Comparisons of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) reproduction within a novel and traditional host: effects of insect natal history, colonized host species and competitors

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Abstract
1 During host-breadth expansion, phytophagous insects incur risk from potentially deleterious novel host environments at the same time as potentially securing a potential escape in space or time from competing species.
2 Bark beetles reproduce under the bark of stems and branches of mature, stressed or moribund trees, and may suffer high mortality from plant defences and inter- and intraspecific competition.
3 An epidemic of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) in western Canada has extended to over 18.1 million hectares of lodgepole pine (*Pinus contorta* Douglas ex. Loudon) forests.
4 In some areas, mountain pine beetles have been found to reproduce within interior hybrid spruces [*Picea glauca* (Moench) Voss × *engelmannii* Parry ex. Engelmann], a normally rare occurrence.
5 Using mountain pine beetles reared from naturally-infested interior hybrid spruce and lodgepole pine hosts, we examined the effect of female natal species and colonized host species on the ability to attract mates and reproduce within spruce and pine logs deployed as a choice assay in a field setting. Additionally, we examined whether the arrival and reproduction of competitors such as pine engravers (*Ips* spp.) was associated with reduced brood production.
6 Females reared from pine and spruce exhibited similar reproductive potentials. Recruitment and establishment of ovipositional galleries, larval galleries and pupal chambers were similar in the typical and novel hosts.
7 Reproduction by mountain pine beetles in spruce, although successful, was significantly lower than in pine. This reduction occurred despite spruce logs being almost entirely free of competing secondary beetles.

Keywords *Dendroctonus ponderosae*, host breadth, host fidelity, interspecific competition, mountain pine beetle, natal effects, novel host, reproduction.

Introduction

Among phytopagous insects, reproductive success can be affected by insect–plant, conspecific and interspecific interactions (i.e. competition). Plant-specific physical and chemical properties can affect maternal fecundity (Awmack & Leather, 2002), patterns of oviposition (Murphy & Feeny, 2006), ovipositional effort (Hopkins & Ekbom, 1999), larval fitness (Reid, 1963; Langor, 1989) and survivorship (Courtney & Kibota, 1990; Cudmore *et al*., 2010). Similarly, intra- and interspecific competition can have important consequences on larval and adult fitness (Anderbrant *et al*., 1985; Langor, 1989; Feder *et al*., 1995; Kaplan & Denno, 2007), survival (Bergvinson & Borden, 1991; Zvereva *et al*., 2010), mate attraction (Anderbrant *et al*., 1985) and reproductive success (Boone *et al*., 2008). Moreover, the availability, physical properties,

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nutritional quality and allelochemistry of host plants can be important mediators of competition (Denno *et al*. 1995).

In addition to host–plant interactions, diet breadth can also affect the population dynamics of phytophagous insects (Ehrlich & Murphy, 1988; Denno *et al*., 1995; Kaplan & Denno, 2007). Population sizes may decrease when preferred hosts are rare (Singer, 1982) but increase if successful oviposition and development occurs on novel plants (Courtney & Kibota, 1990). Novel host use poses potential physiological complications (Bush, 1969; Kelley & Farrell, 1998). Stabilizing selective pressures (e.g. reductions in resource competition) may offset initial increases in mortality and allow insect populations to adapt to the new host plant (Feder *et al*., 1995; Zvereva *et al*., 2010). It is hypothesized that such circumstances can lead to continued use of the novel plant and increase polyphagy among herbivorous insects (Price *et al*., 1980).

In some instances, polyphagy on novel hosts can facilitate range expansions of herbivores (Stastny *et al*., 2006). Colonizing plant hybrids may facilitate the evolutionary and physiological processes of switching to a novel host (Floate & Whitham, 1993; Pilson, 1999).

The bark beetles (Coleoptera: Curculionidae) comprise a taxonomic group that demonstrate close associations with their host plants. These insects typically utilize aggregation pheromones to attract conspecifics and colonize the subcortical tissues of trees. Host plant chemistry is a primary factor in reproductive success because host compounds can repel attacks (Raffa & Berryman, 1983), serve as precursors for mate-attracting pheromones (Seybold *et al*., 2006) and can synergize or inhibit insect responses to pheromones (Erbilgin & Raffa, 2000; Erbilgin *et al*., 2003). Numerous studies have investigated the effects of host trees on various aspects of bark beetle–host interactions, such as host orientation and selection (Shepherd, 1966; Elkinton & Wood, 1980; Campbell & Borden, 2006), host colonization dynamics (Berryman & Ashraf, 1970; Raffa & Berryman, 1983), semiochemical communication (D.L. Wood, 1982; Seybold *et al*., 2006) and reproductive success (Reid, 1963; Amman, 1982; Raffa & Berryman, 1987; Reid & Robb, 1999). Because bark beetles are endophytic phloeophagous herbivores that spend the majority of their life cycle within the confines of the host plant, at within-tree scales, bark beetle reproduction may be significantly affected by plant chemistry (Reid & Gates, 1970; Raffa & Berryman, 1983; Franceschi *et al*., 2005; Boone *et al*., 2011). Additionally, the aggregative behaviour of bark beetles, combined with the necessity to feed on a discreet and limited phloem resource, exposes these insects to direct competition with a variety of confamilial and wood-boring competitors (S.L. Wood, 1982).

