

# Acceptance and suitability of novel trees for *Orthotomicus erosus*, an exotic bark beetle in North America

A. J. Walter · R. C. Venette · S. A. Kells

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**Abstract** To predict whether an herbivorous pest insect will establish in a new area, the potential host plants must be known. For invading bark beetles, adults must recognize and accept trees suitable for larval development. The preference-performance hypothesis predicts that adults will select host species that maximize the fitness of their offspring. We tested five species of North American conifers and one angiosperm for adult acceptance and suitability for reproduction of the Mediterranean pine engraver, *Orthotomicus erosus* (Wollaston). Red pine, *Pinus resinosa* Aiton, and white spruce, *Picea glauca* (Moench) Voss, were accepted by adult beetles and suitable for reproduction to the extent of adult replacement. Others, such as balsam fir, *Abies balsamea* (L.) Mill., eastern hemlock, *Tsuga canadensis* (L.) Carrière, and tamarack, *Larix laricina* (Du Roi) Koch, were acceptable but unsuitable. The presence of tree species that are acceptable to adults but unsuitable for reproduction may affect the ability of *O. erosus* to establish across North America.

**Keywords** Mediterranean pine engraver · Invasion biology · Establishment · Host range expansion · Novel host association · Pinaceae

## Introduction

Establishment success of an invading herbivorous insect depends in part on the ability of the newly arrived insect to accept plants suitable for consumption and oviposition. Herbivores in a new environment must be pre-adapted to distinguish hosts from non-hosts (Jermy 1988). Since host plants from the native range will probably not be present, high motivation to oviposit by the invading adult insects causes them to lower their threshold for host acceptance, leading to the use of plants that would not normally be attempted (Courtney and Kibota 1990; Dethier 1982).

For herbivorous insects whose progeny do not have a high dispersal capacity, the larval host is determined by the ovipositing female (Janz 2002). The preference-performance hypothesis predicts that females will accept plants that are most suitable (maximize the fitness) for their progeny (Jermy 1984; Scheirs and De Bruyn 2002; Wiklund 1975). However, oviposition on sub-optimal or unsuitable hosts may occur because the adults use cues to determine suitability of a novel plant that are not correlated with

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A. J. Walter · S. A. Kells  
Department of Entomology, University of Minnesota,  
219 Hodson Hall, 1980 Folwell Ave, St. Paul,  
MN 55108, USA

R. C. Venette (✉)  
USDA Forest Service, Northern Research Station,  
1561 Lindig St., St. Paul, MN 55108, USA  
e-mail: rvenette@fs.fed.us

larval performance (Gripenberg et al. 2007; Rodman and Chew 1980). The phenomenon occurs during plant invasions; some herbivorous insects will oviposit on introduced plants even though those plants are unsuitable for reproduction (Badenes-Perez et al. 2006; Barre et al. 2002; Casagrande and Dacey 2007; Chew 1977; Courtney 1981; Graves and Shapiro 2003; Harris et al. 2001; Straatman 1962).

The Mediterranean pine engraver, *Orthotomicus erosus* (Wollaston), is a Eurasian bark beetle that has recently invaded California and colonizes several species in the genus *Pinus* (Lee et al. 2005). In its native range, *O. erosus* is considered one of the principal bark beetle pests of managed pine plantations in Israel (Mendel et al. 1985) and northern Iran (Mendel 1988). *O. erosus* is one of the most frequently intercepted bark beetles in cargo and solid wood packing material entering North America (Brockerhoff et al. 2006; Haack 2006). It has successfully invaded South Africa, Swaziland, The Republic of Tajikistan, and Chile (Eglitis 2000), and caused economic losses in pine plantations (Lee et al. 2007). In an initial assessment *O. erosus* was considered a high risk to North America, but with a high degree of uncertainty surrounding the assessment (Eglitis 2000). The risk assessment identified the large potential host range of the beetle as a concern because of the economic value of the tree species it may attack and because a wide host range may allow the beetle to spread over a large area in North America (Eglitis 2000).

If *O. erosus* does spread across North America, it will encounter genera and species of conifers with which it has no history of association. The complete host range of *O. erosus* and its potential for host shifting is unclear. Within its native and adventive ranges, *O. erosus* has been reported on many pines (*Pinus* spp.) (Arias et al. 2005; Mendel and Halperin 1982; Wood and Bright 1992), and it may also utilize Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), oriental spruce (*Picea orientalis* (L.)), Spanish fir (*Abies pinsapo* Boiss.), cedar (*Cedrus libani* A. Rich., *C. atlantica* (Endl.) Manetti ex Carrière) (Pinaceae) (Bright and Skidmore 1997; Wood and Bright 1992) and Mediterranean cypress (*Cupressus sempervirens* L.) (Cupressaceae) (Mendel and Halperin 1982). Recent host testing on 22 conifer species found in North America showed that larvae can develop in all pine (*Pinus*) species tested, as well as Douglas-fir

