a
a
b
b
c
c
c
c
Black + Bait
White + Bait
Black
White
females
males
20
10
0
10
20
30
Monochamus clamator
a
a
b
b
b
b
b
b
Black + Bait
White + Bait
Black
White
females
males
6
4
2
0
2
4
number of beetles (mean ± 1 SE)

TABLE 14. Analysis of variance of the response of three large woodborers to visual and semiochemical stimuli. Experiment 23 combined two levels of a colour stimulus (black or white traps), and two levels of a semiochemical stimulus (attractive bait and no bait).

			MALES			FEMALES		
Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
					Xylotrechus longitarsus			
23	Colour	1	0.9097	21.26	<0.0001	0.3595	6.32	0.0158
	Semiochemical	1	1.1339	26.50	<0.0001	0.7507	13.21	0.0008
	Colour *x* Semio	1	0.2677	6.26	0.0164	0.2037	3.58	0.0653
	Error	42	0.0428			0.0568		
					Monochamus scutellatus			
	Colour	1	0.5056	11.61	0.0015	0.3245	6.32	0.0158
	Semiochemical	1	5.1349	117.88	<0.0001	5.7720	112.46	<0.0001
	Colour *x* Semio	1	0.7993	18.35	0.0001	0.2608	5.08	0.0295
	Error	42	0.0436			0.0513		
					Monochamus clamator			
	Colour	1	0.2337	5.93	0.0192	0.3467	7.20	0.0104
	Semiochemical	1	0.7296	18.52	<0.0001	1.2346	25.63	<0.0001
	Colour *x* Semio	1	0.3263	8.28	0.0063	0.2871	5.96	0.0189
	Error	42	0.0394			0.0482		

corresponding interaction term was only marginally significant in the case of female *X. longitarsus* (Table 14). In this experiment, catches of females of two wood wasps, *Xeris spectrum* (L.) and *Urocerus gigas* ssp. *flavicornis* (F.) (Hymenoptera: Siricidae), revealed contrasting behaviours; the former species did not discriminate among any treatments, but the latter strongly preferred black over white baited traps (Figure 15). White, baited traps were as attractive as black, unbaited traps to *U. g. flavicornis*, and more attractive than white unbaited traps (Figure 15). No male wasps were caught. Males of a round-headed borer, *Buprestis lyrata* Casey (Coleoptera: Buprestidae), were caught in higher numbers in black, baited traps than in all other treatments, although there were no differences among treatments in female catches (Figure 15; Table 15).

FIGURE 15. Results of Experiment 24 for the woodboring insects *Buprestis lyrata*, *Xeris spectrum*, and *Urocerus gigas* ssp. *flavicornis*. In the treatment combinations listed on the right, colour denotes trap colour, and the bait is a combination of α-pinene, ethanol and the bark beetle pheromones ispdienol and ipsenol. Within an experiment and sex, means followed by the same letter are not significantly different by the REGW multiple-range test.


Urocerus gigas
Xeris spectrum
a
b
bc
c
females
a
a
a
a
females
Black + Bait
White + Bait
Black
White
6
4
2
0
3
2
1
0

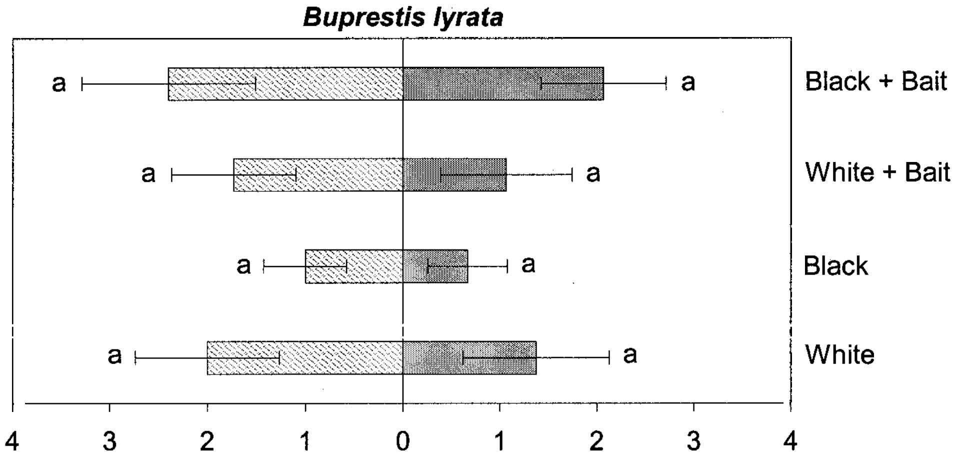

Buprestis lyrata
a
a
a
a
a
a
a
a
Black + Bait
White + Bait
Black
White
4
3
2
1
0
1
2
3
4

TABLE 15. Analysis of variance of the response of three woodboring insects (one Buprestid beetle and two Siricid wasps) to visual and semiochemical stimuli. Experiment 23 combined two levels of a colour stimulus (black or white traps), and two levels of a semiochemical stimulus (attractive bait and no bait). * Female catches only.

