

Effect of natal and colonised host species on female host acceptance and male joining behaviour of the mountain pine beetle (Coleoptera: Curculionidae) using pine and spruce

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Abstract—The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), outbreak in British Columbia and Alberta, Canada, currently extends over 18.3 million ha of pine forest. The principal host of the insect is lodgepole pine, *Pinus contorta* var. *latifolia* Englemann (Pinaceae) although it is a generalist herbivore on pines. Mountain pine beetles do not typically colonise spruce. However, during the current outbreak, several instances of mountain pine beetle attack on interior hybrid spruce, *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex. Engelm (Pinaceae) have been noted in areas where severe lodgepole pine mortality has occurred. Occasionally, beetle reproduction within spruce has been successful. Reproductive behaviours of mountain pine beetles reared from pine and spruce, such as female host acceptance and male joining behaviour, were studied on bolts of pine and spruce in laboratory bioassays. Females more readily accepted spruce host material relative to pine. Females that developed in spruce had higher rates of host acceptance of both pine and spruce host material than females that had developed in pine. We interpret these latter results with caution, however, as inference is partially restricted by sourcing viable insects from one spruce in this study. Implications of these findings to the concepts of host adaptation and population dynamics of this eruptive herbivore are discussed.

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae), is arguably the most ecologically and economically important phloeo-phagous herbivore in western North America due to its irruptive nature, frequent outbreaks, and wide *Pinus* Linnaeus (Pinaceae) host range (Safranyik and Carroll 2006). Mountain pine beetles, like other bark beetles, are intimately associated with their hosts. The majority of the life cycle of the beetle, with the exception of a brief dispersal flight period among adults, is spent under the bark and within the tissues of host trees (Wood 1982).

Female mountain pine beetles are the host-selecting sex. Female beetles use and integrate host-derived air-borne compounds, close-range visual cues, and gustatory and tactile chemical cues to select potential host trees (Safranyik and Carroll 2006; Saint-Germain *et al.* 2007). Lodgepole (*Pinus contorta* var. *latifolia* Englemann) and ponderosa pine (*P. ponderosa* Douglas ex. Lawson) (Pinaceae) are the most commonly used hosts, although mountain pine beetles will reproduce within almost all native or introduced pine species throughout its range (Wood 1982; Safranyik and Carroll 2006).

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The largest outbreak of mountain pine beetles ever recorded is currently occurring in western North America. In British Columbia and Alberta, Canada, the outbreak has resulted in high levels of pine mortality over 18.3 million ha of pine forest since 1999 (British Columbia Ministry of Forests, Lands, and Natural Resource Operations 2013). Within the central interior region of British Columbia, mountain pine beetles have recently been observed attacking interior hybrid spruce, *Picea glauca* (Moench) Voss × *Picea engelmannii* Parry ex. Engelmann (Pinaceae). Observations of mountain pine beetles attacking spruce have been reported occasionally (Hopkins 1905; Furniss and Schenk 1969; Smith *et al.* 1981) and may occur during beetle epidemics (Wood 1982). Successful brood production by mountain pine beetles within spruce hosts is exceedingly rare (Furniss and Schenk 1969; McKee *et al.* 2013), although reproduction in live, standing spruce, has been documented during the current outbreak in British Columbia where the availability of susceptible lodgepole pine has declined sharply in the terminal phases of the outbreak (Huber *et al.* 2009).

A.D. Hopkins used host colonisation patterns of mountain pine beetles to propose the Hopkins' host selection principle, predicting that adult insects prefer to use the host species in which they developed as larvae (Hopkins 1917). Although Hopkins' theory has been well studied in a variety of insect species, the literature is replete with conflicting results (Barron 2001). Few studies have examined the influence of natal species on the host selection behaviour of the mountain pine beetle. While some studies have not shown support for preferential colonisation of hosts conspecific to their natal species within mountain pine beetle (Richmond 1933; Langor and Spence 1991), data from other studies suggest that natal host fidelity may occur in colonised *Pinus* (Baker *et al.* 1971) and *Picea* Dietrich species (Furniss and Schenk 1969; Smith *et al.* 1981).