(*Pseudotsuga menziesii*), and white and black spruce (*Picea glauca* (Moench) Voss, *P. mariana* (Mill.) B.S.P.). A small amount of reproduction occurred on tamarack (*Larix laricina* (Du Roi) Koch) (Pinaceae), but not white fir (*Abies concolor* (Gond. & Glend.) Hildebr.) (Pinaceae), incense cedar (*Calocedrus decurrens* (Torr.) Florin), or coast redwood (*Sequoia sempervirens* Lamb) (Cupressaceae) (Lee et al. 2008). In these host range studies, adult *O. erosus* were placed directly into drilled entrance holes into the phloem of the test species, but the extent to which *O. erosus* will initiate gallery construction in various hosts is unknown.

In a known host, *O. erosus* males will first attack a tree. They chew through the outer bark to the phloem, where they excavate a nuptial chamber. The male will be joined by 1–3 females (Mendel and Halperin 1982). Mating occurs when the females join a male, although up to 97% of *O. erosus* females are already mated when they emerge from the brood log (Mendel 1983). The females construct egg galleries parallel to the vertical axis of the tree. Eggs are laid on both sides of the egg galleries and the larvae construct galleries outward from the egg gallery as they feed on the phloem. Larvae feed on the phloem and etch the outer xylem of the host tree, and the pupal chamber is constructed here as well. When the teneral adult emerges, it will continue to feed in the deteriorating phloem for maturation feeding if the bark is sufficiently moist. If the bark is too dry or when maturation feeding is complete, the insect emerges from the host tree to search for a new host (Mendel and Halperin 1982). Like many bark beetles, *O. erosus* employs a pheromone system to control aggregation onto host material (Giesen et al. 1984).

This paper reports host range testing on *O. erosus* under quarantine conditions. Our objective was to test several eastern North American conifers for acceptability to adults and suitability for reproduction. We test the hypothesis that when confronted with novel hosts, the adult beetles will accept tree species that are suitable for reproduction, and reject those tree species that are unsuitable.

## Methods

In order to investigate host utilization behaviors on novel plant species by *O. erosus*, we examined the

behavior of adults confined on the bark surface and the reproductive potential of groups of beetles forced to colonize cut logs for several novel tree species. The acceptability of the tree species to adults was measured by the probability that beetles would bore through the outer bark and create galleries in the phloem. Our measure of suitability was in terms of beetle reproductive potential, specifically, the number of offspring produced by a group of beetles.

### Beetle colony

Beetles collected from the established population in California were used to start a colony under quarantine condition in St. Paul, MN. Cut logs of Aleppo pine, *Pinus halepensis* Mill., infested with *O. erosus* were collected in Fresno, CA in August 2006, July 2007, and August 2007. Cut logs were held in emergence boxes (Browne 1972) in Davis, CA, and emerged adults were shipped to the MAES/MDA Containment Facility in St. Paul, MN.

The beetles were reared on cut logs of red pine, *Pinus resinosa* Aiton (approximately 50 cm long  $\times$  15–40 cm diameter) collected from the University of Minnesota Northern Research and Outreach Center (Grand Rapids, MN). To minimize desiccation, cut surfaces of the rearing logs were sealed with paraffin wax 1–2 days after harvest (Candle Crafting Products Premium Candle Wax, Yaley Enterprises, Redding, CA). Between harvest and use in the colony, logs were maintained in a greenhouse at a minimum temperature of 7–13°C during the day and 4–10°C at night. The logs were used within 10 weeks after harvest.

At least 20 adults were placed on the surface of each cut log, and the artificially infested logs were placed in 38 cm diameter  $\times$  92 cm length cylinders of 0.75 cm thick cardboard, sealed at each end with a ventilated cap. During rearing, logs were maintained at 25°C, 16:8 L:D in a growth chamber. Under these conditions, beetle generations matured in approximately 6 weeks. New colonies were initiated after one or two generations had developed. Under our rearing conditions and in the field, *O. erosus* adults tend to remain in the brood log rather than emerge as long as the log remains moist enough (Mendel and Halperin 1982). In our colony, this led to severe competition and reduced numbers of the beetle. Therefore, beetles used for the colony or experiments were obtained by peeling the bark and phloem of the

colony logs and manually extracting adult beetles. All handling procedures were approved by the USDA APHIS Plant Protection and Quarantine Division Permit Number 74447.