Exp.	Source of Variation	df	MS	*F*	*P*	MS	*F*	*P*
			*X. spectrum**			*U. gigas flavicornis**		
23	Colour	1	0.0499	1.23	0.2734	0.9685	21.88	<0.0001
	Semiochemical	1	0.1247	3.08	0.0865	1.9948	45.07	<0.0001
	Colour *x* Semio	1	0.0005	0.01	0.9131	0.3624	8.19	0.0066
	Error	42	0.0405			0.0443		
			Buprestis lyrata					
			MALES			FEMALES		
	Colour	1	0.0593	1.90	0.1756	0.0011	0.03	0.8593
	Semiochemical	1	0.1108	3.55	0.0667	0.0557	1.59	0.2138
	Colour *x* Semio	1	0.2465	7.89	0.0075	0.1375	3.93	0.0539
	Error	42	0.0312			0.0349		

4. DISCUSSION

4.1 SPECTRAL REFLECTANCE OF HOST AND NON-HOST BARK

To the human eye, bark of the species studied generally appears dark to light grey, white, or brown, lacking any higher relative reflectance in restricted regions of the spectrum that would give it a noticeable 'hue' and 'chroma' (Endler 1993). Spectral reflectance of this kind is therefore termed 'achromatic', and the spectral analysis confirmed this for most hosts and significant non-hosts examined. An exception was ponderosa pine, *Pinus ponderosa* Dougl., which was incidentally sampled and analysed (N=6), and had a peak reflectance in ca.650–670 nm (data not shown), consistent with its red-brown appearance to the human eye and with the reflectance of the related loblolly pine, *P. taeda* L. (see Strom et al. 1999). There are very few published data on the spectral reflectance of plants, and tree boles in particular. However my results are very similar to those of Lang et al. (2003), who assessed the reflectance ($\lambda = 400–2400$ nm) of daylight in the field from the bark of Scots pine, *Pinus sylvestris* L. and silver birch, *Betula pendula* Roth using a tripod-mounted spectrophotometer. The close similarity of our results also validates the ecological significance of my laboratory analyses.

Because there is no variation in hue among the various trees (e.g. one species does not appear 'green' and another 'yellow'), one would not expect these bark and timber beetles to have evolved hue-specific responses while seeking hosts (Thorsteinson 1960). This expectation is supported by Lindgren et al. (1983) who also analysed the bark reflectance of Douglas-fir and found no dominant hue, and Strom et al. (1999), who concluded that hue was unimportant to host-seeking southern pine beetles, *Dendroctonus frontalis* Zimm..

Despite the general achromaticity, there were considerable differences among tree species in the intensity of reflected wavelengths (Figure 1), particularly between conifers and the non-host angiosperms aspen and birch. Examination of the beetles' probable sensitivity maxima at 450 nm (blue) and 510–530 nm (green) (Groberman and Borden 1981, 1982), reveals that to blue and green photoreceptors, trembling aspen should appear 7.3 and 6.6 times, and paper birch 12.8 and 11.4 times brighter, respectively, than lodgepole pine. These quantitative differences in reflectance intensity could provide accurate information for discriminating between conifers and two predominant angiosperm trees in the habitats of these insects. In agreement with this hypothesis, the western flower thrips, *Frankliniella occidentalis*, is attracted to brighter shades of yellow in a positively linear fashion (Vernon and Gillespie 1990), a behaviour that may be related to the discrimination of young foliage (Jolivet 1998). The observed differences in bark reflectance may complement differences in chemical profile between conifers and angiosperms that can mediate beetle discrimination of hosts from non-hosts (e.g. Huber et al. 2000a).

In contrast to all other trees (and the trap plastics), paper birch strongly reflected short-blue and ultraviolet (UV) light (300-400 nm). Of the few studies that have examined the actual spectral reflectance of plants (e.g. Billings and Morris 1951; Kennedy et al. 1961; Gates et al. 1965; Prokopy 1983), most did not quantify UV reflectance; in fact very few plant tissues have been shown to reflect UV light at all. The flowers of several species have UV-reflecting patterns that may guide pollinators and increase pollen exchange (Kevan and Baker 1983), and the epicuticular wax blooms of cabbage, *Brassica oleracea* var. *capitata*, and onion, *Allium cepa*, reflect light down to 350 nm or near-UV (Prokopy 1983), and appear to influence landing by cabbage root maggots, *Delia radicum*, (Prokopy 1983) and onion maggots (Judd et al. 1988). Similarly, the cuticular blooms of Colorado spruce, *Picea pungens* Engelm., and blue spruce, *P. pungens* Englem. var. *hoopsii*, reflect UV light down to 200 nm, while those of Douglas-fir do not, a difference that may be related to the higher UV exposure (and potential damage) in the higher altitude spruces (Clark and Lister 1975). However, this is apparently the first demonstration of UV-reflectance from the bark of a tree. This reflectance could be the result of specular reflectance from the bark surface and/or reflectance from pigments within bark cells (Vogelmann 1993). Birches have thin bark compared to other trees, and UV-reflecting pigments may have evolved as a mechanism to prevent sunlight from damaging subcortical photosynthetic or vascular tissues (Gates et al. 1965; Clark and Lister 1975; Vogelmann 1993). Supporting an adaptive interpretation, the bark of silver birch, *B. pendula*, contains UV-absorbing phenolics that are over-expressed in response to high UV radiation (Tegelberg et al. 2002) suggesting that both reflectance and absorbance mechanisms may both function to protect birch stems from UV damage. Alternatively, UV reflectance may be pleiotropically correlated with some other bark character, and adaptively neutral. Although the beetles in this study have not been shown to perceive UV light, the possession of a UV-sensitive receptor would allow discrimination of a significant non-host angiosperm, as well as solar UV light that might provide orientation cues to dispersing beetles. For example, the white pine weevil, *Pissodes strobi* Peck, appears to respond to UV over non-UV reflecting white light, possibly to aid dispersal (Droska et al. 1983). Because no insect group has been shown to lack UV receptors, and UV-blue-green vision appears to be ancestral in pterygote insects (Briscoe and Chittka 2001), it is likely that further research would establish both the occurrence and significance of UV light detection in bark beetles.