The present study takes advantage of an enormous outbreak of mountain pine beetle in western Canada (Aukema *et al*., 2006; Raffa *et al*., 2008; Samarasekera *et al*., 2012) to examine questions of novel or atypical host use in an eruptive herbivore. In this system, the female is the host-selecting sex. The beetles vector blue-staining fungi that, in combination with the pheromone-mediated mass attack, can collectively exhaust host defences (Safranyik & Carroll, 2006). During outbreaks, the insect kills its host during reproduction, typically exhibiting a univoltine life cycle. Although the primary host of the mountain pine beetle in British Columbia is considered to be lodgepole pine (*Pinus contorta* Douglas ex. Loudon), the insect will attack most available species of pines, potentially facilitating novel range expansions (Safranyik *et al*., 2010). In western Canada, there is heightened concern of the potential range expansion of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) (Coleoptera: Curculionidae) through a hybrid zone of lodgepole pine × jack pine (*P. banksiana* Lambert) (Pinales: Pinaceae) into the novel jack pine hosts that stretch across the boreal forest of Canada (Safranyik *et al*., 2010; Cullingham *et al*., 2011; de la Giroday *et al*., 2012). Moreover, Huber *et al*. (2009) recently reported the successful reproduction of mountain pine beetle in interior hybrid spruce [*Picea glauca* (Moench) Voss × *engelmannii* Parry ex. Engelmann] (Pinales: Pinaceae), where beetle reproduction within the atypical spruce hosts exceeded reproduction within lodgepole pine hosts attacked nearby. Successful reproduction within alternative hosts by mountain pine beetles may aid in prolonging the beetle outbreak in areas where pine host availability has been reduced by extensive beetle activity. Also, because exposure to novel hosts can pre-adapt insects to other novel hosts (Jaenike, 1983), there is a minimal but not zero concern that mountain pine beetle reproduction within spruce hosts could pre-adapt the beetle to attack other conifer species encountered as the insect continues to expand its geographical range eastward into novel areas of the Canadian boreal forest.

We examined sympatric reproduction of mountain pine beetles in lodgepole pine and an atypical host, interior hybrid spruce (hereafter referred to as 'pine' and 'spruce', respectively). The present study aimed to examine the effects of natal host and colonized host species on the reproductive potential of mountain pine beetles and determine the extent of successful reproductive behaviour in usual and atypical hosts in a field experiment using cut logs. We also measured the arrival and reproduction of naturally recruited competitor species to the infested pine and spruce logs, aiming to examine whether mountain pine beetle reproduction in an atypical host might confer reproductive advantages by reducing interspecific competitive interactions.

Materials and methods

Experimental set-up

Female mountain pine beetles from both spruce and pine were obtained from naturally colonized material. Mountain pine beetle-colonized spruce and pines were harvested near Prince George (53°53′00″N 122°48′00″W) and Crassier Creek (55°38′00″N, 122°15′00″W), British Columbia, respectively. Colonized material was transported to the laboratory and placed in rearing chambers. After emergence, beetles were provided with phloem and stored at 5 °C in an environmental chamber. Only vigorous females (assessed by a visual inspection of activity) that were ≤ 7 days old were selected for use in the experiments.

Uninfested spruce and pines for the bioassays were harvested near Crassier Creek, British Columbia. The sites where tree harvest occurred were located in the SBSwk2 biogeoclimatic zone, a land classification system used in British Columbia.

This ecosystem is found at elevations between 750 and 1200 m and is characterized by a cool, wet climate supporting forests of mixed interior hybrid spruce, lodgepole pine and subalpine fir [*Abies lasiocarpa* (Hooker) Nuttall] (Meidinger & Pojar, 1991). Spruce and pine trees of similar height, growing conditions, and diameter at breast height (diameter measured on the bole at 1.3 m above the ground) were selected from the same geographical area to reduce qualitative and quantitative chemical variation in resin quality (Pureswaran *et al.*, 2004) as a result of environmental or geographical factors. Trees were cut in stands that were free of epidemic beetle activity, and stands in the area were just beginning to exhibit mortality as a result of local immigration events from the larger epidemic (Aukema *et al.*, 2006). Trees were felled and cut into 2.5-m logs. After transport to the laboratory, the ends of the logs were sealed with molten paraffin wax to reduce desiccation. Logs were stored under sealed tarpaulins to avoid colonization by secondary bark beetles such as *Ips* spp. or wood borers (Coleoptera: Cerambycidae and Buprestidae). Within 2 days of collection, the 2.5-m logs were sectioned into smaller experimental logs (length 40 cm) with mean ± SE diameters of 21.1 ± 0.4 cm and 21.9 ± 0.5 cm for spruce and pine, respectively. After sectioning, the cut ends of the experimental logs were sealed with paraffin wax to reduce desiccation.

The present study consisted of four treatments in a 2 × 2 present host × natal host factorial design. Two treatments consisted of previously uninfested spruce and pine logs that had been colonized in the laboratory with female mountain pine beetles reared from spruce. The remaining two treatments consisted of previously uninfested spruce and pine logs colonized in the laboratory with female mountain pine beetles reared from pine.

For laboratory colonization of fresh logs with females, five females were inserted equidistant from each other around the base of each log at a distance of 5 cm from the cut and sealed edge. The females were inserted via 3-mm diameter starter holes drilled through the outer bark into the interface with the phloem layer. A single female was then gently inserted into each hole using soft forceps. A small piece of aluminum screening was used to cover the gallery entrance to reduce female abandonment when tunnelling. The screening was fixed such that a female could exit the starter hole but not escape the log. Inserted females were monitored over a 24-h period for host acceptance and ovipositional gallery construction, judged by visible frass production at the gallery opening. Screening was not removed until transport of logs to the field site had occurred.