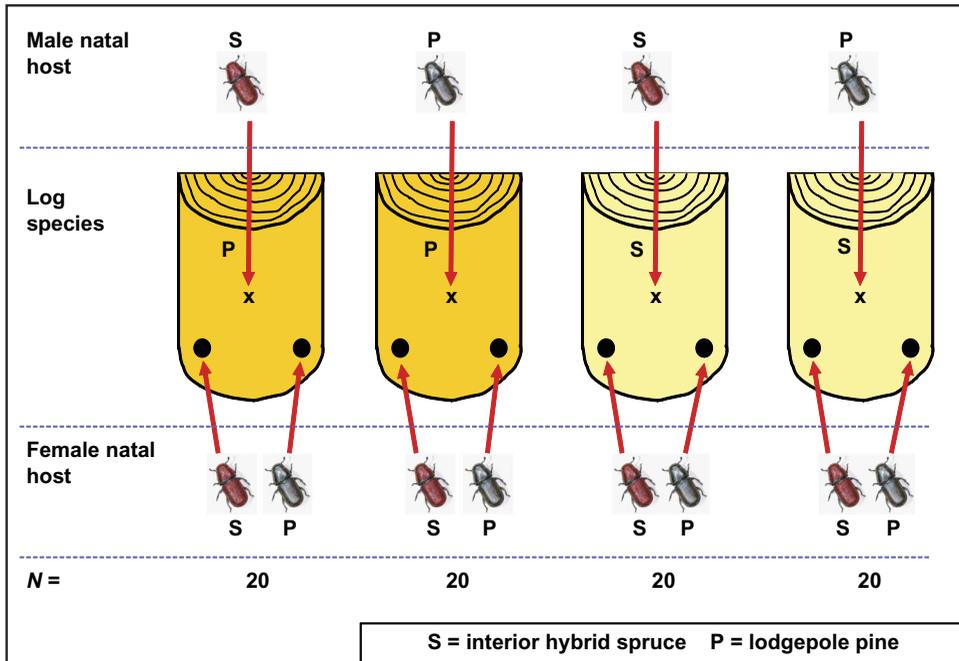
In this study, we took advantage of the rare opportunity of naturally occurring populations of mountain pine beetles developing in lodgepole pine and interior hybrid spruce in a region of British Columbia, Canada, to investigate host selection behaviour of mountain pine beetles from each tree species in cut logs in laboratory bioassays. The objectives of this study were to: (1) test Hopkins' host selection principle by examining the effect of

larval (*i.e.*, natal) host species on host acceptance by female mountain pine beetles, (2) determine if natal host consistency of male and female beetles influences male joining of females in ovipositional galleries within logs of lodgepole pine and interior hybrid spruce, and (3) investigate the effect of host consistency between female natal species and colonised host species on the female-joining behaviour exhibited by males.

Study material of non-infested lodgepole pine and interior hybrid spruce was harvested from a stand near Crassier Creek, British Columbia (55° 38'00''N, 122° 15'00''W). The stand was located in the SBSwk2 (sub-boreal spruce, wet, cool) biogeoclimatic zone, an ecosystem classification system used in British Columbia. This ecosystem is between 750 and 1200 m elevation and has a cool, wet climate supporting forests of interior hybrid spruce, subalpine fir (*Abies lasiocarpa* (Hooker) Nuttall), and lodgepole pine (Meidinger and Pojar 1991). Interior hybrid spruce (hereafter referred to as "spruce") and lodgepole pine (pine) of similar height, health, diameter at breast height (dbh; 1.3 m), and growing under similar site conditions (*i.e.*, soil type, drainage, slope, and aspect) were harvested from a stand judged to be free of outbreaking mountain pine beetles. Two trees of each species were harvested on 5 July 2007. One vehicle transported the nonattacked spruce and pine material, while another vehicle transported infested pine material (see below). Non-attacked logs had the ends sealed with wax to reduce desiccation and were stored outdoors under tarpaulins and used within 10 days of harvest. No colonisation of these logs by secondary bark beetles or wood borers (*e.g.*, Coleoptera: Cerambycidae and Buprestidae) occurred by the time of use.

