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Research article

Mountain Pine Beetle Host Selection Between Lodgepole and Ponderosa Pines in the Southern Rocky Mountains

Daniel R. West,[1,2] Jennifer S. Briggs,[3] William R. Jacobi,[1] and José F. Negrón[4]

[1]Colorado State University, Colorado State Forest Service, 5060 Campus Delivery, Fort Collins, CO 80523-5060 (dan.west@colostate.edu; William.Jacobi@colostate.edu), [2]Corresponding author, e-mail: dan.west@colostate.edu, [3]U.S. Geological Survey, Geosciences and Environmental Change Science Center, Box 25046, M.S. 980, Bldg., 25, Denver Federal Center, Denver, CO 80225 (jsbriggs@usgs.gov), and [4]USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect, Fort Collins, CO 80525 (jnegron@fs.fed.us)

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Abstract

Recent evidence of range expansion and host transition by mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) has suggested that MPB may not primarily breed in their natal host, but will switch hosts to an alternate tree species. As MPB populations expanded in lodgepole pine forests in the southern Rocky Mountains, we investigated the potential for movement into adjacent ponderosa pine forests. We conducted field and laboratory experiments to evaluate four aspects of MPB population dynamics and host selection behavior in the two hosts: emergence timing, sex ratios, host choice, and reproductive success. We found that peak MPB emergence from both hosts occurred simultaneously between late July and early August, and the sex ratio of emerging beetles did not differ between hosts. In two direct tests of MPB host selection, we identified a strong preference by MPB for ponderosa versus lodgepole pine. At field sites, we captured naturally emerging beetles from both natal hosts in choice arenas containing logs of both species. In the laboratory, we offered sections of bark and phloem from both species to individual insects in bioassays. In both tests, insects infested ponderosa over lodgepole pine at a ratio of almost 2:1, regardless of natal host species. Reproductive success (offspring/female) was similar in colonized logs of both hosts. Overall, our findings suggest that MPB may exhibit equally high rates of infestation and fecundity in an alternate host under favorable conditions.

Key words: *Dendroctonus ponderosae*, *Pinus contorta*, *Pinus ponderosa*, host selection, Hopkins' Host Selection Principle

Eruptive populations of the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins; MPB) have caused widespread mortality of pines in western North American, with tens of millions of hectares affected since the 1990s (Raffa et al. 2008). The extent and severity of this recent outbreak are unprecedented in recorded history (Taylor and Carroll 2004, Raffa et al. 2008). The primary host species incurring the majority of mortality from mountain pine beetle has been lodgepole pine (*Pinus contorta* Doug. ex Loudon), but recent studies have identified areas in which the insect is expanding beyond its previously known range (Carroll et al. 2003, Safranyik et al. 2010, de la Giroday et al. 2012). Such range expansion in some cases involves higher elevation ranges, more northern latitudes, and new host species (Safranyik et al. 2010; de la Giroday et al. 2012, McKee et al. 2013, Raffa et al. 2013). Although the mountain pine beetle is a polyphagous insect known to infest numerous native and exotic pine species in western North America, it has not often previously caused significant mortality in more than one host during the same epidemic. Over the past century, mountain pine beetle population outbreaks have generally supported the field observations of A.D. Hopkins, a prominent early forest entomologist, who reported, "a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted" (Hopkins 1916, 1917). Interest in host preference and Hopkins' Host Selection Principle (Allee et al. 1949, Amman 1982, Barron 2001) has increased, as the recent mountain pine beetle epidemic expanded and threatened new geographic regions and hosts (de la Giroday et al. 2012, McKee et al. 2013).

In Colorado, major hosts of the mountain pine beetle are lodgepole pine and ponderosa pine (*Pinus ponderosa* Lawson). Throughout Colorado, ponderosa pine occupies approximately 800,000 hectares (ha) from 1,800 to 2,750 m, while lodgepole pine occupies about 600,000 ha between 2,450 to 3,050 m (Colorado State Forest Service 2012). In 2008, epidemic populations of mountain pine beetle expanded in high-elevation lodgepole pine forests on both the west and east sides of the Continental Divide, and moved into stands containing ponderosa pine in the mixed-conifer ecotone east of the Divide (USFS 2009). Questions arose within the scientific community and among land managers about the potential for extensive mountain pine beetle-induced mortality in ponderosa pines in mixed stands, as well as the vulnerability of adjacent

lower-elevation, ponderosa pine-dominated forests along Colorado's rapidly expanding Front Range wildland–urban interface. For both ponderosa and lodgepole pine hosts to sustain epidemic levels of mountain pine, a transition in host selection preference from lodgepole pine to ponderosa pine would have to occur as populations encountered more ponderosa than lodgepole pine. Alternatively, two mountain pine beetle biotypes or host races—reproductively isolated populations breeding separately within the two hosts—might exist in sympatry (Funk et al. 2002, Smadja and Butlin 2009). The possible presence of biotypes might produce an illusion of alternate host preference while each population actually remained associated with its respective host species.

The mountain pine beetle outbreak in Colorado's Front Range forests in 2008 presented an opportunity to test whether mountain pine beetle populations would remain in lodgepole pine, or would spread into ponderosa pine and cause significant mortality in this alternate, widespread host. Studies testing or addressing Hopkins' principle have had mixed results, both in bark beetles (Coleoptera: Curculionidae: Scolytidae) and other insect groups that exhibit host preferences (Barron 2001 and references therein). Three studies found no support for Hopkins' predictions when bark beetles were offered cut-logs or processed sections of alternate pine host species. Richmond (1933) found that more mountain pine beetles emerged from naturally infested lodgepole pines than ponderosa pines. However, the emerging beetles predominantly infested cut sections of ponderosa pine over lodgepole pine. Wood (1963) recorded similar selection by *Ips paraconfusus* of homogenized phloem disks prepared from ponderosa pine, sugar pine (*Pinus lambertiana* Dougl.), and Jeffrey pine (*Pinus jeffreyi* Grev). Cerezke (1995) identified similar attack rates of mountain pine beetle on logs of jack pine (*Pinus banksiana* Lamb.), lodgepole pine, and limber pine (*Pinus flexilis* James) placed at common field sites in British Columbia. However, the use of cut or processed sections of trees in these studies meant that the trees' defense systems could not have responded to the insects' attacks in the complex interactive process that occurs under natural growing conditions (Raffa and Berryman 1983, Boone et al. 2011).