After the 24-h monitoring period, logs were transported to the field site. The logs were set upon metal stakes 2 m in height. A 12-funnel Lindgren multiple funnel trap (Lindgren, 1983) was hung from the log via a 30-cm length of wood fastened to the top of each log. This trap is particularly effective for capturing larger-bodied insects. Smaller insects were captured using a section of vinyl screening (12.5 × 20 cm) coated with Tanglefoot insect adhesive (The Tanglefoot Company, Grand Rapids, Michigan). These sticky screens were fastened on the surface of each log using black pushpins.

The experiment was deployed in a randomized complete block design in a lodgepole pine stand near Chief Lake, British Columbia, Canada (54°21′00″N 122°59′00″W). The treatments in each block included four artificially infested logs (two spruce and two pine, with one of each species infested with females emerged from pine, and the other infested with females emerged from spruce), as well as two uninfested control logs (one spruce and one pine log) (Fig. 1). Each log was randomly positioned at one of six equidistantly-spaced points within a circular pattern with a radius of 3.5 m. Each log served as the attractant for its associated pair of traps (one Lindgren trap and one sticky screen). In total, 12 blocks each consisting of six trap pairs each were deployed over the period 14–16 July 2007.

Insects were collected both from funnel traps and from sticky screens at 5 day intervals over the predominant flight period for mountain pine beetle from initial field deployment until 16 August 2007. Upon collection, insects were stored at −20 °C
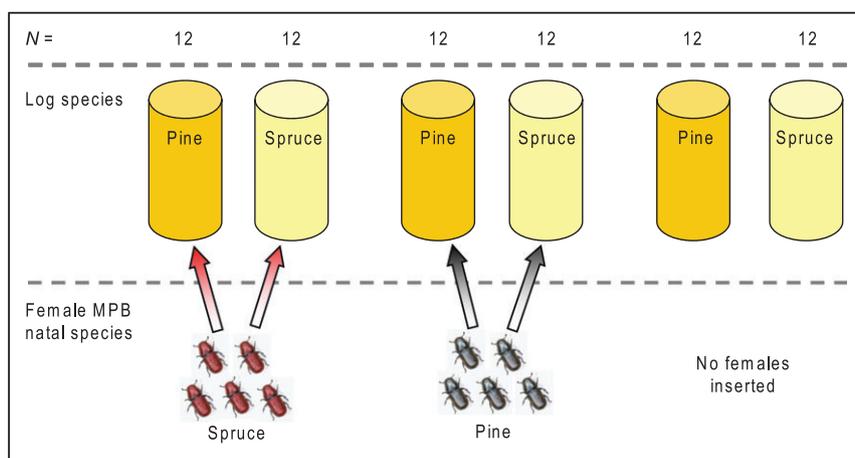

Figure 1 Experimental design for the examination of natal host and present host species effects on the reproductive potential of female mountain pine beetles (MPB) in interior hybrid spruce and lodgepole pine logs. Beetles labelled 'Spruce' and those labelled 'Pine' are individuals reared from interior hybrid spruce and lodgepole pine hosts, respectively. Logs denoted 'Spruce' and 'Pine' are interior hybrid spruce and lodgepole pine, respectively. Control logs did not contain manually inserted female mountain pine beetles.

until they could be identified and counted. On 16 August, all of the logs were transported to the laboratory and were placed in rearing containers in a greenhouse at 24 °C under an LD 15 : 9 h photocycle. Insects that emerged were collected from the rearing containers every 5 days from 22 August until 29 November, after which no further emergence occurred. Collected specimens were stored at −20 °C until identification. Bark was removed from the experimental logs in April 2008 to examine the colonization patterns of various species of bark beetles using the distinctive patterns of reproductive galleries etched in the wood (S.L. Wood, 1982).

Statistical analysis

We used two-factor analysis of variance to analyze the effects of natal species of pioneer females as well as host species on mountain pine beetle attraction measured as the number of beetles captured in the Lindgren trap and the sticky screen. We evaluated two response variables to measure mountain pine beetle attraction: (i) total attraction to each treatment and (ii) total attraction per colonizing female because some females abandoned the logs after transport to the field. Analyses were conducted in a mixed-effects framework with natal and host species as fixed effects and block as a random effect. A subset of analyses excluded the control logs to evaluate the effects of logs containing female pioneer insects on insect attraction. We also tested whether the tree from which the log had been cut, or the log's diameter, influenced attraction. Because these variables did not have any significant effect, the results are not presented.

Upon peeling the bark from the logs after all insects had emerged, we recorded the number of female ovipositional galleries established per log, total ovipositional gallery length per log, ovipositional gallery length per female, number of larval galleries per female, and the number of pupal chambers per female. The number of offspring produced per female was determined by dividing the number of emergent brood per log by the number of established ovipositional galleries per log. The number of offspring produced per log (standardized by phloem surface area) was also determined. Additionally, the number of ovipositional gallery abandonments by females per log was measured (i.e. galleries less than 2 cm in length). All recorded data pertained only to female mountain pine beetles that were manually inserted into the experimental logs within the laboratory. Such females are hereafter referred to as 'pioneer' beetles. We used a similar mixed effects framework for each analysis, with fixed effects of natal species of female beetles and log species, and block as a random effect.

To examine the effects of interspecific competition, we also investigated how the number of mountain pine beetle pupal chambers and emerging progeny within each treatment varied with respect to the number of parental galleries constructed by the secondary bark beetles *Ips pini* (Say), *Pseudips mexicanus* (Hopkins), and *Orthotomicus latidens* (LeConte). Substantial trap catches of *I. pini* in the field allowed statistical analyses to be performed for this species individually. However, as a result of the low catch numbers, *P. mexicanus* and *O. latidens* were pooled with *I. pini* data for the analysis of a generalized competitor complex. The three species also were pooled for all emergence data.