### Collection of trees for experiments

The species used in the experiments were: red pine (*Pinus resinosa*), white spruce (*Picea glauca*), tamarack (*Larix laricina*), eastern hemlock (*Tsuga canadensis* (L.) Carrière), balsam fir (*Abies balsamea*), and paper birch (*Betula papyrifera* Marsh.). Red pine is a suitable host (Lee et al. 2008). Paper birch was considered a likely non-host, and the host status of the other species was unknown. The five conifer species represent five of the eleven genera in Pinaceae; most reported hosts of *O. erosus* are in Pinaceae.

Trees were felled at the University of Minnesota Northern Research and Outreach Center (Grand Rapids, MN). Cut logs (approximately 50 cm long  $\times$  11–34.5 cm diameter) were sealed with paraffin wax and stored in a greenhouse in St. Paul, MN under the same conditions as logs used for rearing until they were used in experiments. Most tree species were collected in 2 years, but because of difficulty in locating specimens, hemlock collections were made only in 2007. Red pine, white spruce, tamarack, and balsam fir were collected 13 September 2006; with an additional red pine and paper birch collection on 22 October 2006. In 2007, a collection of two eastern hemlock trees was made on 13 June, and two trees per species of red pine, white spruce, tamarack, eastern hemlock, balsam fir, and paper birch were collected 3 July.

### Adult acceptance study

For *O. erosus*, acceptance of a potential host tree by adults occurs when an adult bores through the outer bark of a tree, reaches the phloem, and establishes a gallery. In order to capture these behaviors in the quarantine laboratory, we confined adults on the surface of a disc consisting of the outer bark and phloem of the tested tree species, and monitored their subsequent activity in a no-choice assay. Presenting bark beetles with intact or ground discs of bark, phloem, or both is a well-established method for testing host acceptance (Elkinton and Wood 1980; Klepzig et al. 1996; Raffa 1988; Wallin and Raffa

2000, 2004; Wood 1963). Differences between tree species in both entry to the outer bark and length of galleries produced have been observed in disc assays (Wallin and Raffa 2002). We chose to test acceptability of the six species to both males and females because it seemed plausible that mated females could initiate galleries on their own, especially if males are hard to locate, which may be the case for a small establishing population.

A separate arena containing a bark-and-phloem disc from one tree species was constructed for each tested beetle. In a method similar to that of Elkinton and Wood (1980), discs were cut from a log with a 5 cm diameter hole saw and removed with a draw knife. Each disc was embedded in paraffin wax in its own 9 cm diameter plastic Petri dish. With this method, the beetles needed to bore through the outer bark to reach the underlying phloem. Bark disc arenas were constructed the day before the start of each block. A few disc arenas for each tree species were ruined because the bark curled away from the phloem and wax overnight, and beetles were not placed in these arenas.

All beetles used in the acceptance study had been extracted from colony logs 2 days before the start of the block and kept in Petri dishes with moist filter paper in the growth chamber used for colony rearing. One beetle was placed in each bark disc arena for 72 h, and the arena was kept in a growth chamber (25°C, 16:8 L:D). The assay was run for 72 h to maximize the probability that acceptance would be detected (Barton Browne and Withers 2002; Tallamy 2000). In preliminary experiments, we observed a large degree of beetle mortality after 72 h (data not presented). In addition, a 72 h assay has been used in similar acceptance experiments with other species of bark beetles (Wallin and Raffa 2000). At approximately 24 and 48 h, each arena was observed and the status of the beetle was noted (i.e., living and visible, dead, boring, or not visible and not creating boring dust). At the end of the experiment, all the arenas were placed in a frost-free freezer ( $\sim -20^{\circ}\text{C}$ ) for at least 24 h. Later, the arenas were removed from the freezer and dissected. The position of the beetle, its boring activity in the outer bark and phloem, and length of gallery in the phloem layer were recorded.

We intended to assay a total of 30 male beetles and 30 female beetles for each of the two trees for