To obtain insects for bioassays, two spruce, naturally colonised by mountain pine beetles were obtained from Prince George, British Columbia, Canada (N 53°53'00'' W 122°48'00'') on 29 June 2007. Similarly, two pines colonised by mountain pine beetles under natural field conditions were harvested from Crassier Creek, British Columbia, on 5 July 2007. The infested trees each contained teneral mountain pine beetle adults. The infested spruce and pines were split into slabs, keeping the outer bark intact. The slabs were placed in emergence containers in the laboratory at 22 °C under 24 hour illumination. Beetles were collected daily from transparent collecting jars that contained

Fig. 1. Experimental design for the examination of natal host and host species effects on host acceptance by female mountain pine beetles, and the joining behaviour of male mountain pine beetles with females in their ovipositional galleries. Beetles denoted with an “S” and those denoted by the letter “P”, are individuals reared from interior hybrid spruce and lodgepole pine hosts, respectively. Logs denoted “S” and “P” are interior hybrid spruce and lodgepole pine, respectively. The “X” on the logs indicates the point of male release.



moist Kimwipes[®] (Kimberly-Clark Corp., Neenah, Wisconsin, United States of America). Due to heavy predation by cerambycid larvae, and an attempt to use beetles of the same age and vigour, the spruce-reared beetles in this study were sourced from a single tree. Emergent beetles were separated by sex and natal host species, stored at 5 °C as described in Safranyik (1976), and provided either spruce or pine phloem as reared from a spruce or pine host, respectively. Only vigorous females ≤ 7 days old were used in the experiments.

Twenty bolts of each species were cut from the noncolonised spruce and pine trees. Bolts were 15 cm in length with diameters of 14.4 ± 0.6 and 15.9 ± 0.1 cm (mean \pm SE) for the pine and spruce bolts, respectively. Each bolt was then split lengthwise to yield two equal halves (half-bolts). All cut surfaces were coated with molten paraffin wax to reduce desiccation. In total, 40 spruce and 40 pine half-bolts were prepared in this manner.

Two female mountain pine beetles, one reared from spruce and one reared from pine, were

introduced into each half-bolt, using 160 females in total (Fig. 1). Females were introduced to each half-bolt using starter holes located at the bottom of each bolt. The starter holes were 3 mm in diameter, drilled through the bark to the phloem layer, oriented parallel to the cut edge (*i.e.*, horizontally), and spaced as far from each other as possible while maintaining a 3 cm distance from any wood/bark edge (Fig. 1). This would allow female beetles to excavate ovipositional galleries while minimising encounters with potentially desiccating phloem. A single female was inserted into each starter hole using forceps. The hole to which pine-reared and spruce-reared females were introduced was determined randomly. Four females that did not enter the phloem within 1 minute of introduction were not included in the study. Each female beetle was used only once. Aluminium screening stapled over the starter holes allowed a female to exit the starter hole, but not escape. Half-bolts containing a pair of females at the bottom were stored vertically in

individual, ventilated plastic containers in a common rearing room at 22 °C.

Twelve hours after female ovipositional gallery construction, the aluminium screening was removed and a single, vigorous, male beetle ≤ 7 days old was released at the center of each half-bolt. Of the 40 spruce half-bolts, 20 received a male reared from spruce and 20 received a male reared from pine. Males were distributed in an identical manner on the 40 pine half-bolts (Fig. 1). After male release onto the bark, the half-bolts were stored as above for an additional 12 hours.