Similar to analyses of capture of mountain pine beetle, the data for *I. pini* or the competitor complex were analyzed with respect to natal species of female mountain pine beetle and log species with block as a random effect. Again, for quality control, we also determined whether the tree from which the log had been cut or the log's diameter influenced attraction. Because it was found that this was not the case, the results are not presented.

In all analyses, data transformations, such as $\sqrt{(y)}$, were utilized as necessary to satisfy model assumptions of normal distribution of residuals and homoscedasticity. All statistical analyses were performed using R (R Development Core Team, 2009).

Results

Attraction, colonization and reproduction of mountain pine beetles

Mountain pine beetles exhibited differential attraction to the logs deployed in the field because logs with tunnelling beetles captured more than the controls ($F_{5,55} = 3.45$, $P = 0.0088$). There were no differences in the number of arriving mountain pine beetles captured with respect to natal species of the inserted female colonizers ($F_{1,33} = 0.23$, $P = 0.64$) or host species ($F_{1,33} = 0.32$, $P = 0.57$) (Fig. 2a). On average, spruce logs containing spruce- and pine-reared females attracted 55.0 ± 31.1 and 33.9 ± 9.6 (mean ± SE) mountain pine beetles per 5-day period, respectively. Pine logs attracted 29.8 ± 6.5 and 32.5 ± 7.2 beetles, for spruce- and pine-reared females, respectively. Control spruce and pine logs attracted 17.3 ± 3.9 and 22.5 ± 3.5 mountain pine beetles over the same time periods.

We found post-hoc when peeling the logs that female beetles inserted in the laboratory did not always continue tunnelling in the log once deployed to the field. The number of abandonments by pioneer females was greatest in spruce hosts ($F_{1,33} = 5.35$, $P = 0.0271$), regardless of female natal species ($F_{1,33} = 0.98$, $P = 0.33$). Pine- and spruce-reared females averaged 1.3 ± 0.5 and 1.6 ± 0.5 abandonments per spruce host, respectively, whereas such females showed 0.3 ± 0.2 and 0.8 ± 0.3 abandonments per pine host (of five originally inserted females). Four logs of each pine treatment attracted one or two conspecific colonizers in the field, as judged by gallery starts away from the laboratory-inserted females when the logs were peeled. However, despite the occasional abandonment or recruitment, the number of established ovipositional galleries per m² in colonized logs did not vary by treatment ($F_{3,33} = 0.54$, $P = 0.66$). Similar to the number of beetles attracted to the logs, the number of ovipositional galleries established by female pioneers was neither influenced by host species ($F_{1,33} = 1.03$, $P = 0.32$), nor the natal species of the inserted females ($F_{1,33} = 0.035$, $P = 0.85$). Colonized pine logs had a mean ± SE of 14.5 ± 0.9 and 15.3 ± 1.2 ovipositional galleries per m² for pine- and spruce-reared females, respectively, whereas colonized spruce logs had 14.0 ± 2.1 and 12.6 ± 1.7 ovipositional galleries per m² for pine- and spruce-reared females, respectively.
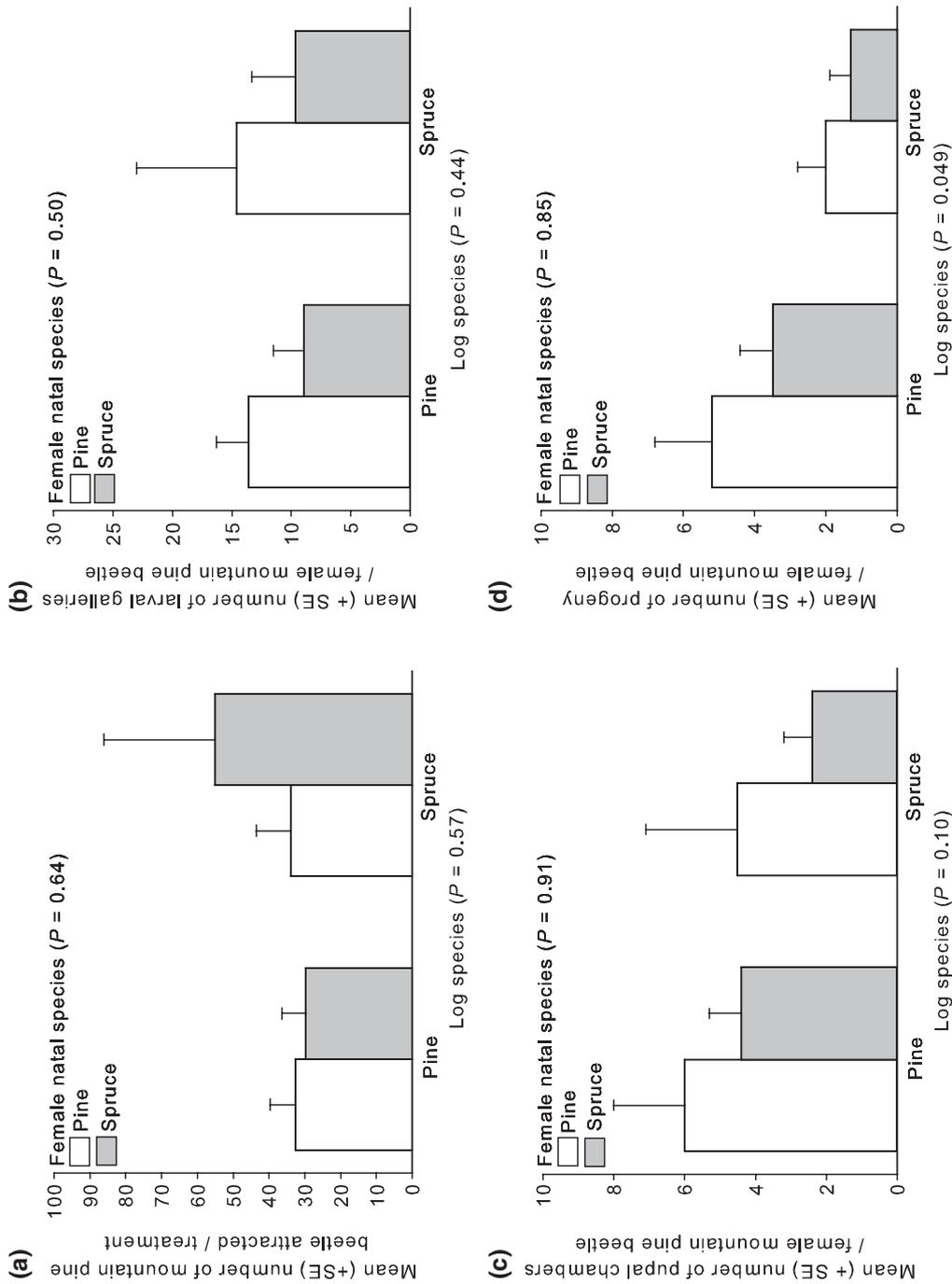
Figure 2 Effect of natal host of origin and present host on the reproduction of mountain pine beetle. White and grey shading represent logs laboratory-colonized with female mountain pine beetle (*n* = 5) reared from pine and spruce natal hosts, respectively (*n* = 12 replicates per log- and female mountain pine beetle natal-species combination). (a) Mean ± SE number of mountain pine beetles attracted to each treatment during the study period. (b) Mean ± SE number of larval galleries per manually inserted female mountain pine beetle per treatment. (c) Mean ± SE number of pupal chambers per manually inserted female mountain pine beetle per treatment. (d) Mean ± SE number of brood produced per manually inserted female mountain pine beetle per treatment.

