Host preference by *Saperda calcarata* Say (Coleoptera: Cerambycidae)

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ABSTRACT

We conducted five laboratory and one field experiments to examine potential host selection mechanisms of *Saperda calcarata* Say in British Columbia. Olfactory bioassays indicated that female (and possibly male) beetles were attracted to volatiles from leafy twigs of trembling aspen, *Populus tremuloides* Michaux. However, wounding of the bole, ethanol baiting, or both, did not result in significant orientation toward or attack of trembling aspens in the field. Feeding preferences for trembling aspen were strong for both sexes in choice bioassays, but in no-choice bioassays, females did not discriminate between trembling aspen and black cottonwood, *P. trichocarpa* Torrey & Gray. Scouler's willow, *Salix scouleriana* Barrat in Hooker, was fed upon the least by both sexes. When diameter of bolts offered as oviposition hosts was equalized, frequency of oviposition was similar among the three hosts. Our data suggest that feeding preference is the predominant mechanism of host selection by *S. calcarata*.

INTRODUCTION

The poplar borer, *Saperda calcarata* Say (Coleoptera: Cerambycidae: Lamiinae) attacks living poplars from the sections Populus (*P. tremuloides* Michaux, *P. alba* L., *P. grandidentata* Michaux), Aigeiros (*P. deltoides* Bartram, *P. fremontii* Watson, *P. nigra* L. 'Italica'), and Tacamahaca (*P. angustifolia* James, *P. balsamifera* L., *P. trichocarpa* Torrey & Gray) throughout their range in North America (Hofer 1920, Baker 1972, Drouin & Wong 1975, Nebeker *et al.* 1985). The beetle also attacks poplar hybrids (*P.* x *acuminata*) (Hofer 1920) and willows (Baker 1972). *Populus* spp. are susceptible from approximately three years of age (Abrahamson & Newsome 1972), or 4-5 cm diameter at breast height (dbh = 1.3 m) (Hofer 1920, Drouin & Wong 1975, Nebeker *et al.* 1985). *Saperda calcarata* adults reportedly discriminate among poplar hybrids for feeding (Garland & Worden 1969) and there are differences in attack rates among *P. deltoides* clones (Nebeker *et al.* 1985).

In British Columbia (BC), *S. calcarata* adults emerge in late June to July, undergo a short period of maturation feeding (Linsley 1959) and mate. Females oviposit into oblong niches chewed in the bark of host trees. Young larvae mine in the inner bark and sapwood, then move deeper creating large, irregular galleries throughout the sapwood and heartwood (Hofer 1920). Frequently a single tree is repeatedly attacked forming a 'brood' tree. Attacked trees are identified by their deformed bole, oviposition scars, sap stains spreading down the bark, and frass piles at their base. The life cycle takes three to four years in Canada, but is probably shorter in the south (Hofer 1920, Peterson 1947, Baker 1972).

Saperda calcarata is considered a major pest of poplars (Solomon 1987) and frequently becomes prevalent within stands (Bird 1930, Nebeker *et al.* 1985). Physical damage to the boles from larval galleries makes trees susceptible to breakage. Openings from oviposition niches and woodpeckers lead to increased incidence of pathogens like *Hypoxylon mammatum* (Wahlenberg) Karsten (Graham & Harrison 1954) or *Phellinus tremulae* (Bondartsev)

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Bondartsev & Borisov (Hofer 1920) which girdle the bark or stain and rot the wood, and attacked trees may be further damaged by other insects, e.g., *Agrilus anxius* Gory or *Poecilonota cyanipes* (Say) (Hofer 1920).

Because attacks by beetles may be prevalent in poor sites, e.g., dry slopes (Hofer 1920, Bird 1930, Morris 1963), or in decadent hosts (Graham & Harrison 1954), *S. calcarata* is assumed to prefer weakened hosts that remain alive during attack (Hanks 1999). In agreement with this hypothesis, less attack was observed on *P. deltoides* clones from southern provenances which grew most vigorously (Nebeker *et al.* 1985). In contrast, Baker (1972) noted that brood trees were larger and faster growing than neighbouring trees, and Abrahamson & Newsome (1972) concluded there was no difference in attack level on different quality sites. Olfaction is generally believed to play a large role in cerambycid host location (Linsley 1961, Hanks 1999, Allison *et al.* 2004).