In contrast, aerial detection surveys conducted by the USDA Forest Service and its partners across western pine forests over many decades found that outbreak populations of mountain pine beetle tend to remain primarily in the host species in which they initially developed (USDA, Aerial Detection Survey, http://www.fs.usda.gov/detail/r2/forest-grasslandhealth/, last accessed 1 Novovember 2015; Annual Biological Reports, USDA Forest Service, Rocky Mountain Region, Forest Health Management). The results of three observational studies under natural conditions in Wyoming were also consistent with Hopkins' predictions: mountain pine beetle-induced mortality remained greater over time in the insects' initial host species in mixed stands containing lodgepole pine and either whitebark pine (*Pinus albicaulus*; Baker et al. 1971, Raffa et al. 2013) or limber pine (Dean 2007). Each of these studies attributed their findings to the beetles' continued preference for their natal hosts—those in which they developed. Two recent field surveys found high levels of infestation of both ponderosa and lodgepole pine growing in mixed or adjacent stands in Colorado and British Columbia, respectively (Klenner and Arsenault 2009, West et al. 2014). However, none of these studies directly measured host selection behavior in the field, nor could they evaluate whether beetles emerging from one host were equally exposed to the alternate host species present in the stands.

As epidemic populations of mountain pine beetle expanded in Colorado, we initiated a series of studies in both field and laboratory settings to evaluate the susceptibility of lodgepole versus ponderosa pine hosts. We investigated four aspects of mountain pine beetle population dynamics and host selection behavior in the two species: emergence timing, sex ratios, host choice, and reproductive success. First, we asked whether the emergence phenology (seasonal timing) of mountain pine beetles from trees growing in sympatry differed between lodgepole pine and ponderosa pine. Differences in emergence timing of natal host populations of beetles from lodgepole pine and ponderosa pine might indicate reproductive isolation between populations emerging from the two hosts. Both Bentz (1999) and Amman (1982) found that adult mountain pine beetles emerged significantly earlier from ponderosa pine than from lodgepole pine logs in laboratory studies when temperature was controlled. Our second assessment investigated whether sex ratios of beetles emerging from the two host trees differed over the duration of the emergence period. Because female mountain pine beetles initiate new attacks on trees, differences in sex ratios of beetles emerging from the two natal host species might reflect differences in host selection behavior, as well as differences in the quality of the host selected (Amman 1982).

Our third investigation evaluated whether the mountain pine beetle preferred to infest lodgepole pine over ponderosa pine under controlled conditions without the physical host defenses of resin flow present, both in the field and laboratory. We conducted two different experiments that separated the insects' primary versus secondary host selection behaviors. The mountain pine beetle uses several methods to find suitable host trees, including detection of tree volatiles (Seybold et al. 2006), visual cues (Campbell and Borden 2006), and random landing (Pureswaran and Borden 2005). Once a tree has been selected, gustatory (feeding) acceptance allows bark and phloem mining to occur (Raffa et al. 2005). These processes are commonly referred to as primary host selection. As beetles tunnel into the subcortex to construct their oviposition galleries, volatile compounds present in the tissues of the host trees are oxidized and emitted from the beetles and their frass (feces-phloem mixture) as monoterpenes (Seybold et al. 2006). In the process known as secondary host selection, host monoterpenes are pre-cursors to aggregation pheromones and are oxidized by attacking beetles, which serve to attract other foraging mountain pine beetles that may join the attack and assist in overcoming the defenses of the tree (Raffa and Berryman 1983). We were unable to monitor the associated microorganisms in the beetle–host complex, though we acknowledge that these microbes are implicated as important contributors to successful beetle colonization and reproduction in pines by concentrating nitrogen (Ayres et al. 2000) or by producing sterols (Bentz and Six 2006). To evaluate the outcome of both primary and secondary host selection, we conducted a controlled choice experiment in the field, in which naturally emerging beetles from both host species were offered logs of either species for infestation. We also conducted a laboratory assay in which individual female beetles from each natal host were offered bark sections of both pine species in closed containers. This laboratory assay tested only primary host selection behavior by the individual insects, as there were no opportunities for aggregation pheromones to assist in host selection.

Our final question asked whether reproductive success differed between mountain pine beetles infesting lodgepole pine versus ponderosa pine. We reared the brood from the infested logs in our controlled-field-choice experiment to adult emergence, and compared the number of offspring, the brood size per female, and the length of oviposition galleries between the two hosts. Reproductive success of mountain pine beetle has been shown to differ among hosts (Amman 1982; Cerezke 1995, Gross 2008, Raffa et al. 2013) and may be highly relevant to insects' host selection preferences (Amman 1982), but the relative success rates of mountain pine

beetle in each host species examined have not been consistent across previous studies. We speculated that if the rates of host selection, reproductive success, or both were greater in ponderosa pine than lodgepole pine in Colorado's Front Range, the resulting larger beetle populations developing in this host could cause similar or greater levels of mortality in ponderosa pine forests compared with higher elevation lodgepole pine forests over time.