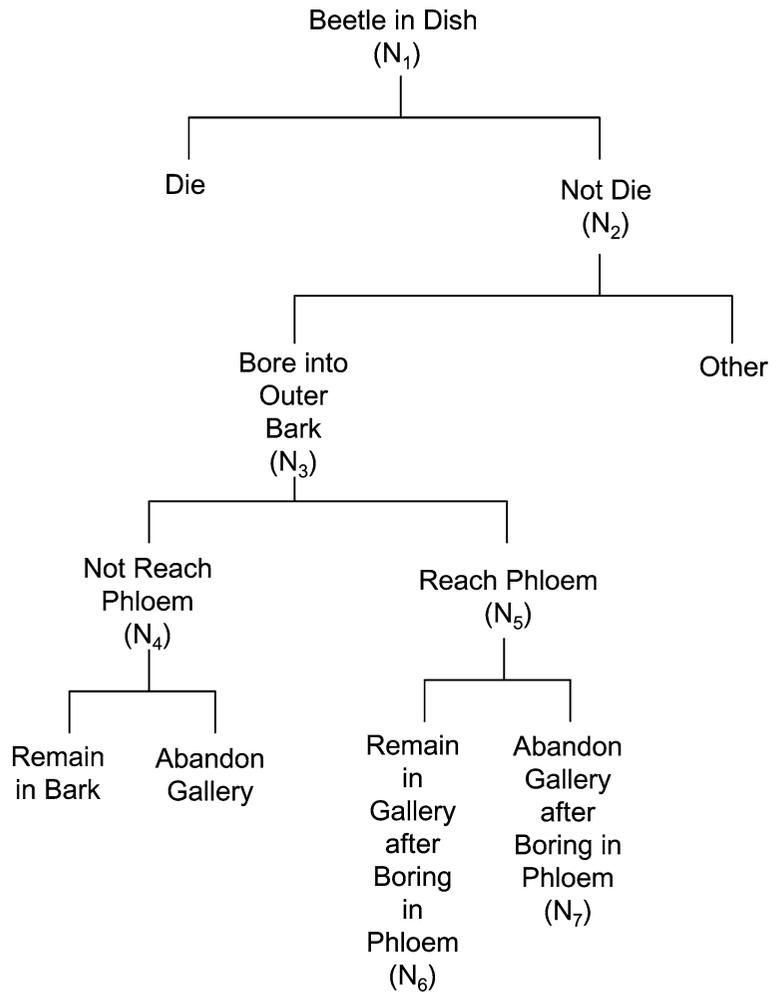
the six tree species and an equal number from negative control treatment consisting of a 'blank' arena containing wax but no bark and phloem disc (120 beetles per tree species, a total of 840 beetles). The actual number of beetles assayed was slightly lower because a few of the arenas were ruined overnight (see above). The experiment was run as a randomized complete block design. Six blocks were replicated in time between 17 July and 8 October 2007, with five male and five female beetles started in arenas from each tree species in every block.

The process of entering the outer bark, boring through the outer bark of a tree, reaching the phloem and establishing a gallery involves several behavioral steps (Fig. 1). The precise behavioral step(s) where a host acceptance decision by *O. erosus* occurs is unknown. *Ips paraconfusus*, a close relative of *O. erosus*, appears to reject some non-host trees after sampling the outer bark or phloem (Elkinton et al. 1980). Therefore, we looked for differences in the probability that *O. erosus* would complete each step in the behavioral sequence (Fig. 1).

The probability that the beetles would complete each step of the behavioral sequence was analyzed with logistic regression. The candidate explanatory variables were beetle sex, host species, block, and all two-way interactions. Explanatory variables were added or removed from the model by using forward, backward, and stepwise selection. In all cases, the selection methods yielded the same explanatory variables with  $\alpha = 0.05$ . Contrasts among the treatments were conducted for each significant explanatory variable at each behavioral step (PROC LOGISTIC, SAS Institute Inc. 2004).

The observed data for length bored in phloem by the beetles that bored into the outer bark and reached the phloem did not pass the Shapiro-Wilk test for normality ( $W = 0.678$ ,  $P < 0.0001$ , PROC UNIVARIATE, SAS Institute Inc. 2004). A nonparametric Kruskal–Wallis test was used to test for differences in gallery lengths between beetles that remained in their galleries and those that abandoned them (PROC NPAR1WAY, SAS Institute Inc. 2004). Using the Kruskal–Wallis test with a Bonferroni-adjusted  $\alpha$  of 0.0033 to maintain an overall  $\alpha$  of 0.05, comparisons of gallery length were then made between tree species for beetles that abandoned their galleries and those that remained.

**Fig. 1** Flow chart showing the possible decisions made by a bark beetle during the host acceptance bioassay. The number of beetles that reached each node ( $N_x$ ) is given in Table 1



**Larval suitability study**

The suitability of a tree for *O. erosus* reflects the effects that the selected plant will have on the reproductive potential of the beetle. Suitability may include effects on insect behavior (i.e., the number of eggs a female chooses to oviposit) and/or physiological effects of the plant on the insect (i.e., egg hatch or larval development rate). We measured the suitability of a tree species as the number of larvae produced by a parent population forced to colonize a log.

The methods for our suitability study were similar to those of Lee et al. (2008). Using a power drill with a brad point bit, three holes (3.125 mm diameter) were drilled through the bark and phloem and just into the sapwood of logs. Two males were inserted

into each hole and escape was prevented by taping a piece of metal screening over the hole. Two males were inserted per hole to ensure that at least one male per entrance hole would survive. Two days later, three female beetles were added to each hole and the screening was replaced. Three females were introduced because one to three females usually join a single male in an entrance hole (Mendel and Halperin 1982). Using this method, bark beetles will form galleries and oviposit in a wide variety of suitable and unsuitable tree species (Furniss 1976; Lee et al. 2008).