We commonly observe *S. calcarata* attack in trembling aspen, *P. tremuloides*, in BC, but not in black cottonwood, *P. trichocarpa*, or willow, *Salix* spp. Our objectives were to determine: if olfactory attraction occurs to trembling aspen, the apparent preferred host, and if there are different levels of feeding or oviposition among these three hosts.

MATERIALS AND METHODS

Saperda Colonies. We collected ca. 2.5 m³ *S. calcarata*-attacked trembling aspen bolts from trees felled near 70 Mile House, BC in April or May of 2002 to 2004. Adults emerged from the caged bolts during June and July for two successive years. A total of 76 and 101, 46 and 30, and 11 beetles emerged each year from bolts harvested in 2002, 2003 and 2004, respectively. Timing of emergence was in agreement with Garland & Worden (1969). Adults were kept on aspen branches in water in 1.2 x 1.8 x 0.6 m outdoor enclosures until used in bioassays. Beetles were used once in any one type of bioassay, except for feeding bioassays in 2002, when tested beetles were returned to the holding cage from which test subjects were removed.

Plant material. Leafy aspen branches were collected periodically, mostly from various interior BC locations, but also from Burnaby and Maple Ridge on the coast. Branches were kept with the cut ends in water at 4 °C, and used in bioassays within one week. Both Scouler's willow, *Salix scouleriana* Barrat in Hooker, and black cottonwood branches were collected in Burnaby, BC the same day bioassays were performed. In total, four to five genotypes of each species were tested.

Olfaction experiments. In 2003 and 2004, responses to volatiles were investigated in the laboratory using a still air olfactometer (Figure 1). Randomly assigned treatment and control jars contained either a small jar of water with a small, leafy branch of aspen, or just water, respectively. The arena ceiling was a sheet of clear Lexan (GE Polymershapes, Coquitlam, BC). A video camera was positioned above the arena. To induce the photopositive beetles to approach the stimuli, a fluorescent light was placed under the platform between the two jars. The entire apparatus was covered with a black cloth. Three to five adults of a single sex taken directly from the holding cage were placed into each arena. Presence of beetles in the concentric rings above the treatment or control jars were determined at 30 sec intervals for 2 h. Fourteen trials were recorded. Feeding damage to the perforated centres above control and treatment stimuli was assessed for both recorded and unrecorded trials. Jars were washed and the paper covering replaced before each assay. Assays commenced any time between 0800 and 2400 h.

A field experiment was set up in a trembling aspen grove near Sabiston Lake, northeast of Savona, BC, on 28 June, 2002. Apparently healthy trees, spaced approximately 20 m apart, received one of four treatments in a randomized block design (n = 14): 4 axe cuts on opposite sides of the
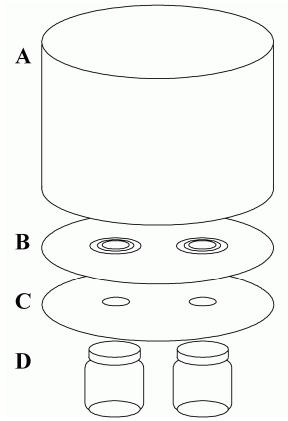
Figure 1. Schematic of olfactometer used to test olfactory responses of *S. calcarata* to trembling aspen leaf volatiles. A 60 cm diameter circular arena consisted of a black cylinder 60 cm high (A) placed on a white coroplast (GE Polymershapes, Coquitlam, BC) platform (C) with two holes, 5.5 cm in diameter with centres 28 cm apart. This platform was covered with white paper (B) perforated 41 times with a pin in a uniform, radial pattern above the openings. Three concentric rings 5.5, 12.5, and 19.5 cm diameter were drawn on the paper (B) above each hole. The platform (C) rested on glass cookie jars (aperture 11 cm diameter) (D), centred below each hole.

tree at ca. 1.5 m; ethanol bait stapled at ca. 2 m; 4 axe cuts plus ethanol bait; or no treatment. Ethanol is a ubiquitous kairomonal indicator of stressed trees (Kelsey & Joseph 1998 and references therein). The basal 3 m of the trees were examined for oviposition in 2003 and 2004.