Unlike trembling aspen and paper birch, red alder bark reflected considerably less light across all wavelengths, and in most cases, was as dark grey as lodgepole pine and Douglas-fir. Alder and all three conifers were indistinguishable from one another over 400–580 nm, although interior fir had the highest reflectance. Black traps were not statistically different in reflectance from either Douglas-fir or lodgepole pine, and thus provided good visual models for these species, but as predicted, were less so for interior fir. While no tree species reflected as intensely as the perfectly white trap plastic over the range of visible wavelengths (Groberman and Borden 1982), the high reflectance and qualitative similarity made these traps acceptable models of trembling aspen and paper birch boles. Moreover, small imperfections in the bark (e.g. lenticels in birch) would have been detected by the close range spectrophotometer as having different spectral reflectances (lowering the overall reflectance intensity), but would become more difficult to resolve with increased distance from the tree. Thus, white traps, trembling aspen and paper birch may have been even more similar in the field.

4.2 BEHAVIOURAL RESPONSES

4.2.1 BARK BEETLES

Host-seeking bark beetles should use accurate and easily assessed cues that provide ecologically relevant information on potential hosts. All three bark beetles inhabit 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 host selection (Moeck and Simmons 1991; Tunset et al. 1993; Byers 1995, 2000; Huber et al. 1999), beetles could also use the distinctive visual appearance of at least two predominant angiosperms to identify them as non-hosts (Figure 1). The prediction that beetles would prefer host model (black) traps, and avoid non-host (white) traps was consistently met for all three bark beetle species.

The avoidance of white traps by the two *Dendroctonus* species is consistent with similar results for southern and western pine beetles (Strom et al. 1999, 2001). The southern pine beetle also avoided yellow traps, but did not discriminate among black, blue, brown, grey, green or red traps (Strom and Goyer, 2001). Schonherr (1977) also found a preference for black and brown traps by both *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, baited traps.

When the visual stimulus was combined with olfactory cues of non-host angiosperms, there was an additively repellent effect, with some redundancy. This additive-redundant trend is consistent with Borden et al. (1998), Huber and Borden (2001), and Zhang and Schlyter (2003), who found that repellent non-host angiosperm volatiles acted in an additive/redundant manner when combined. These authors hypothesised that this was because beetles should have evolved a generalized avoidance of diverse angiosperm volatile blends, rather than specific responses to individual compounds or particular combinations that might deter beetles from too wide an area, and cause foragers to miss suitable hosts in heterogeneous stands. I suggest that this hypothesis should be extended to include visual and olfactory stimuli. Beetles would benefit from an integrated response to cues from both sensory modes, which would allow non-host discrimination in a greater variety of ecological contexts and spatial scales. For example, certain monoterpenes are often stereotyped as 'conifer' volatiles, while many simple hydrocarbons (e.g. green leaf volatiles) are stereotyped as angiosperm volatiles, despite the fact many of these are common to both conifers and angiosperms (Byers 2000; Huber et al. 2000a). In cases where chemical cues alone were too complex, random, or evenly distributed to allow discrimination, visual cues could act in concert with volatiles to facilitate in-flight discrimination. Redundancy of the effects of tree stimuli across sensory modes would allow beetles to switch between cues depending on their accuracy e.g., in different light environments or stand densities (Fawcett and Johnstone 2003). The results of Experiment 16 support these hypotheses: in clusters where host volatiles were evenly distributed among traps, beetles used the visual cues to decide where to land. However, beetles could also be 'persuaded' to ignore visual cues when accompanied by a putatively accurate host chemical.

In addition, the results of experiments with unnatural combinations of antiaggregation pheromones and antiaggregants + NHVs suggest that this pattern is more generalized and that beetles can combine diverse, and in some cases anomalous, combinations of repellent stimuli in an additive manner. This knowledge could be exploited in devising management tactics that incorporate diverse stimuli for different sensory modes (e.g. Epsky and Heath 1998).

The MPB exhibited the most consistent avoidance of white traps, and was also the only species which preferred black to white *unbaited* traps in the initial test of visual preference (Experiment 10; Figure 4), although the DFB also exhibited this preference in Experiment 3 (Figure 2). The ANOVA results (Tables 3-5, 8, 9) reveal that the MPB also had the least number of significant interactions of colour and semiochemical factors, suggesting that visual preferences were consistent across semiochemical treatments.

Actual independence of the two sensory modes is not implied by these results, however, given the redundant trend discussed above.