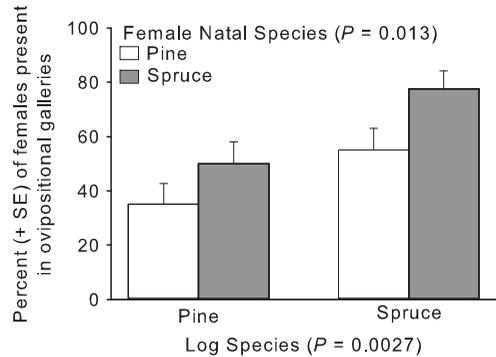
After 12 hours (24 hours from experiment initiation), the bark was removed from each half-bolt to record female host acceptance and male presence within female ovipositional galleries. Female host acceptance was defined as being present within an ovipositional gallery excavated by the beetle with boring dust present. Female host rejection was an abandonment of the starter hole, or, having not initiated ovipositional gallery construction. Males were recorded to have joined a female if the ovipositional gallery contained the male. Because body size can influence the mate selection behaviours of mountain pine beetles (Reid and Baruch 2010), male and female beetles were measured for size using the width of the pronotum at the widest point. Since there was no effect of body size influencing beetle mate-joining behaviours (analysis of variance, $F(1,11) = 1.02$, $P = 0.33$), the results are not shown.

Host acceptance by females was first examined from a female natal-species perspective (*i.e.*, do females preferentially accept hosts that are conspecific to their natal host?) and second from a host-species perspective (*i.e.*, do females prefer spruce versus pine hosts regardless of natal species?). Data were analysed using a generalised linear mixed effects model incorporating female host acceptance/rejection as the binomial response variable, female natal species and host species as fixed effects, and half-log (replicate) as a random effect. Statistical analyses were performed using R (R Development Core Team 2009).

Because only 25 males were found in ovipositional galleries at the end of the experiment, we were unable to analyse natal or present host species effects with respect to male joining patterns (*i.e.*, objectives 2 and 3) and these results are not presented.

Females reared from the spruce had higher rates of host acceptance of both pine and spruce host

Fig. 2. Percentage (+SE) of female mountain pine beetle acceptance of interior hybrid spruce or lodgepole pine hosts by females reared from interior hybrid spruce or lodgepole pine hosts. Host acceptance was defined as the presence of a female within an ovipositional gallery 24 hours after introduction to a pine or spruce log. $n = 40$ females per treatment.



material, relative to females that were reared from pine ($Z = 2.484$, $P = 0.013$). In addition, females reared from either host species were more likely to accept spruce rather than pine material ($Z = 3.003$, $P = 0.0027$) (Fig. 2).

The results of this study do not support Hopkins' host selection principle, since female mountain pine beetles did not preferentially colonise the species of log that was conspecific to their natal host. However, our finding that the female mountain pine beetles reared from the spruce demonstrated higher rates of host acceptance than those reared from pine is consistent with the theory that the frequency of genotypes promoting host discrimination declines with increasing population size (Raffa and Berryman 1983; Wallin and Raffa 2002, 2004). During mountain pine beetle outbreaks, the most suitable hosts are preferentially colonised early and are thus not available to beetles in the later phases of the infestation (Amman 1972; Safranyik and Carroll 2006). Hence, beetles colonising spruce may be a symptom of declining host specificity exhibited by the highest density populations coupled with the lowest availability of pine hosts, at the centre of the outbreak. The progeny of such beetles may be genetically or environmentally predisposed to attack non-hosts, as has been seen during past outbreaks (Wood 1982).

Although it would have been more desirable to collect pine-reared and spruce-reared beetles from multiple hosts within the same geographic region, this was not possible due to the scarcity of colonised pines remaining in the centre of the outbreak where we obtained colonised spruces, and the rarity of successful spruce colonisation on the northern edges of the outbreak where the lodgepole pines had not yet been exhausted (Aukema *et al.* 2006; Huber *et al.* 2009). Because the host types for rearing insects were thus necessarily confounded with location and population density, we are not able to unequivocally evaluate the effects of spruce and pine on host acceptance behaviour and exclude alternate hypotheses such as those involving population density. Previous work with *Dendroctonus rufipennis* (Kirby) in spruce, however, has demonstrated that development within well-defended hosts can elevate rates of host entrance relative to individuals from weaker hosts (Wallin and Raffa 2004). A decline in discrimination with increased population density and possible increased aggressive tree-killing behaviour by progeny reared from spruce are consistent with the female colonisation behaviour noted in this study.