Feeding bioassays. Choice and no-choice feeding bioassay experiments were performed to investigate feeding preferences of *S. calcarata* among trembling aspen, black cottonwood and Scouler's willow. Three small branches, each with three to five leaves, were placed in water-filled vials inside 17x16x12 cm plexiglass boxes. A single *S. calcarata* adult was allowed to freely feed on plant material overnight. No-

choice bioassays contained one of the three potential hosts, and choice bioassays contained one branch of each. Before an assay, the leaves were traced onto paper. After the bioassay ended, leaves were attached to their traced counterparts, scanned, and the leaf area consumed was quantified using Scion Image software (Scion Corporation, Frederick, Maryland). A total of 17 choice and 14 no-choice bioassays were performed during July of 2002 and 2003.

Oviposition bioassays. In 2002 we tested oviposition by *S. calcarata* in holding cages on eight freshly cut bolts of varying diameter of each of the above three species. In 2003, two apparently healthy trembling aspen, black cottonwood, and

Scouler's willow trees of similar diameter were felled on 1 and 18 July 2003, bucked and transported to SFU where they were kept refrigerated until needed. Six to eight beetle pairs were placed in 13 outdoor cages, 90 x 90 x 90 cm, with one randomly positioned bolt of each species and a central water jar containing leafy trembling aspen branches for seven days. Bolts were ca. 50 cm in length, and diameters taken from their midpoint. Oviposition was determined in both experiments by opening all niches cut in the bark.

Statistical analyses. In all cases α = 0.05. For olfaction bioassays, one-tailed paired t-tests were used to determine if the frequency of observations in each of the concentric rings was greater over treatment than control jars. Chi-square tests were performed for each sex to compare the frequency of feeding damage above treatment *vs.* control stimuli against the null hypothesis of no discrimination between stimuli. Data from feeding and oviposition bioassays were transformed by $x^{\frac{1}{2}}$ and $\log(x+1)$, respectively, to correct for non-normality and heteroskedasticity, then analyzed as randomized complete blocks by ANOVA with PROC GLM (SAS Institute 1990). Because it was not possible to perform all no-choice feeding assays at the same time, the analysis included trial date and host species effects. The final model did not include interaction effects. Multiple comparisons were performed with REGWQ (SAS Institute 1990).

RESULTS

Olfaction experiments. There were no differences in the occurrence of beetles in the middle and outside rings bordering the perforated area above treatment (i.e. trembling aspen leaves) and control stimuli for both sexes (middle ring, females, t = 0.69, $P = 0.26$, males, t = -0.80, $P = 0.23$; outer ring, females, t = 0.76, $P = 0.24$, males, t = 0.95, $P = 0.19$). Females (but not males) were present more frequently above the treatment than the control stimulus (Table 1). Often, females and males fed on the perforated paper directly above the treatment stimulus, but in one instance females fed above the control as well (Table 1). Females also chewed curvilinear patterns in the paper covering the arena floor that were reminiscent of oviposition niches, but no eggs were found.

Very few attacks were found on trembling aspen treated to release host volatiles (axe cuts) or baited with ethanol. A total of 8 oviposition chambers in two replicates were found: 1 niche on an ethanol-treated tree; 1 and 3 niches on two axe-cut trees; 2 and 1 niches on two trees with both treatments and none on control trees. None of these niches developed into successful larval galleries.

Feeding bioassays. We observed feeding on both the petioles and leaves as did Garland & Worden (1969), but only quantified the more abundant foliar damage. When given a choice (Figure 2), both sexes clearly preferred trembling aspen over both black cottonwood and Scouler's willow (females $F_{2,32} = 41.15$, $P < 0.0001$; males $F_{2,32} = 42.68$, $P < 0.0001$). There were also significant differences in feeding in the no-choice experiment (females $F_{2,34} = 20.53$, $P < 0.0001$; males $F_{2,33} = 26.96$, $P < 0.0001$). However, females accepted trembling aspen and black cottonwood equally, and males fed on black cottonwood more vigorously than on Scouler's willow (Figure 2).