Unlike the DFB and WBBB, the MPB is also the most aggressive of the three species at high population densities, and colonises standing, living trees almost exclusively. This is in contrast to the interior DFB, which will attack both severely weakened and fallen hosts, and the WBBB, which prefers tall stumps as well freshly fallen trees (Furniss and Carolin 1977; Garbutt 1992; Humphreys 1995). Thus the MPB may have a correspondingly narrow range of attractive host profiles, and may also have highly specialised behavioural responses to these standing trees. Prokopy and Owens (1978) hypothesized that specialist foragers should have evolved specific orientation responses to host stimuli, and in particular to visual stimuli. They suggested that 'visual specialists' should be easily deterred in foraging efforts by slight deviations from their preferred host cues, while visual generalists ought to be less easily deterred. All three species, but in particular the MPB, may be examples of visual specialists. Similarly, Strom et al. (2001) concluded that the southern pine beetle was more of a visual specialist than the closely related western pine beetle, and suggested that this was because of greater aggressiveness in the former species.

There was also evidence of variation in visual responses. Female DFB, for instance, did not discriminate between black and white traps in Experiment 2 (Figure 2), although this may have been due to the low numbers of beetles captured. In Experiment 3, there were insignificant reductions of male and female DFBs in white *versus* black baited traps although both sexes preferred black to white unbaited traps, females were repelled by white traps when they were also baited with an NHV, and there was a highly significant effect of colour for both sexes overall (and no interaction; Table 3). This beetle is far less aggressive than the MPB, and particularly on the coast, colonises fallen more readily than living hosts (Atkins 1966a; Humphreys 1995). Fallen trees on the forest floor may present fewer, or less accurate visual cues than standing stems, and the use of both classes of host may explain the more variable response of this species. This may also explain the insignificant effect of colour with female *Dr. confusus* in Experiment 9. However, this experiment caught relatively few females, and was conducted after the peak flight; males caught in this experiment may have been re-emergent males seeking second hosts (L. Maclauchlan, *personal communication*). Coastal and interior DFB beetles exhibited similar stimulus preferences (Figures 2 and 3), suggesting that observed differences in host use between interior and coastal habitats have not selected for differing responses to visual or semiochemical cues in this species.

There was also evidence that the visual responses of bark beetles can be contingent on the olfactory context. For example, there were often no differences in catches in black and white traps in the absence of olfactory stimuli. However, responses to semiochemicals probably occur at distances greater than those at which beetles can visually perceive the traps (Prokopy 1986), and there was evidence that the MPB and DFB visually discriminated between black and white unbaited traps. In Experiment 8, mixed sexes of *Dr. autographus* did not discriminate between *exo*-brevicomin baited black and white traps, but did prefer black over white traps when the traps also released host volatiles (Figure 8). A similar trend was observed with *Dr. confusus* (Figure 5). Thus, visual characters may be important to these species, but only when the appropriate olfactory cues are present. These data are evidence for sensory integration while discriminating between potential hosts and non-hosts, and suggest that synergism[2] of olfactory and visual inputs during host-selection mediates landing decisions.

The evidence that visual and semiochemical stimuli interacted in a non-additive (e.g. synergistic) manner (see also §4.2.2), led to the cluster experiments, which tested the hypothesis that the MPB would demonstrate similar visual preferences when the attractive pheromones were no longer directly on the target silhouette. Experiment 15 demonstrated that MPBs would prefer black over white traps in a small area redolent with attractive semiochemicals. The low number of replicates, however, resulted in an apparently weak colour preference by male beetles in this experiment. Experiment 16 was designed to elucidate the interplay of visual and olfactory host cues, and non-host colour when the attractive pheromones were decoupled from the 'tree' stimuli. The results (Figures 9, 10) clearly confirm that the mountain pine beetle 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.

First, long range attraction to groups of target silhouettes is mediated by an attractive kairomone (myrcene), consistent with the general expectation (Dethier 1982; Prokopy 1986) that olfactory cues mediate long-range behavioural responses. There were exactly twice as many 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 treatments with myrcene only on one trap colour, and significantly lower catches (generally <1 beetle on average) in clusters without myrcene

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[2] I define 'synergism' in a general sense, as the phenomenon of a combination of treatments having a non-additive effect detectable as a significant factorial ANOVA interaction (Sokal and Rohlf 1995; Slinker 1998). This definition does not depend on the magnitude or direction of the effect (i.e. attraction *vs.* repellency).

(Figure 9; Table 10A), suggesting that neither the two bark beetle pheromones, nor the traps are attractive in the absence of an appropriate host olfactory stimulus. Myrcene is not the only host volatile that synergises the attractiveness of *exo*-brevicomin and *trans*-verbenol (Billings et al. 1976; Miller and Borden 2000), and is found in low quantities in lodgepole pine bark and foliage (Pureswaran and Borden 2004), however it provided a suitable model stimulus for testing the importance of visual stimuli. These results suggest that the increased release of myrcene caused greater attraction of beetles to clusters, or caused greater arrestment of beetles orienting to the centrally placed pheromones, and the dose-dependent effect of this host volatile corroborates previous experiments (Borden et al. 1987; Miller and Borden 2000; Lindgren 2003 *personal communication*).