Materials and Methods

Emergence Phenology

To evaluate evidence for the existence of sympatric mountain pine beetle biotypes, we recorded the number of beetles emerging weekly from trees of both host species in 2 yr (May-October of 2010 and 2011) at two sites in the lodgepole–ponderosa pine ecotone along the Front Range, Arapaho-Roosevelt National Forest, Colorado, USA (Molly Lake site in 2010, UTM NAD-83 Easting Northing: 13N 449861 4512902, 2,590-2,620 m elevation; Pennock Pass site in 2011, UTM 13N 458090 4492379, 2,620-2,650 m elevation; Fig. 1). We attached emergence cages in May, prior to adult emergence, on the north side of trees at 1.4 m from the forest floor. Cages were 0.18 m^2 and constructed of bronze screen with glass jars affixed at the bottom. Each year, 30 new trees of each species were arbitrarily selected within 200 ha at the Molly Lake site and 33 ha at the Pennock Pass site. Cages were attached to the north aspects of sample trees, as greater densities of brood have been recorded on north aspects of lodgepole pine trees (Reid 1963, McCambridge 1964, Shepherd 1965); however, no aspect differences were detected in ponderosa pine (Negron et al. 2001, Schmid, 1972). Each week from mid-June to mid-October, we counted the adults that emerged from each tree, and determined their sex by identifying the presence of the stridulating organ in males on the seventh abdominal tergum (Hopkins 1909, Lyon 1958). To investigate differences in emergence timing, we averaged the weekly adult cage collection counts for each host species and calculated half least significant difference (LSD) values for confidence bounds (Proc Means; SAS 9.2, SAS Institute, Cary, NC). We used a mixed model (Proc Glimmix; SAS 9.2) with an alpha set at 0.05 to assess the effects of host species, year, and weeks within a given year on the average weekly adult cage collection counts. Log_{10}-transformations were performed on the average weekly cage counts to reduce the influence of high leverage points from any one tree. Mean estimates were back-transformed from log_{10}-values and the weekly collections were divided by the total collections to calculate the percent of total beetles collected per week.

Sex Ratio of Emerging Beetles

To investigate whether sex ratios of emerging beetles varied between the two host species over time, we counted all males and females in weekly cage collections from each tree from which less than 30 beetles had emerged. If more than 30 insects emerged from a given tree in a week, we randomly sampled 30 individuals from the collection. Using a mixed model, we compared the mean ratio of emerged females with total emerged beetles per tree per week for each host species. We included year, species × year interaction term, week within year, and species × week within year as fixed effects in the model (Proc Glimmix; SAS 9.2). Log_{10}-transformations were performed on the sex counts to reduce the influence of high leverage points from any one tree. To perform the logit transformation, we eliminated weeks where insects had not emerged from both tree species and/or only males or females were present. Thus, sex ratios were compared across the 5 wk of greatest emergence for both species for both years, 2010–2011 (July 23 through August 21). For significant effects, upper and lower confidence bounds were calculated for the mean number of collected females (mean ± 1/2 LSD), which is equivalent to Fisher's protected LSD.

Host Selection: Controlled-Field Experiment

To address the question of whether mountain pine beetle preferentially selected lodgepole or ponderosa pine, controlled-field experiments were conducted at the same two sites used in the phenology study. These sites had incipient-epidemic (Safranyik and Carroll 2006) beetle populations that were infesting both lodgepole and ponderosa pine trees. Within the Molly Lake and Pennock Pass sites, we selected 12 pairs of trees that had been mass-attacked the previous year and attached emergence cages to them. Each pair of trees was the same natal host species (six pairs of ponderosa pine, six pairs of lodgepole pine) and served as the source of beetles. From the emergence cages attached to each tree, we placed a 5-cm-diameter PVC pipe leading into a single choice arena on the forest floor that contained vertically oriented cut-log sections of both ponderosa pine and lodgepole pine (Fig. 2). Emergence cages were placed high enough on the stem to allow the insects to travel downward in the PVC pipes into midpoint of the choice arenas. Arenas (122 by 61 by 61 cm) were constructed of oriented strand board (OSB) bases, six vertical frame supports (5 by 8 by 61cm), and wood framed tops, covered with aluminum screening, which allowed ambient temperature fluctuations and air circulation. This design allowed beetles to naturally emerge from their natal host trees, travel down the pipes, enter the arenas, and select a host species to infest, either lodgepole or ponderosa. In all replicates, each tube supplied freshly emerged adults from an emergence cage affixed to one of the two trees.

We identified the source trees as mass attacked if: 1) beetle entrance wounds (often with pitch tubes) covered the entire circumference of the stem; 2) frass was present around the entire tree base; and 3) foliage had begun to fade. Additionally, attack status was verified through bark sampling on the south aspect of each tree. The densities of attacks on natal host trees were not standardized, as trees were selected for the experiment based on their high number of attacks and their location adjacent to another mass-attacked tree of the same species, so that beetles from two different trees could supply each choice arena.

To provide breeding tree material for these choice experiments, one tree of each host species from the same stand was felled and limbed each week and 50–60-cm sections were placed in the choice arenas directly after the tree was cut. Trees were selected if they met the following criteria: no visible insect damage or disease; growing under similar conditions in the same stand as the experimental host trees; similar diameter as the host trees (<2.5 cm difference; >20 cm dbh); and similar taper for the 12 log sections. Cut ends of sections were sealed with a water-based wax emulsion to reduce desiccation (Waxlor End Sealant, Forestry Suppliers). Log sections of each host were matched by diameter and vertically positioned at each end of the arenas. The order in which the logs of the two tree species were placed at each end of the arenas was randomized each week. Log sections were replaced every 7 d for 5 wk from July 21 to September 1, 2010 and July 14 to August 22, 2011.