On a per-female-basis, female pioneers reared from either natal host species within spruce logs attracted approximately two-fold greater numbers of mountain pine beetles than females with conspecific natal species within pine logs ($F_{1,32} = 5.33$, $P = 0.0276$). Each pine- and spruce-reared female within spruce logs attracted a mean $\pm$ SE of 12.1 ± 3.2 and 16.1 ± 8.1 mountain pine beetles per 5-day period, respectively. Pine- and spruce-reared females in pine logs attracted a mean $\pm$ SE of 6.4 ± 1.5 and 7.9 ± 2.0 mountain pine beetles, respectively. Mountain pine beetle attraction per female pioneer was not affected by the females' natal host species ($F_{1,32} = 0.27$, $P = 0.60$).

The total length of female ovipositional gallery constructed per log did not differ across treatments ($F_{3,33} = 1.92$, $P = 0.15$). On a per female basis, ovipositional gallery lengths in pine logs showed a mean $\pm$ SE of 15.8 ± 2.8 cm and 13.1 ± 2.0 cm for pine- and spruce-reared females, respectively. In spruce logs, per female ovipositional gallery length showed a mean $\pm$ SE of 14.0 ± 5.1 cm and 11.0 ± 2.2 cm for pine- and spruce-reared females, respectively. These lengths were similar with respect to female natal host species ($F_{1,32} = 0.09$, $P = 0.76$) and log species ($F_{1,32} = 1.75$, $P = 0.20$). The SD for ovipositional gallery length per pioneer female was also similar with respect to female natal species and log species because neither factor influenced this measurement ($F_{1,32} = 0.04$, $P = 0.85$ and $F_{1,32} = 1.39$, $P = 0.25$, respectively).

Ovipositional behaviour and larval performance was similar in both hosts, regardless of the host of origin of the female pioneers. The mean number of larval galleries per pioneer did not vary with female natal species ($F_{1,32} = 0.47$, $P = 0.50$) or the species of log colonized ($F_{1,32} = 0.620$, $P = 0.44$) (Fig. 2b). On average, there were 13.6 ± 2.9 and 8.9 ± 2.6 larval galleries per female for pine- and spruce-reared individuals within pine logs versus 14.8 ± 8.4 and 9.6 ± 3.7 larval galleries per pine- and spruce-reared female, respectively, within spruce logs. The numbers of pupal chambers per female were approximately one-third the numbers of larval galleries. The mean $\pm$ SE number of pupal chambers within pine logs was 6.0 ± 2.0 and 4.4 ± 0.9 for females reared from pine and spruce hosts, respectively. The mean $\pm$ SE number of pupal chambers in spruce logs per female was 4.5 ± 2.6 and 2.4 ± 0.8 for pine and spruce-reared females, respectively. Again, neither female natal host ($F_{1,32} = 0.01$, $P = 0.91$) or log species ($F_{1,32} = 2.80$, $P = 0.10$) affected this measurement (Fig. 2c).

Although the establishment and colonization dynamics of female mountain pine beetles were similar among natal hosts and log species, there were differences in reproductive output. The number of brood produced per mountain pine beetle female was higher in pine versus spruce ($F_{1,32} = 7.95$, $P = 0.0493$). Brood production in pine logs containing pine- and spruce-reared females showed a mean $\pm$ SE of 5.2 ± 1.6 and 3.5 ± 0.9 offspring, respectively. Brood production in spruce logs was less than half of that observed in pine logs, showing a mean $\pm$ SE of 1.9 ± 0.9 and 1.3 ± 0.6 offspring for pine- and spruce-reared females, respectively (Fig. 2d). There were no effects of female natal species on the number of progeny ($F_{1,32} = 0.18$, $P = 0.67$). The results did not change when emergence results were standardized by log (i.e. phloem) surface area. Host species ($F_{1,33} = 9.84$, $P = 0.0036$) but

not maternal natal species ($F_{1,33} = 1.75$, $P = 0.20$) influenced brood production. Thus, it appeared that colonization and establishment were similar up to the pupal life stages, where many developing mountain pine beetles died in spruce.