Having responded to (and potentially entered) a cluster, beetles apparently choose to land by integrating visual and olfactory information. In clusters with myrcene on traps of both colours, (i.e. where semiochemical information was equal among traps), beetles chose black traps more often than white (Table 10B; Figures 9, 10). Similar discrimination was exhibited in clusters with myrcene on black traps only (Table 10B), 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 catches in white traps in the control clusters (Figure 9). However, in clusters with myrcene on white traps only, there were equal catches of beetles in black and white traps (Table 10B; Figure 9), indicating that discrimination using a visual stimulus can depend on the presence of kairomones, which may be more accurate host cues, and override visual stimuli even within the close range of the cluster. A complementary interpretation is that the attractiveness of this chemical was exactly negated by the repellency of the non-host (relative to the host) visual cue. Similar numbers of beetles were caught in myrcene-on-black and myrcene-on-white clusters, supporting the hypothesis that integration occurred within, rather than outside the cluster.

The significant effect of treatment on the percent difference between black and white traps (Figure 10; Table 10A) also supports the hypothesis that visual and olfactory information is integrated during landing decisions. Males demonstrated the greatest discrimination when host volatile and visual stimuli were combined (clusters with myrcene on black traps only) (Figure 10), further supporting the hypothesis that beetles assessed individual traps for both olfactory and visual information within the 2.5 m radius clusters. Conversely, females preferred black over white traps to the same extent whether myrcene was on all four traps, or only black traps (Figure 10). The reason for this difference remains unclear. Females may process information at a different scale than males, i.e. at a greater distance. Alternatively, just as there is redundancy in the putative non-host message, there may also be redundancy in the host stimulus message. Females may 1) orient to host odours, 2) perceive visual stimuli (black trap, tree) associated with those odours (e.g. outside the cluster) and 3) decide to land, with subsequent olfactory cues within the cluster being redundant. In clusters with myrcene only on white traps, this sequence of stimulus integration would have been disrupted 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 and Michael 1973; Ryker and Rudinsky 1976). Females, on the other hand, are probably the sex with the greater reproductive investment, and might benefit more from avoiding the costs of close-range 'fly-by' assessment once the appropriate combination of visual and olfactory stimuli had been perceived. Overall, while the MPB clearly exhibits marked visual and olfactory preferences, it is capable of integrating both types of stimuli in making the decision to land on a target.

Models of host selection have speculated that bark beetle landing decisions are either 1) based on assessment of potential host quality (e.g. Gries et al. 1989), or 2) are random before (e.g. Byers 1996) or after (Payne 1986) initial attraction to olfactory stimuli such as aggregation pheromones. In the case of the MPB, non-host volatiles can *disrupt* responses to aggregation pheromones (Borden et al. 1998), and the results of Experiments 10-12 (Figure 4) demonstrate clearly that a putative non-host visual stimulus can also disrupt beetle responses to pheromones. The results of Experiment 16 also suggest that beetles could enter a mixed stand of pine and non-host angiosperms that contained a beetle-attacked tree (and was redolent with pheromones), and orient to individual trees using vision, but could also assess the trees within the stand at relatively close flying range using olfaction.

Similar hypotheses have been suggested for several other insects. For example, Jang et al. (2000) concluded that the parasitic wasp *Diachasmimorpha longicaudata* (Ashmead) utilises olfaction at long range, visual cues at mid range, and at close range, makes a final olfactory assessment that mediates actual landing on fruit likely to contain host fruit flies. The dipteran parasitoid *Apocephalus paraponerae* Borgmeier orients to host visual cues (body size), but final host acceptance (Wood 1982a) is mediated by short range detection of, or contact with, epicuticular hydrocarbons (Morehead and Feener 2000). Plum curculios, *Conotrachelus nenuphar* (Herbst), also use visual cues, but ultimately locate host fruit using close range odours (Butkewich and Prokopy 1993). Finally, 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 (i.e. numbers of fruit in a cluster on a branch) however, flies start to integrate olfactory cues (Aluja and Prokopy 1993).

Where chemical cues are more accurate host indicators, insects would benefit from prioritizing olfactory information up to the point of landing, as seen in Experiment 16. This is the first time this ability has been shown for bark beetles, and the results: 1) refute the hypothesis that the MPB relies on a random landing mechanism to locate suitable hosts in this context (cf. Byers 1996), and 2) implicate a flexible continuum of sensory integration, with various modes predominating at, rather than restricted to (e.g. Lanier 1983), different stages of the host selection process.