After 7 d, each log section was removed from the arena and placed in a rearing box located in a temperature-controlled laboratory (20.4 C ± 0.02; mean ± SE). Rearing boxes were constructed of OSB (61 by 61 by 61 cm) with stapled aluminum screened fronts covered with black landscape fabric to reduce light and humidity. Emerged insects were collected weekly in glass jars affixed to holes

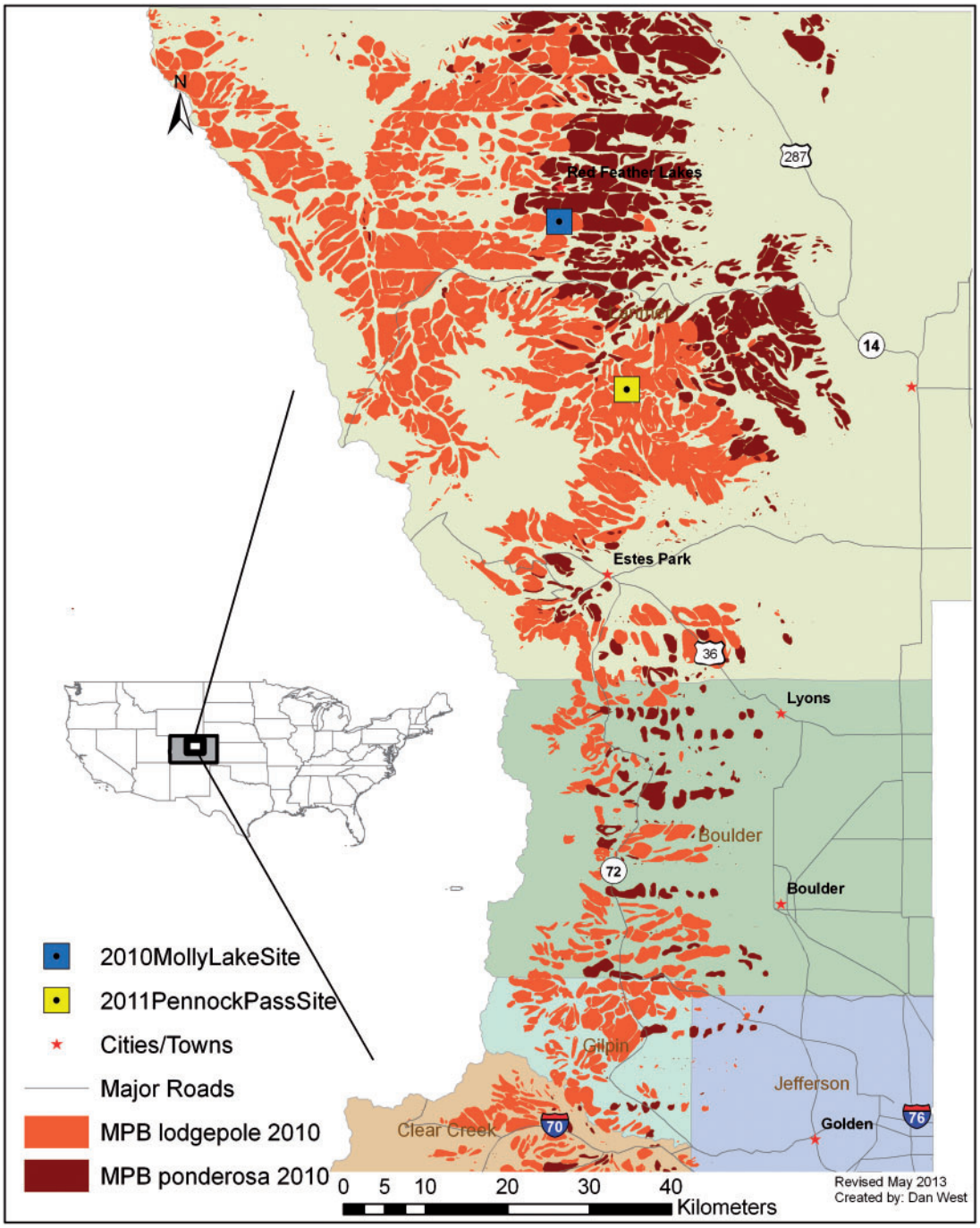

Fig. 1. Mountain pine beetle-caused mortality in lodgepole and ponderosa pines from 2010 aerial detection survey along the Front Range, CO, with lodgepole–ponderosa pine ecotone site locations for 2010 and 2011.

in the bottom of the rearing boxes. Weekly collections of emerged beetles were tallied.

Each log section was assessed after beetle emergence ceased. Log diameters (center and ends), length, phloem layer thickness on each end, and the number of mountain pine beetle emergence holes were recorded. To test for differences in mean diameters and phloem thickness in response to the fixed effects of choice species, we used a mixed model where natal trees ($n = 48$) and natal trees by species (lodgepole pine, ponderosa pine) were treated as random effects in the model (Proc Mixed; SAS 9.2). The bark from each log was peeled in approximately 13-cm-wide strips and oviposition galleries were measured using a map distance wheel.

We evaluated the host selection behavior of mountain pine beetles by comparing the number of oviposition galleries per square meter constructed in lodgepole pine versus ponderosa pine log sections. Female mountain pine beetles initiate oviposition gallery construction and make one gallery each (Reid 1962); therefore, the number of galleries is synonymous with the number of selections of each host by each mated female. We also assessed whether the mean number of galleries per log differed between natal host species and

Fig. 2. Host selection experiment with two ponderosa pine natal hosts providing freshly emerged mountain pine beetle to offered lodgepole pine and ponderosa pine cut-logs. Choice logs were replaced weekly (July and August) for 5 wk in 2010 and 2011. Photo: Dan West

choice log species, using a mixed model analysis in which year (2010, 2011), natal host species (lodgepole pine, ponderosa pine), and choice log species (lodgepole pine, ponderosa pine) were fixed effects, while natal trees ($n = 48$) within natal species (lodgepole pine, ponderosa pine) by year (2010, 2011) and choice log species by natal trees within natal species by year were random effects (Proc Mixed; SAS 9.2).