Effects of competitors on the emergence of mountain pine beetles

Overall, the competitor complex arriving to and reproducing within logs was much higher for pine than spruce logs. More *I. pini* were captured arriving to traps baited with pine logs versus spruce ($F_{1,33} = 7.31$, $P = 0.0107$), showing a mean $\pm$ SE of 10.4 ± 3.9 for pine compared with only 1.7 ± 0.3 per 5 day for spruce, pooled across treatments, respectively. Natal species of female mountain pine beetle colonizers did not affect trap captures ($F_{1,33} = 0.94$, $P = 0.34$). A similar pattern was noted when all of the competitors (*I. pini*, *P. mexicanus* and *O. tomicus*) were pooled. The attraction of the competitor complex was not related to natal species of female mountain pine beetle colonizers ($F_{1,33} = 1.13$, $P = 0.30$), although it was related to host species ($F_{1,33} = 25.89$, $P < 0.0001$), with pine being more attractive. Traps baited with pine logs captured between 5.6- and 16.7-fold more individuals than spruce logs (Fig. 3a). *Ips pini*, *O. latidens* and *P. mexicanus* accounted for 74%, 20% and 6% of captured competitors ($n = 165$) within pine logs colonized by pine-reared female mountain pine beetles. Pine logs colonized by spruce-reared female mountain pine beetles attracted 266 competitors, of which, *I. pini*, *O. latidens* and *P. mexicanus* accounted for 61%, 19% and 20%, respectively. The attraction of the competitor species to spruce logs was extremely low compared with pine. Traps baited with spruce logs colonized by pine-reared female mountain pine beetles captured a total of 29 competitors consisting of 25 *I. pini*, 1 *O. latidens* and 3 *P. mexicanus*, whereas traps baited with spruce logs colonized by spruce-reared female mountain pine beetles captured 14 *I. pini* and only one *O. Latidens* in total.

The density of ovipositional galleries constructed by competitor species was greatest within the colonized pine logs compared with spruce ($F_{1,33} = 46.20$, $P < 0.0001$). Pine logs containing female mountain pine beetles reared from pine or spruce showed a mean $\pm$ SE of 44.2 ± 7.6 and 50.0 ± 13.4 competitor galleries per m^2, respectively. The density of competitor galleries was much lower in spruce logs, showing a mean $\pm$ SE of only 7.8 ± 5.1 and 3.4 ± 1.2 galleries per m^2 for logs containing pine- and spruce-reared female mountain pine beetles, respectively. Gallery density within treatment logs was not influenced by the natal species of the female mountain pine beetle colonizers ($F_{1,33} = 0.17$, $P = 0.68$).

Patterns of emergence for the competitor complex from mountain pine beetle-colonized logs were similar to those observed for attraction. The emergence success of these competitors was highly influenced by host log species ($F_{1,33} = 29.28$, $P < 0.0001$) but not natal species of mountain pine beetle colonizers ($F_{1,33} = 0.47$, $P = 0.50$). The mean $\pm$ SE number of competitors of all species emerging per 5-day period from pine logs containing female mountain pine beetles reared from pine and spruce was 30.6 ± 12.1 and 38.8 ± 18.3, respectively. Of all competitors, *I. pini* was the most numerous
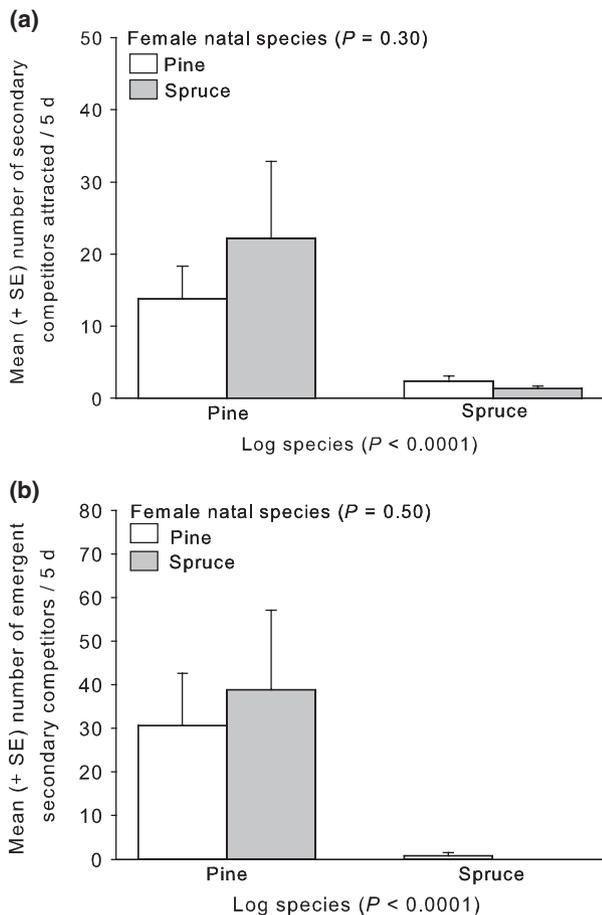
(a)

(b)