4.2.2 AMBROSIA BEETLES

In contrast to the bark beetles, none of the ambrosia beetles strongly avoided white traps in the initial experiments, and overall, did not demonstrate strong colour-based discrimination among traps. Visual cues may not figure as prominently during host selection by these beetles. One reason for this may be that ambrosia beetles do not consume plant tissues directly, and have a wider host range than bark beetles because of the polyphagous nature of their symbiotic fungi (Beaver 1989; Shore 1998). As relative generalists, ambrosia beetles may not have evolved strong, specific responses to visual cues (Prokopy and Owens 1978). In addition, ambrosia beetles almost always colonise fallen host trees (Shore 1998; but see Kühnholz et al. 2001 for exceptions). Having fallen, a host stem would lie among other fallen trees on a variety of substrates on the achromatic forest floor (Endler 1993), and due to the poor chromatic contrast between the substrate and the stem, a fallen tree might not provide useful colour information to a flying beetle as to its identity or suitability. Furthermore, although many of their host conifers are visually quite similar (Figure 1), host characteristics important to ambrosia fungi may require olfactory assessment (e.g. ethanol concentration, Kelsey and Joseph 1999). Organisms are predicted to balance the assessment costs and accuracy of different cues when using them (Fawcett and Johnstone 2003). Olfactory cues such as ethanol and α-pinene concentrations (Graham 1968; Vité and Bakke 1979; Kelsey and Joseph 1999) may be sufficiently accurate to flying ambrosia beetles searching the forest floor, and may be economical to assess if host discrimination is accomplished in flight. The cost of landing to discriminate visually between hosts and non-hosts at close range also may have selected against the evolution of visual discrimination (Endler 1992). Finally, coastal *T. lineatum* are most likely to encounter red alder as a predominant non-host, which, unlike trembling aspen and paper birch, is similar to host conifers (Figure 1), lowering the utility of visual discrimination in this habitat.

Interestingly, the DFB has, on average, 42% more ommatidia than *T. lineatum* (Chapman 1972). Although these measures did not correct for body size (there was a weak, positive correlation between body length and ommatidia number for the DFB in this study), it is possible that the evolution of strong olfactory host finding mechanisms in this ambrosia beetle may have constrained the evolution of certain visual apparatus (e.g. ommatidia), or that these anatomical differences are related in some other way to host location or dispersal behaviours. Further work is required to test this hypothesis, and it should be noted that *Dr. autographus* has even fewer ommatidia than *T. lineatum* (Chapman 1972).

The fact that visual cues were not used as obviously by ambrosia beetles as by bark beetles does not mean that the former do not use visual cues. In the case of *G. sulcatus* (Experiment 22), there was a significant model effect of colour for both sexes (Table 13), but this effect was too weak to cause significant differences between black and white traps for any semiochemical treatment. With *T. lineatum*, there was strong evidence that reliance on visual cues depends on the presence of appropriate semiochemical cues. In Experiments 18 and 20, neither sex discriminated between black and white traps baited with the pheromone lineatin alone (Figures 11, 13). However, males in both Experiments 17 and 19 preferred black to white traps when the attractive baits comprised lineatin with the host kairomones α-pinene and ethanol (Table 11; Figure 11). Similarly, males preferred black over white traps in Experiment 8 ($F_{1,40}$=5.88, P=0.02), and marginally so in Experiment 9 ($F_{1,61}$=3.6; P=0.06) when the traps were baited with the WBBB pheromone *exo*-brevicomin[3]. Thus, beetles may orient to tree visual cues only when they are accompanied by certain kairomonal (as opposed to conspecific) semiochemical cues, a finding that supports a similar hypothesis by Vité and Bakke (1979; see also Kerck 1972) and corroborates results of Borden et al. (1982) and Lindgren et al. (1983). Results from experiments 17–20 suggest that visual and semiochemical host cues are used in an integrated (synergistic) fashion, with visual responses being contingent on olfactory context.

Complementing these results is evidence that interior *T. lineatum* did avoid the non-host visual cue when it was accompanied by a specific, corresponding non-host semiochemical cue. In Experiment 20, white traps were only repellent when the

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[3] *Exo*-brevicomin (a putative kairomone) was attractive to both male ($F_{1,40}$=20.79, P<0.0001) and female ($F_{1,40}$=4.12, P=0.049) *T. lineatum* in experiment 8 (*cf.* Tømmerås and Mustaparta 1989).

semiochemical treatment included the non-host volatile salicylaldehyde (Figure 13). Beetles did not discriminate between trap colours for the other two treatments, and the resulting interaction of semiochemical × visual factors was significant for females, and marginally so for males (Table 13). Thus, the use of a visual cue to avoid non-host angiosperms may depend on the detection of a complementary olfactory stimulus such as salicylaldehyde, which is a volatile of angiosperm, but not conifer bark (Huber et al. 2000a; Zhang et al. 2000a; Pureswaran and Borden *unpublished data*). This cue would presumably be more accurate than a visual stimulus, but the combination may be even more accurate to foraging beetles. Supporting this hypothesis is the finding of Kerck et al. (1978) that beech-infesting *T. domesticum* (Olivier) preferred white to black stem models baited with ethanol. These results suggest the hypothesis that there is a synergism between olfactory and visual cues in the attraction to hosts *and* avoidance of non-hosts by *T. lineatum*, with visual responses being contingent on olfactory information in both cases. This is apparently the first evidence of a synergistic interaction of visual and semiochemical cues to *reject* a non-host.

My results do not support Dubbel et al. (1985), who found that both sexes of European *T. lineatum* were significantly deterred from landing on white, pheromone-baited traps. Reasons for this difference could be phylogeographic differentiation between ecotypes of *T. lineatum*, as proposed by Borden et al. (1982) based on different responses to attractive semiochemicals by *T. lineatum* in B.C. and the United Kingdom, or the fact that Dubbel et al. (1985) used flat barrier traps unlike the vertical traps used in this study. In addition, the bait used in that study (LINOPRAX®) was a blend of 0.04 % lineatin, 2.4 % α-pinene, with the balance being an uncharacterized mixture of water and ethanol (Grégoire 2004 *personal communication*). The addition of the host olfactory stimuli may have elicited a colour preference as in Experiments 8, 17 and 19 for male *T. lineatum* (Figure 11).