Oviposition bioassays. When bolt diameter was not controlled in 2002, *S. calcarata* females oviposited preferentially in trembling aspen and black cottonwood, the species with the largest diameter bolts (Table 2). When bolt diameter was equalized in 2003, there was no preference in oviposition among the three host species (Table 2).

We observed some larvae feeding in the bark of all three species, but they did not survive long as bark quality deteriorated rapidly because of infection by *Cytospera chrysosperma* (Persoon: Fries) Fries, distinguished by characteristic orange conidial tendrils (Callan 1998).

Table 1.

Comparison of behavioural activity by male and female *S. calcarata* within perforated centres of arena floor above treatment (i.e. trembling aspen leaves) and control jars in the still-air olfactometer.

Observations	Females	Males
Observations of beetles within arena circle circumscribing perforated area above treatment or control stimulus, 30 sec intervals for 2 h.		
no. replicates	7	7
mean no. observations ± SE		
treatment stimulus	55.4 ± 18.5	41.9 ± 8.8
control stimulus	26.3 ± 10.8	41.9 ± 18.5
t-value	1.99	0.00
Probability	0.047	0.50
Observations of feeding on perforated area of arena floor above treatment or control stimulus		
no. replicates	8	11
no. times most feeding above treatment stimulus	7[1]	6
no. times most feeding above control stimulus	0	0
no. times no feeding damage observed	1	5
Chi-square value	7.00	6.00
Probability	0.008	0.01

[1] In one trial feeding damage was observed above both stimuli, but damage was much greater over the treatment stimulus.
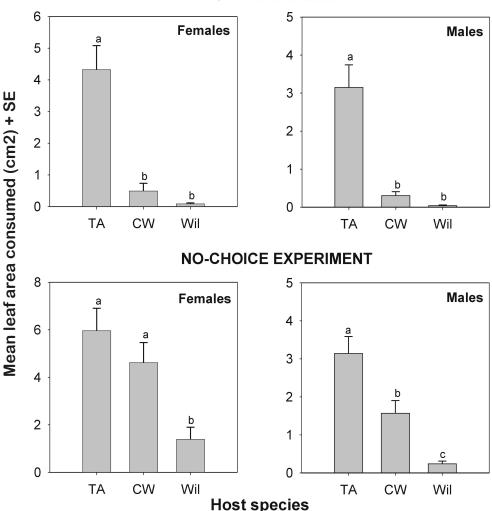
DISCUSSION

Our results indicate that *S. calcarata* can locate potential hosts by olfaction, can discriminate among tree species through gustatory cues, and may reject trees for oviposition if their diameter is too small.

Females were attracted to the volatiles from leaf-bearing twigs of trembling aspen in an arena olfactometer (Table 1). The fact that males chewed the paper above treatment but not control stimuli suggests they too are attracted to host volatiles. In the field experiment, we had hypothesized that *S. calcarata* brood trees would produce ethanol, and possibly other metabolites caused by wounding, and that the combination would be attractive. The positive response to leafy twigs, and the failure to induce significant attack on trees that were wounded, ethanol-baited, or both, suggests that initial orientation is to volatiles from leaves on which adults feed. Oviposition tends to be located in the upper parts of the bole beneath the canopy (Peterson 1947),

requiring little movement by feeding beetles. Similarly, in an unpublished study conducted by C.L. Broberg and R. Gries (SFU), 15 antennally-active volatiles from the bark of trembling aspen were identified by coupled gas chromatographic electroantennographic detection analysis. However, in six field-trapping experiments, no *S. calcarata* were captured to various partial or complete blends of these compounds. These results may indicate that *S. calcarata* use leaf volatiles in orientation toward suitable hosts during flight.