Host Selection: Bioassays With Individual Beetles

Bioassays were conducted to test primary host selection by individual beetles, without any influence of secondary pheromone presence from previous beetle attack. In each replicate, one adult female beetle was placed in a plastic container (2450 cm^3) with sections of bark/phloem from both ponderosa and lodgepole pines (Fig. 3). To obtain the bark/phloem sections, six uninfested trees of each species were selected from the study site in 2010 and replicated in 2011, felled, limbed, and cut into 60-cm lengths. Log sections were marked in sequence to match the taper between each tree species so that the bark sections came from similar diameter and height locations on both species. Directly upon transporting the logs to the laboratory, we removed the outer bark and phloem intact in 32-cm^2 units from log sections from each species at a minimum of 12 cm from the cut ends. In plastic storage containers, one bark unit from lodgepole pine and one unit from ponderosa pine were suspended with the bark side up in paraffin wax. The paraffin reduced desiccation of the phloem while rendering the cut ends of the phloem unavailable for direct feeding. To retain leverage points for possible entry by beetles under bark flakes and furrows, the bark surface was not covered with wax or otherwise altered. We obtained mountain pine beetles for this experiment from log sections of naturally infested trees that had been felled the previous fall and stored in unheated storage sheds. Female mountain pine beetles were chosen at random as they emerged from these lodgepole pine and ponderosa pine logs. Beetles were used in the bioassays if their vigor was such that they could climb the sides of a petri dish and right themselves when placed on their dorsal side.

During each bioassay, we placed one female beetle on the middle of either the lodgepole or ponderosa pine bark unit. The order of placement was randomized for each replicate. The beetle behavior was observed four times daily, for approximately 2 min per replicate, until the beetle selected a host species. The criteria we used to identify host selection were penetration of the outer bark layers of each bark/phloem unit coupled with sustained feeding of the phloem. Sixty-four replicate tests were conducted in 2011–2012, half with female beetles that had developed in lodgepole pine and half with female beetles from ponderosa pine. Replicates in which the insect died without penetration of the bark/phloem unit or sustained feeding were reported as such without a retrial. We used chi-square tests of independence to determine whether the proportion of host species chosen was affected by the beetles' natal host species. To determine whether the proportions of lodgepole versus ponderosa pines selected were equal, we performed binomial proportion exact tests.

Reproductive Success

We used a mixed model to analyze the variation in emerged adults from each natal-tree and choice-log treatment in the field experiment, treating the number of emerging adults as the dependent variable. To

Fig. 3. Bioassays for mountain pine beetle host selection between fresh bark/phloem units from lodgepole (left) and ponderosa pines (right). Individual females from either lodgepole pine or ponderosa pine were offered a choice between the two alternate host bark/phloem units (32 cm^2). $N = 64$; half from each natal host. Photo: Dan West

quantify female fecundity, the counts of emerged adults from each log section were divided by the number of oviposition galleries constructed per female and tested as the dependent variable in a similar model, in which natal-tree and choice-log species were the independent variables. Finally, we used the continuous length of each oviposition gallery as a metric of host suitability and tested for differences between treatments. We performed $\log_{10}$-transformations to reduce the influence of high-leverage points in the data sets for several variables: gallery counts, emerged adults, adults per female, and gallery length per female. Mean estimates were back-transformed from $\log_{10}$-values to improve interpretation of the results. Upper and lower confidence bounds were calculated through $\log_{10}$-back-transformed values (mean ± 1/2 LSD).

Results

Emergence Phenology

Mountain pine beetle emergence timing from lodgepole and ponderosa pines did not differ over the course of two summers. The "peak emergence" for both species occurred over a 2-wk period, the last week of July and the first week of August, for both years (Fig. 4). Emergence occurred over 65 and 72 d in 2010 and 2011, respectively, with peak emergence in late July and early August (Table 1). In 2010, beetles first emerged from our caged sample trees ($n = 60$) on June 25; two ponderosa pine trees produced one adult each. One week later on July 2, the first mountain pine beetle emerged from 1 of the 30 lodgepole pines. The same pattern was seen in 2011, though the first emergence occurred 2 wk later than in 2010. Single mountain pine beetles were collected from four individual ponderosa pine trees on July 9, 2011, while one lodgepole pine produced the first mountain pine beetle on July 15 (Table 1). On September 24, 2010 the last of the beetles emerged from both hosts. In 2011, beetles stopped emerging after September 27 for lodgepole pine and October 18 for ponderosa pine (Table 1).

Our analyses identified significant differences in the number of emerged beetles between species, between both years, weeks within a given year, and species × weeks within each year. Across all sampled weeks for both years, more insects emerged from lodgepole pine (mean [lower half LSD, upper half LSD]; 3.4 MPB/m^2/week/year [3.1, 3.6]) than ponderosa pine (2.3 MPB/m^2/week/year [2.1, 2.6]; $P < 0.0001$, $F_{1,\ 1447} = 18.2$), while more emerged overall from both hosts in 2010 (3.3 MPB/m^2/week/year [3.0, 3.5]) than in 2011(2.4 MPB/m^2/week/year [2.2, 2.6]; $P = 0.0003$, $F_{1,\ 1447} = 13.1$).

Sex Ratios

No differences were detected in the average female to male ratio between beetles emerging from the two pine species ($P = 0.61$, $F_{1,\ 417} = 0.26$) during the 5 wk of high emergence each year (2010: July 23, 30; August 6, 13, 21; 2011: July 22, 29; August 5, 12, 21). For lodgepole pine, the overall average proportion of emerged females to males during this period in 2010 was 0.41; for ponderosa pine in 2010, it was 0.39. In 2011, the values were 0.53 and 0.66 for lodgepole and ponderosa, respectively. We found differences in the average female ratio between years, over the selected 5-wk high emergence period in 2010 and 2011, (2010: 0.40; 2011: 0.59; $P = 0.046$, $F_{1,\ 417} = 3.99$), and among weeks within years ($P < 0.0001$, $F_{8,\ 417} = 5.50$). Across both species, female emergence was greater than male emergence early in the 5-wk period by