Finally, with respect to *Gnathotrichus sulcatus*, it should be noted that the closely related *G. retusus* (LeConte) has recently been observed colonising red alder (Kühnholz et al. 2000) and may also colonise *Populus trichocarpa* Torr. & Gray (Wood 1982). Wood (1982) suggests that there may in fact be a sister species to *G. retusus* which infests red alder. If there is a wider range of hosts (and host stimulus profiles) among subspecies or ecotypes in this genus than previously thought, this may have constrained the evolution of specific visual and olfactory host selection behaviours. This hypothesis is supported by the finding that some green leaf volatiles enhance, while others disrupt, *Gnathotrichus* responses to pheromones (Deglow and Borden, 1998a,b).

4.2.3 LARGE WOODBORING INSECTS

My results show that both sexes of all three cerambycid species use vision when deciding to land on attractant-baited silhouettes (Figure 14). Catches of *Monochamus clamator* and *Xylotrechus longitarsus* in white, baited traps were not significantly different from those in unbaited traps. *Urocerus gigas flavicornis* (Hymenoptera: Siricidae), also avoided white, baited traps, extending the range of coniferophagous insect orders known to respond to visual cues. Like the ambrosia beetles, these large woodborers are polyphagous, and often colonise fallen trees and logs (Furniss and Carolin 1977; Hanks 1990), and yet unlike the ambrosia beetles, they exhibited a strong visual preference. However, many large woodborers also rapidly colonise standing trees damaged by fire or bark beetles (Allison et al. 2004), and these trees may provide more prominent visual cues. Also in contrast to the ambrosia beetles, large woodborers do not rely on fungal symbionts (and thus may have a more narrow range of acceptable host stimulus profiles) and are not known to use aggregation pheromones to locate host material, relying instead on general host semiochemicals such as α-pinene, ethanol (Chénier and Philogène, 1989) or phloeophagous bark beetle pheromones (Allison et al. 2001, 2003). This reliance on tree-produced cues may include a visual component that would allow adaptive discrimination of host conifers and non-host angiosperms.

4.3 GENERAL REMARKS

4.3.1 POTENTIAL OBJECTIONS

There are three possible objections to an ecological interpretation of white trap avoidance as an indication that beetles could potentially use similar visual cues to avoid certain non-host trees.

Lack of apparency

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 electroretinal sensitivity maxima for blue and green wavelengths (Groberman and Borden 1982), which are reflected abundantly from the white traps (in contrast to the black traps). Second, two of these beetles, the Douglas-fir beetle and *T. lineatum*, both oriented *toward* sources of blue and green light in laboratory bioassays of walking beetles (Groberman and Borden 1981), yet exhibited contrasting behaviours in my field experiments. Finally, even when black traps were preferred to white traps, there were often large numbers of beetles caught in white traps, indicating that some beetles chose to land there.

Colour-dependent bait volatility

Theoretically, lower relative catches in white traps might have occurred due to differential trap temperatures affecting the volatility of the attractive baits. As confirmed by the spectral analyses (Figure 1), black traps absorbed considerably more visible (and presumably far-red and infrared) radiation than white traps. If these differences resulted in black traps having relatively higher temperatures, this could have increased bait volatility, possibly explaining the behavioural differences. However, if this were true, one would predict the same response to white traps by all species, which clearly did not occur. In addition, Strom et al. (1999) found no difference in elution rates of southern pine beetle baits from black and white painted, Lindgren multiple-funnel traps, suggesting that any colour-specific temperature differences do not influence bait volatility in a systematic fashion.

Correlation of trap and tree spectra

Another possible objection pertains to the greater reflectivity of white traps than trembling aspen and paper birch bark, and to the suitability of these traps as mimics of non-host boles. 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. Such aberrations would probably not be resolvable at a greater distance by a flying beetle prior to landing. In addition, Strom and Goyer (2001) caught low, but similar numbers of southern pine beetles in both white and yellow traps, and postulated that it was the high intensity of these trap hues which was repellent. To a green photoreceptor responding maximally at 530 nm, the yellow paint used in that study would have a relative intensity of ca. 0.43, while paper birch and trembling aspen have reflectance intensities of 0.57 and 0.34 at that wavelength, respectively (Figure 1). The similar trap catches in both yellow and white traps, and the fact these yellow traps had a peak reflectance intensity more closely approximating that of the principal non-host angiosperms examined in this study, support an ecological interpretation of my data.