Figure 3 Effect of natal host of origin and present host on the attraction and reproduction of competitors of mountain pine beetle. White and grey shading represent logs laboratory-colonized with female mountain pine beetles ($n = 5$) reared from pine and spruce natal hosts, respectively ($n = 12$ replicates per log- and female mountain pine beetle natal-species combination). (a) Mean ± SE pooled attraction per treatment per 5-day period by the secondary bark beetle species *Ips pini* (Say), *Pseudips mexicanus* (Hopkins) and *Orthotomicus latidens* (LeConte). (b) Mean ± SE pooled emergence per treatment per 5-day period by the secondary bark beetle species complex *Ips pini* (Say), *Pseudips mexicanus* (Hopkins) and *Orthotomicus latidens* (LeConte).

species to emerge, followed by *P. mexicanus* and *O. latidens*. Numbers were highly variable, however. In pine logs colonized by pine-reared female mountain pine beetles, *I. pini*, *P. mexicanus* and *O. latidens* accounted for 69%, 29% and 2%, respectively, of the total of 367 beetles. Within pine logs colonized by spruce-reared female mountain pine beetles, *I. pini* emergence dropped to 54% of total species emergence, whereas *P. mexicanus* rose considerably to account for 44% and *O. latidens* constituted the final 2% ($n = 466$ beetles).

By contrast, competitor emergence from spruce logs was extremely low, with only one *I. pini* and nine *P. mexicanus* emerging from logs colonized by pine-reared female mountain pine beetles. We did not observe successful *O. latidens* emergence from this treatment, and no competitors emerged from any of the spruce logs colonized by spruce-reared female mountain pine beetles (Fig. 3b).

The emergence of *I. pini*, *P. mexicanus* and *O. latidens* from the logs did not affect the emergence of mountain pine beetle brood ($F_{1,35} = 0.02$, $P = 0.89$). Similarly, there was no association between the number of combined *I. pini*, *P. mexicanus* and *O. latidens* ovipositional galleries and brood emergence of mountain pine beetles ($F_{1,35} = 63.99$, $P = 0.95$).

Discussion

In the present study, reduced interactions with potential competitor species within an atypical host, spruce, did not affect the reproduction of mountain pine beetles. Previous work has demonstrated both negative (Rankin & Borden, 1991; Boone *et al.*, 2008) and positive (Smith *et al.*, 2011) effects of *I. pini* and *P. mexicanus* on the brood success of mountain pine beetles, respectively. The lack of any host-mediated reductions in mortality as a result of interspecific competition in the present study is unexpected, given that each of the competitor species is solely (or predominantly, in the case of *I. pini*) a pine specialist (Furniss & Carolin, 1977). Although spruce-infesting competitors such as *Ips perturbatus* (Eichhoff) and *Ips tridens* (Mannerheim) are common in the study region (Furniss & Carolin, 1977), we did not capture any representatives of those species in this experiment. Live, standing, *Picea* spp. hosts and/or logging slash were rare within the immediate study area, although interior hybrid spruce was abundant in nearby lowlands, drainages and surrounding forest. Also, all of these species utilize semiochemical-mediated resource partitioning (Hunt & Borden, 1988) and their development, emergence and mating may be phenologically separated in time (Koopmans, 2010), resulting in optimized spacing of beetles within the available phloem or avoidance of occupied hosts. Interactions between *P. mexicanus*, *O. latidens* and mountain pine beetles are likely minimized via temporal separation of dispersal flight and host selection activities. However, as a result of the multi-voltinism and multiple flight periods of *I. pini*, it is likely that competitive interactions between *I. pini* and mountain pine beetles occur under some circumstances. Competition is a mortality factor of sufficient importance in bark beetle systems (Anderbrant *et al.*, 1985; Rankin & Borden, 1991; Boone *et al.*, 2008) such that reduced intraspecific competition can result in increased reproduction in standing, live, atypical hosts (Huber *et al.*, 2009).

The similar attraction of mountain pine beetles to each of the four treatments containing inserted female colonizers suggests that the behavioural activity of the mountain pine beetle pheromone blend is maintained across pine and spruce hosts. Host phytochemistry is an important determinant of host selection in phytophagous insects (Ehrlich & Murphy, 1988) and the ubiquitous terpenoid-based chemistry throughout the Pinaceae (Huber *et al.*, 2004) may evoke reproductive behaviour in mountain pine beetles across a broad host spectrum. Females with developmental histories in spruce must manufacture, either via host tissue-derived precursors (Hunt *et al.*, 1986; Seybold *et al.*, 2006) or possibly via *de novo* synthesis (Hall *et al.*, 2002; Seybold & Tittiger, 2003), pheromones that are functionally equivalent to those produced by females with developmental histories in lodgepole

pine. Pheromone consistency among hosts is advantageous for a pine-feeding generalist herbivore to maintain intraspecific functionality (Raffa *et al.*, 2007). Moreover, because the developmental history of mountain pine beetles in the present study did not influence ovipositional gallery establishment, ovipositional gallery length, number of larval galleries, number of pupal chambers or brood emergence on a per-female-basis within either host, female mountain pine beetles with spruce developmental histories may have equal fitness to beetles reared from pine.

Although host species did not influence attraction on a per log basis, the approximate two-fold increase of beetle recruitment in response to females within spruce logs on a per female basis suggests that subtle variations in pheromone production (Birgersson *et al.*, 1984; Pureswaran *et al.*, 2000; Pureswaran & Borden, 2003), possibly combined with variability of host-derived chemical pheromone precursors, attractant volatiles and/or synergists (Miller & Borden, 2000; Erbilgin *et al.*, 2003; Reddy & Guerrero, 2004; Aukema *et al.*, 2010), may be responsible for this effect because total ovipositional gallery lengths were similar. For example, quantitative differences in spruce and pine resin (Pureswaran *et al.*, 2004) may contain different levels of pheromone precursors that influence downstream pheromone production by the insect. Such differences in attractiveness to pheromone blends have been noted previously with pine engravers tunnelling within various hosts (Erbilgin & Raffa, 2000; Aukema *et al.*, 2004).