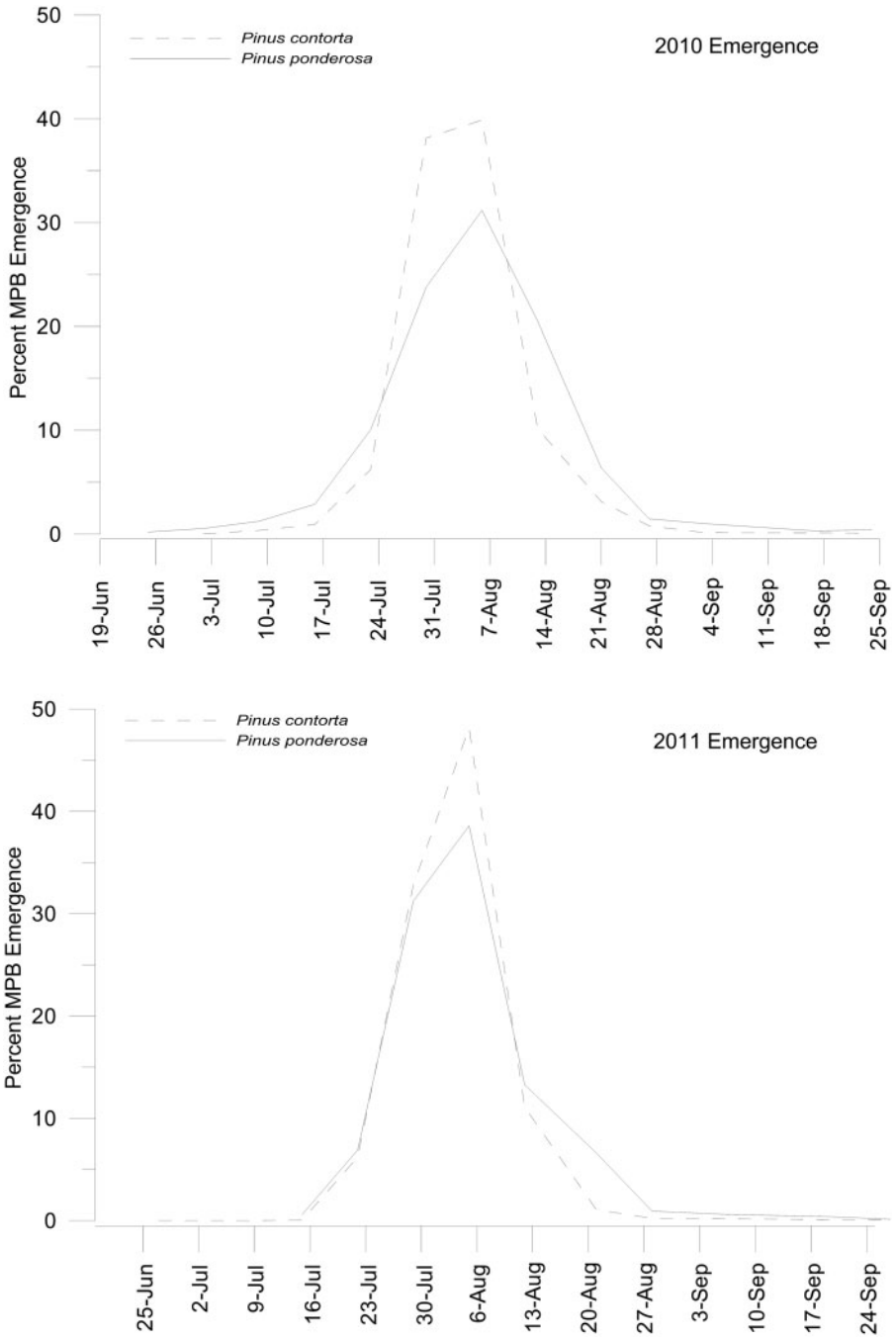

Fig. 4. Percent of total emerged mountain pine beetle from naturally infested lodgepole pine and ponderosa pine in 2010 and 2011. Trees were randomly located within two sites in the lodgepole–ponderosa ecotone between 2,590 to 2,650 m of elevation on the Arapaho-Roosevelt NF, CO. $N = 60$ emergence cages (0.18 m^2) split between species per year.

approximately 2:1 (Fig. 5). Female emergence declined after the peak emergence period in both years, resulting in female ratios of approximately 1:1 by August 21 (Fig. 5).

Host Selection: Controlled-Field Experiment

Our field-choice experiments indicated mountain pine beetle preferred ponderosa pine log sections over lodgepole pine approximately 2:1, with an average of 102.1 versus 49.2 egg galleries/m^2 per infested log per species, respectively; $F_{1,\ 20} = 10.99$, $P = 0.003$. Of the 240 paired-choice logs offered over the 10 wk of controlled-field experiments during 2010 and 2011, 68.3% or 164 logs were selected overall (75 logs were infested and 45 uninfested for lodgepole pine; 89 infested and 31 uninfested for ponderosa pine). The choice preference behavior was likely not influenced by the mean diameter of the cut-logs (lodgepole: 27.1 cm; ponderosa: 27.2 cm), the mean thickness of the phloem (lodgepole: 2.26 mm; ponderosa: 2.38 mm), or the mean surface area of the logs (lodgepole: 3718 cm^2; ponderosa: 3750 cm^2); no differences were detected in these variables between the host species ($F_{1,\ 215} = 0.01$, $P = 0.97$; $F_{1,\ 215} = 3.84$, $P = 0.051$, $F_{1,\ 215} = 0.2$, $P = 0.6$, respectively). On average, more insects entered the choice arenas from lodgepole pine

Table 1. Emerged mountain pine beetles (per m^2 of each tree) and the number of trees with emergence per week from lodgepole pine (*P. contorta*) and ponderosa pine (*P. ponderosa*) between 2,590 and 2,650 m of elevation