4.3.2 SENSORY INTEGRATION DURING HOST SELECTION

My results demonstrate that coniferophagous bark and woodboring beetles are able to integrate both visual and olfactory cues, and respond in a putatively adaptive manner. In particular, the synergism of olfactory and visual tree stimuli shows that several species are capable of more complex discrimination than previously thought. Relatively few studies have aimed to characterize sensory integration. Chiussi and Diaz (2001) found that fiddler crabs, *Uca cumulanta* Crane, exhibited visually mediated escape behaviour only in the presence of chemical cues associated with predators. However, these authors used visual stimuli (flat shapes) that did not have natural analogs, and did not simultaneously test both olfactory conditions. The leafhopper *Dalbubus maidis* (DeLong and Wolcott) is attracted to both green and yellow light, and host maize volatiles synergise the attractiveness of green light to this species, while volatiles of marginal hosts and non-hosts do not (Todd et al. 1990b). Mathieu et al. (1996) found a significant ANOVA interaction between visual and olfactory cues in mesh cage trapping experiments with the coffee berry borer, which strongly preferred red to white traps, but at particular doses of attractive semiochemicals. Finally, when the haematophagous bug *Triatoma infestans* is presented with a pair of patches, (one black, one coloured), it aggregates preferentially on black patches for shelter (Reisenman et al. 2000). However, when presented with black, empty patches and red patches with conspecific faecal scent cues, bugs prefer the red cues; when blue is substituted for red, visual preference is negated (equal); and when faecal cues are on both the coloured and black patches, bugs revert to using the visual cue, and prefer the black (Reisenman et al. 2000). These results, while compiled from several separate experiments, suggest that olfactory and visual cues operate synergistically for this bug; they also correspond extremely well with the results of Experiment 16 (Figures 9, 10), in which beetles also used visual cues when olfactory cues were equal among traps, and in which the visual preference could be overridden by a host olfactory cue.

Other studies have focused on responses in individual sensory modes, and have failed to appreciate multi-modal integration even with supporting data. For example, Epsky et al. (1995) observed indications of visual-olfactory synergism in the Mexican fruit fly, *Anastrephus ludeus* (Loew), which had different trap colour preferences when the bait release device was different, but did not analyse their data to test this finding, e.g. by using a factorial model (Slinker 1998). Similarly, Chapman et al. (1981) had evidence for colour-dependent attraction of aphids, *Cavariella aegopodii* (Scopoli), to the host monoterpene carvone, although they did not test this hypothesis in their analysis. Drost and Cardé (1992) found that the gypsy moth parasitoid *Brachymeria intermedia* (Nees) learned to associate host presence with host habitat visual cues (tree mimics), but also did not attempt to elucidate the interplay of visual and potential semiochemical cues. Teulon et al. (1999) concluded that there was no chemically induced visual response in the western flower thrips. However, there was strong evidence (and a significant ANOVA interaction between sensory modes) for a *visually* induced olfactory preference. Greenhouse thrips discriminated between baited and blank traps (i.e. using olfaction) when the visual cue was a black trap, but not a yellow trap. Yellow is a potentially "supernormal" foliage cue (Moericke 1969; Prokopy and Owens 1983) and may be more important than semiochemicals during host finding by this species, which may use olfaction in the absence of a suitable visual stimulus.

The study of sensory integration by foraging insects can provide unique insight into host selection by many species, and could suggest novel management tactics for pests (e.g. Epsky and Heath 1998). My results add to this small, and slowly growing body of literature that has tested (rather than simply alluded to) the complex interdependence of stimuli in different sensory modes. To focus on one sensory mode to describe host selection by insects, as many investigators do, is to reduce a multidimensional phenomenon to one dimension. Such an approach fails to appreciate both the complex information that insects must process while foraging, and the full range of behaviours that may ensue.

4.4 CONCLUSIONS

1. My results show that foraging bark beetles could utilise visual information to avoid non-hosts, can combine non-host visual and semiochemical cues in an additive manner, and can respond differentially to visual cues depending on the olfactory and

ecological contexts. This is consistent with their specialised host use (Prokopy and Owens 1983).

2. Experiments with the MPB demonstrate that this species does not land randomly on vertical silhouettes after having responded to aggregation pheromones (Gara et al. 1965; Hynum and Berryman 1981), but rather integrates visual and olfactory cues. I have further shown that this species can process a host olfactory cue emanating from a target silhouette at relatively close range, suggesting that beetles may in fact prioritize olfactory cues when deciding to land. These results are consistent with the expectations of an optimally foraging insect (Pyke et al. 1977), even in the context of extreme population densities, but counter the hypothesis that the MPB finds individual hosts in a random manner (e.g. Byers et al. 1996; Pureswaran and Borden 2004). Foraging tactics of this species may be far more complex and integrated than previously thought.
3. My results indicate that ambrosia beetles do not use visual cues as prominently as bark beetles. This is consistent with their patterns of host use, and the type of information they might encounter while searching for those hosts.
4. In the case of *Trypodendron lineatum*, I have shown that a non-host visual cue is repellent only in the presence of a non-host olfactory cue, and that visual discrimination in this species may, in general, be contingent on olfactory inputs. This is apparently the first evidence of a synergistic integration of stimuli to *reject* a non-host.
5. All the target woodboring cerambycids and a woodboring wasp strongly avoided white traps. While these species have similar host ranges to the ambrosia beetles, the woodborers do not use pheromones to communicate host suitability, and may rely

more on tree-produced cues (host odour and visual appearance, and the odours of intraguild bark beetles) to orient to hosts.

6. I contend that host selection by all these beetles apparently relies on the total stimulus profile ('gestalt') of the target silhouette, a rarely tested assumption of foraging insects.
7. Finally, I advise that tests of sensory integration and synergism between modes should endeavour to use factorial designs (or a similar technique, e.g. Nelson and Kursar 1999), to allow comparisons among all combinations of stimuli, and permit detection of synergistic interactions among stimuli.

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