Aspects of spruce chemistry may have promoted its acceptance by female beetles relative to pine material. For instance, β -phellandrene, δ -3-carene, α -pinene, β -pinene, and limonene stimulate ovipositional gallery initiation and construction activities by mountain pine beetles (Raffa and Berryman 1982). Resins of interior hybrid spruce contain greater quantities of δ -3-carene, α -pinene, and β -pinene relative to lodgepole pine, although the latter does contain more limonene and β -phellandrene (Pureswaran *et al.* 2004). Physical properties of the phloem such as moisture content and thickness may also have differed between host types and affected female colonisation behaviour (Amman 1972). Care was taken, however, to harvest host material from similar sites, visually assessing host vigour and processing experimental material in identical manners to minimise differences in tree and/or phloem characteristics.

Aside from plant characteristics, lipid content of insects may affect propensity to accept hosts (Wallin and Raffa 2004). Lipid content in mountain pine beetles is positively correlated with beetle size (Graf *et al.* 2012). In this study there were no

significant differences between beetles from spruce and pine (F.R.M., unpublished data), so lipid content likely did not influence host selection behaviours by females.

We note some limitations of our study. First, caution must be exercised in casting wide inference regarding natal effects of insects emerging from spruce, as the spruce-reared insects used in the bioassays were reared from a single tree. This limitation makes it difficult to determine unequivocally if Hopkins host selection principle is upheld by this study, although the data suggest it is not, as the highest rates of female host acceptance did not occur consistently within the natal host species of spruce-reared and pine-reared females. Second, our assays used harvested logs rather than live trees. Under natural conditions, trees resist beetle attack by employing toxic terpenoid-based compounds (Trapp and Croteau 2001; Huber *et al.* 2004) in a complex and dynamic defensive strategy involving constitutive and induced resin defences that interacts with colonising bark beetles to influence or prevent host colonisation (Raffa and Berryman 1983). Finally, host-species and geographic effects are necessarily confounded for the insects used in this study. Recent studies, however, do not support host-associated genetic divergence of mountain pine beetles (Kelley *et al.* 2000; Mock *et al.* 2007). Moreover, long distance dispersal of mountain pine beetles in the present outbreak (de la Giroday *et al.* 2011) reduce localised genetic divergences (Samarasekera *et al.* 2012). Thus it is unlikely that genetic traits arising from host or geographic origin would have influenced the behaviours of the insects in our study.

The most prominent barrier to sustained use of spruce hosts by mountain pine beetles is likely the susceptibility of spruce to beetle attack. Successful reproduction of eruptive bark beetles is often dependent upon the death of all, or part, of the host tree (Wood 1982). Host susceptibility and subsequent suitability are thus critical factors governing the reproduction of bark beetles (Raffa and Berryman 1983). Our study and the work of others (Furniss and Schenk 1969; Smith *et al.* 1981; Safranyik and Linton 1983; Huber *et al.* 2009) suggest that all potential pine and spruce hosts within a forest exist on a bi-axial continuum of susceptibility and suitability. The constitutive and induced defensive capacity of spruce usually

renders the tree highly unsusceptible to mountain pine beetle colonisation (Furniss and Schenk 1969; Smith *et al.* 1981). However, these hosts may be quite suitable for mountain pine beetle brood development if host constitutive and induced defences can be overcome (Huber *et al.* 2009; McKee *et al.* 2013).

Previous studies have demonstrated that mountain pine beetles can successfully reproduce within the tissues of *Picea* species (Furniss and Schenk 1969; Smith *et al.* 1981; Safranyik and Linton 1983; Huber *et al.* 2009). In the present study, we demonstrated that mountain pine beetles that develop within naturally colonised spruce exhibit an increased propensity to colonise both spruce and pine host material relative to beetles reared from pine hosts. Although spruce-reared beetles under natural conditions may exhibit an increased aggressiveness when colonising spruce and pine hosts, the rarity of successful spruce colonisation events in the central interior of British Columbia strongly suggests that widespread mortality of spruce is highly unlikely even within regions containing extremely dense beetle populations and low pine host availability.

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