At the end of the suitability experiment, the bark and phloem were peeled from the logs and all life stages of *O. erosus* were counted. The appropriate time period for the experiment was determined by

monitoring a set of red pine logs in the *O. erosus* colony that were initiated concurrently with the experiments. The experiment was ended when the beetle population in the colony logs consisted of mainly adults and early instar larvae (indicating that the second generation was starting). We counted all life stages present, with the exception of very small larvae in red pine (the second generation). All individuals that were counted (larvae, pupae, and adults) were assumed to represent viable adults in the next generation. Because of this our measure of suitability does not account for different development times of *O. erosus* on the different tree species.

We had intended to count the number of egg galleries initiated in the logs. However, in logs of various tree species, beetles laid eggs in winding galleries that were very different in shape from the egg galleries reported in the literature (Mendel 1983). Beetles would also tunnel in the phloem without constructing an obvious egg gallery. We were therefore unable to accurately count the number of egg galleries initiated by the nine females introduced to each log. *Orthotomicus erosus* is known to form different gallery patterns on different hosts (Eglitis 2000).

The suitability experiment was divided into two blocks in a randomized incomplete block design. The first block was started on 27 October 2006 and included two logs per tree from three red pine trees (two red pine trees from the Sept 2006 collection and one from October 2006), and two logs per tree from two white spruce, tamarack, and balsam fir trees, and one paper birch tree (20 logs total). Block 2 was started on 21 August 2007 and included two logs per tree from four eastern hemlock trees (two trees collected June 2007, and two from July 2007) and two logs per tree from two red pine, white spruce, tamarack, balsam fir, and paper birch trees (28 logs total).

The number of offspring produced per log was tested for normality by using the Shapiro-Wilk test (PROC UNIVARIATE, SAS Institute Inc. 2004). The effect of species, block, variation among logs from the same tree trees, and variation among trees from the same species on the number of viable offspring observed per log was analyzed using ANOVA followed by Tukey's HSD with  $\alpha = 0.05$  (PROC MIXED, SAS Institute Inc. 2004).

The proportion of individuals in various life stages (adult, teneral, pupa, large larva, or small larva) recovered from the logs was analyzed by ordinal logistic regression with species, block, and their interaction as explanatory variables (PROC LOGISTIC, SAS Institute Inc. 2004). Variables were selected with forward, backward, and stepwise selection options with  $\alpha = 0.05$ . All three selection methods for the regression model yielded the same result.

In a separate analysis, the 95% confidence interval was estimated for the mean number of viable offspring produced in each species (PROC TTEST, SAS Institute Inc. 2004) to determine whether the mean was less than, equal to, or greater than 15 viable offspring per log (the replacement rate).

## Results

### Adult acceptance study

We viewed host acceptance by *O. erosus* as a stepwise series of behaviors (Fig. 1), and we analyzed the host acceptance behaviors independently of each other. The numbers of beetles analyzed at a certain step in the host acceptance sequence was determined by the number of beetles that completed the previous steps (i.e., the number of beetles analyzed for passing from  $N_2 \rightarrow N_3$  depends on the number of beetles that reached  $N_2$ ) (Table 1). Thus, as host acceptance progressed, the design became more and more unbalanced, and the number of replicates declined at each step.

About one-tenth of the beetles that were used in the study died during the first 2 days of the assay

**Table 1** Total number of beetles arriving at stages of the host acceptance sequence for each potential host species

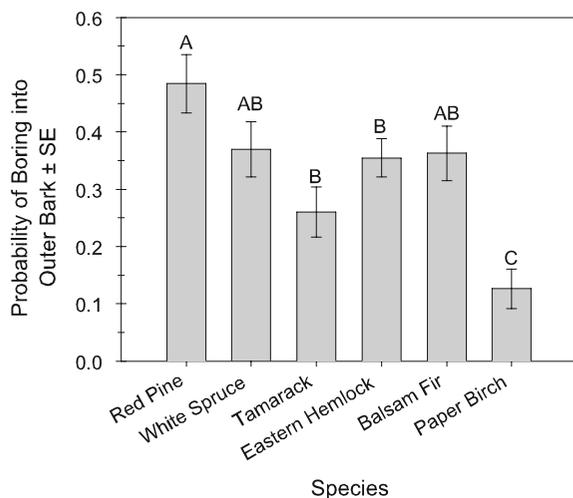
	$N_1$	$N_2$	$N_3$	$N_4$	$N_5$	$N_6$	$N_7$
Red pine	119	97	49	15	34	30	3
White spruce	118	100	38	6	32	31	0
Tamarack	121	100	26	10	16	15	1
Eastern hemlock	239	201	74	22	52	43	7
Balsam fir	119	101	37	16	21	18	3
Paper birch	110	95	12	6	6	6	0

$N_x$  labels refer to Fig. 1

without any boring activity. Tree species, beetle sex, block, and their interactions did not meet the criteria for inclusion in a logistic regression model of the probability of remaining alive ( $N_1 \rightarrow N_2$  in Fig. 1); these factors therefore did not affect the survivorship of the beetles.