Year: 2010		25-June	2-July	9-July	16-July	23-July	30-July	6-Aug.	13-Aug.	21-Aug.	27-Aug.	3-Sept.	17-Sept.	24-Sept.	1-Oct.
P. contorta	Number trees	–	1	9	18	25	28	28	24	20	14	5	3	3	–
	Total MPB	0	5	81	135	1,157	7,282	7,185	2,653	662	188	27	48	27	0
P. ponderosa	Number trees	2	5	8	14	18	22	26	26	20	9	8	3	4	–
	Total MPB	11	27	97	145	850	2,239	1,954	829	328	97	48	16	22	0
Year: 2011		25-June	2-July	9-July	15-July	22-July	29-July	5-Aug.	12-Aug.	21-Aug.	28-Aug.	6-Sept.	20-Sept.	27-Sept.	18-Oct.
P. contorta	Number trees	–	–	–	1	20	25	27	26	12	4	3	2	2	–
	Total MPB	0	0	0	5	1,227	5,721	4,801	1,232	156	43	32	11	16	0
P. ponderosa	Number trees	–	–	4	5	21	25	27	25	19	6	4	3	1	2
	Total MPB	0	0	22	32	312	1,528	1,512	474	301	91	54	27	11	43

Collections were conducted near Molly Lake area (2010) and Pennock Pass areas (2011) on the Arapaho-Roosevelt NF., CO. In total, 60 trees were randomly selected in mid-June each year; 30 traps were attached to lodgepole pine and 30 to ponderosa pine.

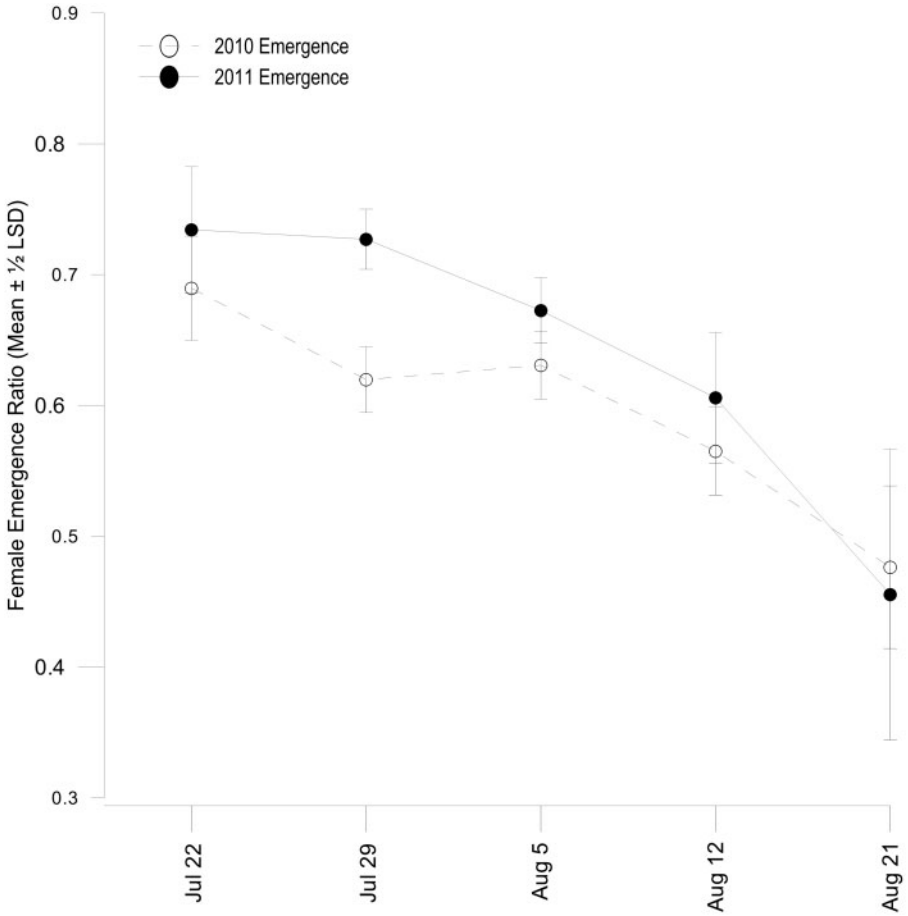

Fig. 5. Female to male ratio of mountain pine beetles emerged from combined lodgepole pine ($n = 60$ trees) and ponderosa pine ($n = 60$ trees) in 2010 and 2011 (Mean ± ½ LSD; $N = 120$ trees split between species per year; emergence cages covered 0.18 m^2/tree). Trees were randomly located in the lodgepole–ponderosa ecotone between 2,590 to 2,650 m of elevation on the Arapaho-Roosevelt NF, CO.

natal hosts and chose a log for infestation (8.1 female egg galleries per log were made by beetles that had emerged from lodgepole) than from ponderosa pine natal hosts (3.9 female egg galleries per log were made by beetles that had emerged from ponderosa; $F_{1, 20} = 12.16$, $P = 0.002$; Table 2; Fig. 6). Overall, more insects chose a host within the arenas in 2010 (1,771 female egg galleries) than in 2011 (1,383 female egg galleries), most likely because more insects entered the arenas in 2010 from the mass-attacked host trees used in the study ($F_{1, 20} = 6.84$, $P = 0.017$).

Because more mountain pine beetles entered the arenas from lodgepole pines than ponderosa (see earlier), the effect of the parental source species (natal host) on the number of emerging brood in the second generation was significantly greater for lodgepole pine ($F_{1, 20} = 7.98$, $P = 0.010$; Table 2). However, over the two seasons and all choice logs, about twice as many brood on average emerged from ponderosa pine (52 MPB per log [37, 71]; mean ± 1/2 LSD) than from lodgepole pine (19 MPB per log [14, 28]; $F_{1,20} = 8.41$, $P = 0.009$; Fig. 7).