The lack of a strong olfactory response by *S. calcarata* is not surprising. As a specialist of weakened hosts that may support multiple generations on the same tree (Hanks 1999), *S. calcarata* is not likely subject to strong selection pressure to adapt to finding new hosts. Furthermore, *Populus* spp. are pioneer species and often occur in locally abundant populations. Thus emergent *S. calcarata* may not need to disperse

CHOICE EXPERIMENT

NO-CHOICE EXPERIMENT

Figure 2. Leaf area consumed by female and male *S. calcarata* when presented with the three potential hosts simultaneously (choice experiment) or separately (no-choice experiment). Bars within an experiment and sex with the same letter are not significantly different, REGWQ test, $P < 0.05$. TA = trembling aspen, CW = black cottonwood, Wil = Scouler's willow.

long distances to find a suitable host. In contrast, stressed hosts which are moribund and can only support one generation of beetle (Hanks 1999) are often rare and/or patchy in distribution. Cerambycid specialists on these hosts have evolved strong long-distance response mechanisms that often involve orientation to host volatiles from recently downed or injured trees, smoke volatiles from burned trees, or pheromones produced by secondary bark beetles pheromones (Allison *et al.* 2004). Although these cerambycids mate and ovi-

posit on these newly found hosts, they engage in maturation feeding on healthy trees (Hanks 1999). Weakened host specialists like *S. calcarata* can use a single individual for all functions; thus even the malformed emergent adults incapable of flight observed by us and others (Peterson 1947; Drouin & Wong 1975), can experience reproductive success without long range dispersal and olfactory orientation to suitable hosts.

Both sexes clearly preferred trembling aspen in choice feeding bioassays and re-

Table 2.

Comparison of oviposition by *S. calcarata* on bolts from three different hosts when bolt diameters were unequal or similar.

Experimental description	Species	Bolt diameter (cm)		Mean no. ovipositions ± SE [1]
		Range	Mean ± SE [1]	
Bolt diameters unequal (2002)	Trembling aspen	6.3 - 13.2	9.5 ± 0.8 a	21.0 ± 9.6 b
	Black cottonwood	8.9 - 16.7	12.2 ± 0.9 a	27.5 ± 9.4 a
	Scouler's willow	3.2 - 5.5	4.6 ± 0.3 b	0.4 ± 0.2 c
Bolt diameters similar (2003)	Trembling aspen	7.8 - 17.1	13.5 ± 0.6 a	4.4 ± 2.1 a
	Black cottonwood	8.1 - 17.3	13.1 ± 0.6 a	8.0 ± 3.2 a
	Scouler's willow	9.2 - 17.0	12.6 ± 0.6 a	8.3 ± 2.8 a

[1] Means within an experiment and column followed by the same letter are not significantly different, REGWQ test, $P < 0.05$. ANOVA statistics as follows: 2002 bolt diameter $F_{2,18} = 33.83$, $P < 0.0001$; oviposition $F_{2,18} = 21.17$, $P < 0.0001$; 2003 bolt diameter $F_{2,24} = 2.57$, $P = 0.10$; oviposition $F_{2,24} = 1.17$, $P = 0.33$.

jected other species, but in the no-choice bioassays, females did not discriminate between trembling aspen and black cottonwood, and males accepted black cottonwood more than Scouler's willow (Figure 2). Females may have higher nutritive requirements than males and therefore cannot afford to be as selective. Preference for trembling aspen could be a result of local adaptation to a species that comprises 4.6 times more wood volume in BC than black cottonwood (BC Ministry of Forests 1998). *Saperda calcarata* is mobile enough to sample numerous trees before finding one that is suitable for feeding.

There are few records in BC of *S. calcarata* attack on *Salix* spp. In Saskatchewan, however, both *Salix* and *Populus* spp. were reported to be "readily eaten" by adults (Peterson 1947). Thus, there could be host-related ecotypes in different regions of North America.

The lack of discrimination between hosts for oviposition when trembling aspen leaves were available for maturation feeding, and diameters of bolts from the three species were equalized, indicates that host volume is more important than species for larval feeding and development (Table 2). Oviposition in large-diameter hosts would be adaptive in ensuring that most hosts did not suffer breakage during the three to four years required for larval development.

In conclusion, lack of evidence for long-range olfactory orientation to new hosts, correlation between *S. calcarata* incidence in BC and gustatory preferences, high mobility, and lack of discrimination between hosts for oviposition, suggest that feeding preference constitutes the predominant mechanism of host selection by *S. calcarata* in BC.

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