There were significant differences among tree species in the probability that beetles would initiate boring into the outer bark ( $N_2 \rightarrow N_3$  in Fig. 1,  $df = 6$ ,  $\chi^2_{kw} = 28.25$ ,  $P < 0.0001$ , Fig. 2). Beetles had the highest probability of boring into red pine, white spruce, and balsam fir. White spruce, tamarack, eastern hemlock, and balsam fir formed an intermediate group. The lowest probability of boring was associated with paper birch. Beetle sex, block, and the interactions among the explanatory variables did not meet the criteria for inclusion in the logistic regression model of probability of boring in the outer bark.

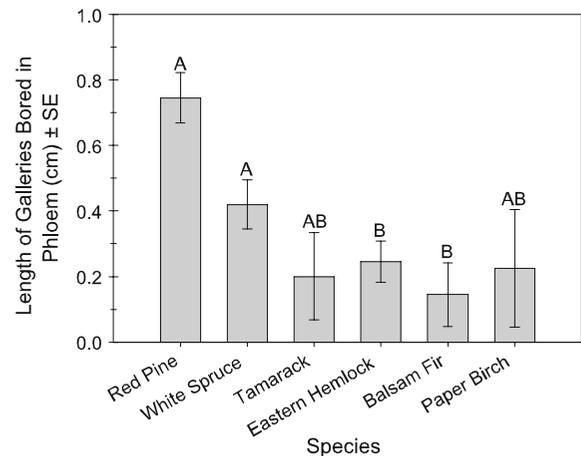
There were no differences in the behaviors between the initiation of boring in the outer bark and the amount of boring that took place in the phloem ( $N_3 \rightarrow N_5 \rightarrow N_6, N_7$  in Fig. 1). None of the explanatory variables met our criteria for inclusion in logistic regression models. Thus, the proportion of the beetles that bored into the outer bark that subsequently reached the phloem did not differ among species, and there were no differences among tree species in the proportion of



**Fig. 2** Probability ( $\pm$ binomial standard error) of *Orthotomicus erosus* boring into the outer bark of bark-and-phloem discs from potential host species. Bars with the same letter are not significantly different in a protected mean separation procedure in logistic regression

beetles that abandoned their galleries after reaching the phloem.

Once beetles had bored into the outer bark and reached the phloem, the length of galleries formed in the phloem was different depending on whether the beetles subsequently abandoned the disc ( $N_5 \rightarrow N_6$  and  $N_5 \rightarrow N_7$  in Fig. 1,  $df = 1$ ,  $\chi^2_{kw} = 7.6009$ ,  $P = 0.0058$ ). Beetles that later abandoned their galleries constructed shorter galleries than those that did not abandon their galleries. For the beetles that remained in their galleries, the length of the galleries differed between red pine and eastern hemlock ( $df = 1$ ,  $\chi^2_{kw} = 17.6787$ ,  $P < 0.0001$ ), red pine and balsam fir ( $df = 1$ ,  $\chi^2_{kw} = 18.5654$ ,  $P < 0.0001$ ), white spruce and eastern hemlock ( $df = 1$ ,  $\chi^2_{kw} = 9.3448$ ,  $P = 0.0022$ ), and white spruce and balsam fir ( $df = 1$ ,  $\chi^2_{kw} = 12.5248$ ,  $P = 0.0004$ ) (Fig. 3). The length bored by beetles in paper birch was not different from that in any of the conifer species, but this value is probably due to the small number of beetles that bored in birch ( $N_6 = 6$ ), and the influence of one beetle in particular that constructed a very long gallery. None of the explanatory variables affected the length of galleries in the phloem in the tree species for the twelve beetles that reached the phloem and subsequently abandoned their galleries.