Similar larval survival and subsequent pupation within each host species during this experiment supports the hypothesis that spruce may be an equally suitable host as pine (Huber *et al.*, 2009). Inferring equal host quality from egg and larval survival (Reid & Gates, 1970), however, must be carried out with caution because egg niches could not be counted within spruce logs as a result of reduced etching of the sapwood by tunnelling beetles.

We note that reproductive failure for mountain pine beetles within spruce hosts did not occur until pupation. Delayed, deleterious host effects on mountain pine beetles infesting spruce implies that spruce phloem may sometimes lack moisture or nutritional requirements for pupal development. Symbiotic fungi, for example, are an important source of nutrition for larvae (Coppedge *et al.*, 1995; Bentz & Six, 2006; Bleiker & Six, 2007) and can influence brood development and emergence (Barras, 1973; Six & Paine, 1998). Zhang and Schlyter (2004) suggest that symbiotic fungi of coniferophagous bark beetles may not survive within nonhosts. Although the fungal associates of the mountain pine beetle *Grosmannia clavigera* (Robinson-Jeffrey and Davidson) Zipfel, de Beer and Wingfield and *Ophiostoma montium* (Rumbold) von Arx are able to colonize spruce phloem (K. P. Bleiker, unpublished data), the extent of colonization has not been quantified. It is possible that fungal proliferation in spruce phloem is reduced compared with pine phloem. *Grosmannia clavigera* and *O. montium* growth is dependent upon physical (Bleiker & Six, 2009a), chemical (Paine & Hanlon, 1994) and nutritional (Bleiker & Six, 2009b) characteristics within the phloem. Moreover, beneficial bacteria that prevent the growth of antagonistic fungi (Cardoza *et al.*, 2006; Scott *et al.*, 2009) may be reduced within alternate hosts (Shifrine & Phaff, 1956), resulting in reduced larval fitness.

An alternative (but not mutually exclusive) explanation for the developmental complications during pupal maturation in spruce may be chronic, sublethal effects as a result of the terpenoids present within the constitutive resin of spruce, which differ quantitatively and qualitatively from those in lodgepole pine (Pureswaran *et al.*, 2004). Mountain pine beetle may not be well adapted to this chemical legacy in a different host (Clarke *et al.*, 2012). Finally, parasitism of late-instar larvae and pupae could have been higher in spruce, although we did not rear any parasitoids from the material when returned to the laboratory.

By contrast to the present study, Huber *et al.* (2009) report that mountain pine beetles that colonized standing, live, spruce hosts in central British Columbia produced more progeny per female than conspecifics colonizing nearby pine. Huber *et al.* (2009) attribute the greater reproductive success of mountain pine beetles in spruce to reduced intraspecific larval competition for resources resulting from lower parental gallery densities in the spruce hosts. Despite such findings, it is possible that spruce hosts are less optimal than pines for mountain pine beetle reproduction. Reduced intraspecific larval competition in the spruce versus pine hosts of Huber *et al.* (2009) may have offset any deleterious effects of (potentially) lower-quality spruce phloem resources and resulted in greater brood production per female relative to the beetles in the pine hosts. As a comparison, the densities of the parental galleries within the pine and spruce logs of the present study were not significantly different. Therefore, it is likely that resource availability for larval development within the pine and spruce host types were similar. The lower reproductive success of female mountain pine beetles in the spruce logs reported in the present study versus the results reported by Huber *et al.* (2009) may reflect our use of harvested logs rather than live, standing hosts for reproductive studies of mountain pine beetles. Our logs may have contained higher concentrations of resin, for example. It is also possible that degradation of pine phloem occurred at a slower rate than spruce phloem after being cut. Higher phloem quality in pine logs throughout the present study would certainly benefit bark beetle brood production (Amman, 1972; Reid & Robb, 1999; Redmer *et al.*, 2001), perhaps by facilitating the proliferation of fungal and microbial associates that condition the host and benefit reproduction (Bentz & Six, 2006; Cardoza *et al.*, 2006; Bleiker & Six, 2007).

The results of the present study demonstrate that, although brood production within spruce may be significantly lower than within pine, a spruce host may function as a source of beetles rather than a sink, and insect population replacement may be possible if the insects are able to colonize susceptible spruce (Huber *et al.*, 2009). Differential reproduction of mountain pine beetles among different host species (Langor, 1989), as well as the apparent interspecific functionality of progeny, could extend outbreaks in certain instances. Our work also demonstrates that the pheromone signal from a novel host is sufficient to attract conspecifics, and can even be more attractive to the herbivore than a pheromone signal from the primary host. This is a concern as the insect spreads eastward through Canada's boreal forest (Safranyik *et al.*, 2010; Cullingham *et al.*, 2011; Samarasekera *et al.*, 2012), and has now become sympatric with novel jack pines (Cullingham *et al.*, 2011). Continued eastward movement by the spreading mountain pine beetle

population will also bring the beetle into contact with other potential *Pinus* hosts such as red pine (*P. resinosa* Solander ex Aiton) and eastern white pine (*P. strobus* Linneaus). More work is critically needed aiming to examine attraction to (and reproduction within) these potential host species under laboratory and field conditions.

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