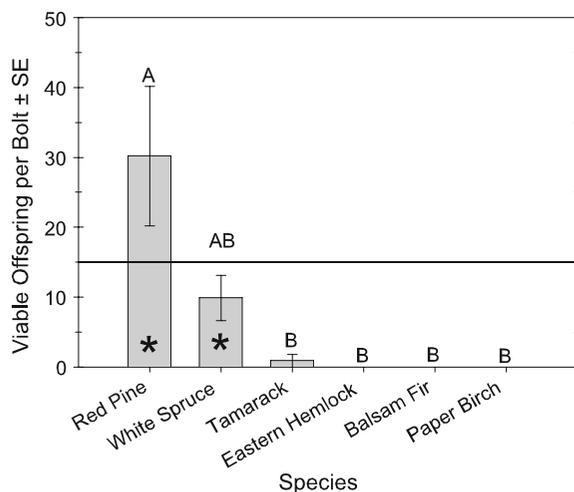
**Fig. 3** Length (mean  $\pm$  SE) of galleries bored in the phloem of bark-and-phloem discs of potential host species by adult *Orthotomicus erosus* that bored into the outer bark of each species, reached the phloem, and did not subsequently abandon their galleries. Bars with the same letter are not significantly different according to multiple nonparametric Kruskal–Wallis comparisons. For the entire test,  $\alpha = 0.05$ ; the Bonferroni adjustment was used to obtain the pairwise  $\alpha$  level of 0.0033

## Larval suitability study

Tree species affected the total number of offspring produced per log ( $df = 6$ ,  $F = 5.16$ ,  $P = 0.0005$ ) (Fig. 4), but there was no effect of block ( $df = 1$ ,  $F = 0.86$ ,  $P = 0.3596$ ). The most offspring were produced in red pine. No offspring were recovered from the eastern hemlock, balsam fir, or paper birch logs. The number of offspring produced in white spruce was statistically equivalent to the number produced in red pine. The number of offspring produced in white spruce and tamarack were statistically no different from zero.

There were no differences among tree species in the proportion of offspring from various life stages (larva, pupa, and adult). The single tamarack log where viable offspring were observed contained 29% adults, 14% pupae, and 57% larvae. White spruce logs with viable offspring contained 24% adults, 9% pupae, and 67% larvae; red pine logs with viable offspring contained 47% adults, 6% pupae, and 47% larvae. The explanatory variables did not meet our criteria for inclusion in logistic regression models.

The confidence interval for the number of offspring observed in individual logs included values



**Fig. 4** Total viable offspring produced (mean  $\pm$  SE) in logs of each potential host species by six male and nine female parents of *Orthotomicus erosus*. Bars with the same letter are not significantly different according Tukey's HSD with  $\alpha = 0.05$ . The horizontal line represents the number of offspring required to replace the parent beetles introduced to the log (replacement rate). \* Indicates host tree species where the 95% confidence intervals for viable offspring produced overlap the replacement rate

greater than or equal to the number of parent beetles introduced (the replacement rate) only in red pine (95% CI 7.64–52.76 offspring) and white spruce (95% CI 2.25–17.50 offspring). The confidence interval for number of offspring produced in tamarack logs included zero (95% CI 0–2.94 offspring).

## Discussion

We expected that adult *O. erosus* would accept all or a subset of novel host species that were suitable for larval development and reject unsuitable species. However, we found that the set of tree species that were accepted by *O. erosus* (red pine, white spruce, balsam fir, and to some extent tamarack and eastern hemlock) was larger than the set of species that were suitable for *O. erosus* development (red pine and white spruce). When faced with novel host plants during an invasion, adult *O. erosus* may oviposit in tree species that are unsuitable for larval development. This result is contrary to the preference-performance hypothesis. The accuracy of the preference-performance hypothesis depends on an evolutionary history of association between an herbivore and members of the plant community. When associations are recent, as with biological invasions, the hypothesis may not hold.

By analyzing differences in each step of host selection (Fig. 1), we are able to show that, for the tree species we tested, differences in host acceptance by *O. erosus* are driven by differences in the proportion of beetles boring into the outer bark. Therefore, the signals used in host selection by *O. erosus* can be expected to occur in the outer bark. Many bark beetle species appear to accept hosts after they have sampled the outer bark or the phloem (Elkinton and Wood 1980; Hynum and Berryman 1980; Pureswaran and Borden 2003; Raffa and Berryman 1982). Some species, such as *Ips paraconfusus* Lanier, are unable to distinguish between the outer bark of hosts and certain non-hosts (Elkinton and Wood 1980), and make their host determination only after sampling the phloem (Elkinton and Wood 1980; Raffa et al. 1993; Wood 1963).

An interesting result of the host acceptability experiment was that male and female beetles had the same probability of host acceptance on the species tested despite the fact that males are considered the host-finding sex (Mendel and Halperin 1982). Similar female gallery initiation behavior has been reported

under experimental conditions in other bark beetle species where males are reportedly the host-finding sex. For instance, female *Ips paraconfusus* initiated their own galleries 10% of the time when caged on logs, even though the logs were not crowded and males had already established galleries and were emitting attractive pheromones (Wood 1963). In a field experiment, 4 out of 20 *I. paraconfusus* in galleries in a baited log were lone females (Elkinton and Wood 1980). Since aggregation is not necessary for beetles colonizing dead trees, and crowding can incur a serious fitness cost in these situations (Byers 1989; Zhang et al. 1992), it may be advantageous for mated females to establish galleries on their own without advertising the presence of the food resource or their offspring to competitors and natural enemies. If this behavior occurs in the field, it could also increase the probability of establishment of an invading beetle population since mate finding after leaving the brood log would be unnecessary.

The host acceptability test reflects the acceptance of dead host material by *O. erosus*, not attack of live and healthy trees. Such acceptability tests result in higher levels of host acceptance than are observed for standing live trees (Raffa 1988). Like most members of the Ipini, *O. erosus* is a secondary pest at low population levels and feeds primarily on freshly killed or dying trees. Adult *O. erosus* only switch to live trees when beetle densities are very high (Arias et al. 2005). At the beginning of an invasion, populations of *O. erosus* may be too small to successfully mass-attack live trees, and we expect that the beetles would initially attack dead or dying trees. Therefore, our host acceptability test is appropriate for determining what types of dead host material would be required to allow the establishment of a population of *O. erosus* but not which live tree species the beetle would attack if it reached high population levels.

The results of our suitability testing are very similar to those obtained by Lee et al. (2008). These results support field observations that *O. erosus* uses species of both pine (*Pinus*) and spruce (*Picea*) as hosts (reviewed in Lee et al. 2008; Wood and Bright 1992). *Orthotomicus erosus* has been collected on one species of fir (*Abies pinsapo* Boiss) (Wood and Bright 1992); other fir species were not suitable in laboratory experiments (Lee et al. 2008, this study). In Europe, introduced tree species congeneric with

their native hosts are suitable for native bark beetles (Sauvard 2004).

The results presented here do not address the host-searching behavior of *O. erosus* before the beetles are in contact with the bark surface. Many bark beetles have rather indiscriminate landing behavior (Elkinton and Wood 1980; Hynum and Berryman 1980; Moeck et al. 1981; Schroeder 1992), possibly because the volatile profiles of many conifers are qualitatively similar (Pureswaran et al. 2004) or host acceptability decisions incorporate prior landing encounters (Wallin and Raffa 2002). Bark beetles have been reported to respond to volatile (Byers et al. 2000; Huber et al. 2000; Pureswaran and Borden 2005; Schroeder 1992; reviewed in Seybold et al. 2006; Zhang et al. 2002) and non-odor (Campbell and Borden 2006) host cues at long range. However, a searching beetle that does not encounter attractive cues will eventually have to land due to exhaustion or because conditions become unsuitable for flight. After landing, if a beetle contacts woody material it will encounter short range cues that may lead to acceptance of a tree that was not attractive at long-range.

The presence of aggregation pheromones may result in different patterns of acceptance than would be predicted by these experiments. We have not yet tested pheromone production by *O. erosus* in acceptable, unsuitable tree species. Pheromone emission by beetles from unsuitable trees would exacerbate the effects of these trees on an invading population. Conversely, if pheromones were produced only on suitable hosts, it would improve the ability of adults to distinguish suitable trees from unsuitable ones.

Adult acceptance of unsuitable plants is known from systems involving invasive plants and native insects (Badenes-Perez et al. 2006; Barre et al. 2002; Casagrande and Dacey 2007; Graves and Shapiro 2003; Harris et al. 2001). However, the effect of this behavior on the success of an invading insect is rarely considered. If accepted but unsuitable plants were prevalent enough, or preference for these species was strong, accepted unsuitable plants could act as a reproductive sink. Our results suggest that after adults contact bark, *O. erosus* will accept unsuitable tree species, which would be a reproductive dead end. If a beetle population was able to persist in an area over several generations, we should expect strong selection against the acceptance of unsuitable tree species. Therefore, over time this behavior should disappear.

However, if members of a newly-introduced population accept unsuitable tree species, this could create a population sink, decreasing the probability of successful establishment even if suitable host resources were present.

Most species introduced to a new habitat do not establish (Mack et al. 2000; Williamson 1996). Others establish in only some of the areas where they are introduced or have much larger effects in some areas than others (Houston and Valentine 1977; Tobin and Whitmire 2005; Williamson 1999). These experiments show that adults of invading *O. erosus* populations are likely to accept some tree species that are not suitable for the development of their larvae. Laboratory choice experiments and field work will be needed to assess whether unsuitable hosts can act as reproductive sinks. If they do, this would decrease the risk of establishment by invading populations of the beetle. The presence of non-host species that affect insect behavior may help to explain the difficulty in predicting invasion success by potential pest species or biological control organisms (Mack et al. 2000; Williamson 1999; Worner 2002).

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