Table 2. Effect significance in a mixed-model analysis of mountain pine beetle female host selection (mean number of galleries constructed per log), offspring production (total emerged brood), brood per female, and gallery length per female (y = response) between lodgepole and ponderosa pine in controlled-field-choice experiments conducted in the Arapahoe-Roosevelt NF, CO (2010–2011; $\alpha = 0.05$)

Effect	Response variables					
	y = Female host selection	y = Emerged brood	y = Brood per female	y = Gallery length per female	Numerator df	Denominator df
Natal species	**0.002**	**0.011**	0.094	0.591	1	20
Choice log species	**0.004**	**0.009**	0.053	0.073	1	20
Natal species × choice species	0.719	0.679	0.770	0.090	1	20
Year	**0.017**	**0.041**	0.162	0.561	1	20
Natal species × year	0.369	0.534	0.740	0.518	1	20
Choice log species × year	0.595	0.808	0.987	0.238	1	20
Natal species × choice log species × year	0.900	0.965	0.773	0.661	1	20

Bold values indicate the significant effects in each of the four models

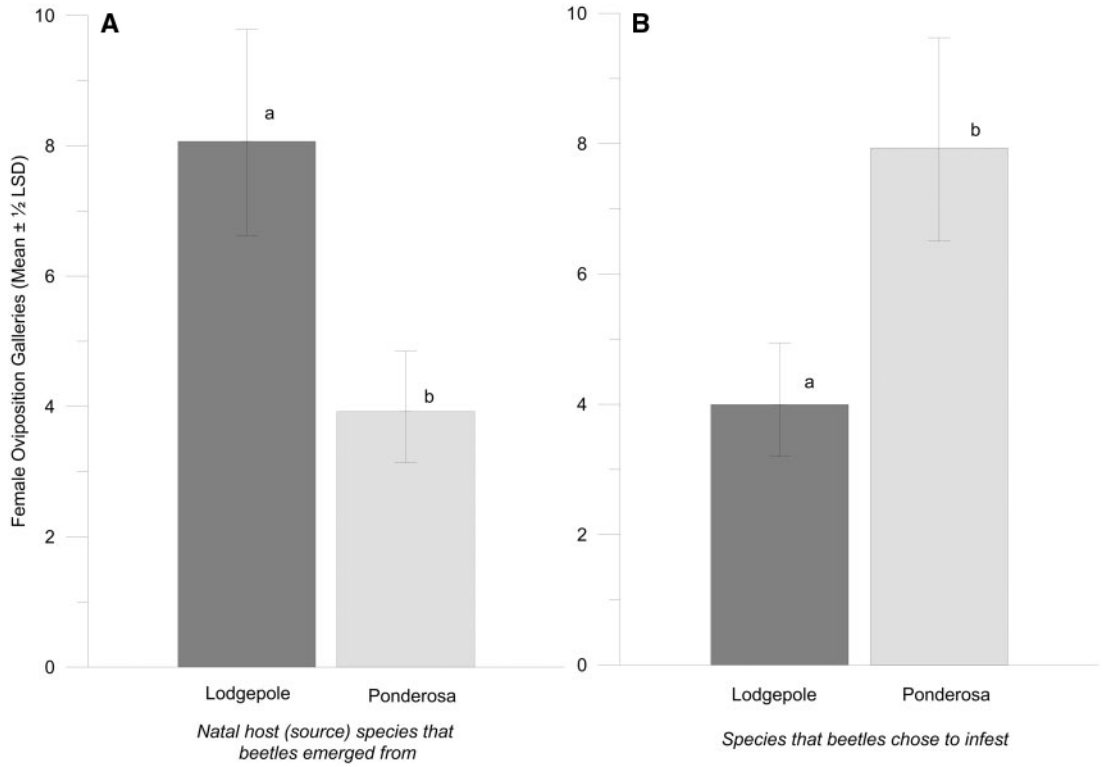

Fig. 6. Mountain pine beetle oviposition galleries created on sections of logs cut from lodgepole and ponderosa pine trees on the Arapahoe-Roosevelt NF, CO; 2010–2011. A. Beetle source species: Mean number of oviposition galleries constructed on log sections by mountain pine beetles that had parental lines of either lodgepole or ponderosa pine host trees (source species). $N = 240$ log sections (120 sections from arenas with lodgepole as natal source of beetles, 120 from arenas with ponderosa as natal source of beetles). (Mean ± ½ LSD). Differing letters indicate statistical separation of means in a mixed-model analysis ($\alpha = 0.05$). B. Beetle choice species: Mean number of mountain pine beetle constructed oviposition galleries in log sections of lodgepole or ponderosa pine chosen by beetles from both natal tree species. $N = 240$ log sections (120 sections of ponderosa as choice species, 120 sections of lodgepole as choice species) (Mean ± ½ LSD). Differing letters indicate statistical separation of means in a mixed-model analysis ($\alpha = 0.05$). *A significant year effect was detected, though not depicted in the figure. More insects emerged from source trees in 2010 than 2011, though year effect has little ecological relevance. 183 by 129 mm (600 by 600 DPI)

Host Selection: Bioassays With Individual Beetles

In our bioassays, 50% of adult female beetles from lodgepole pine chose ponderosa pine bark units ($n = 16$) and 31% chose lodgepole pine bark units ($n = 10$). A greater percentage of females from ponderosa pine also chose ponderosa pine bark units (59%; $n = 19$) over lodgepole pine bark units (25%; $n = 9$). Thus, in two-thirds of the trials, beetles preferred ponderosa pine over lodgepole pine ($Z = -2.3$, $P = 0.019$). The natal source species, either ponderosa or lodgepole pine, did not have an effect on the choice of species selected ($\chi^2_1 = 0.458$, $P = 0.50$); beetles from both natal hosts preferred ponderosa pine. Across both years, 6 of 32 beetles from lodgepole pine natal hosts died before clearly selecting a bark unit (19%), while 5 of 32 beetles from ponderosa pine died (16%).

Reproductive Success

The average brood per female produced from the chosen log sections did not differ between natal host species or choice host species

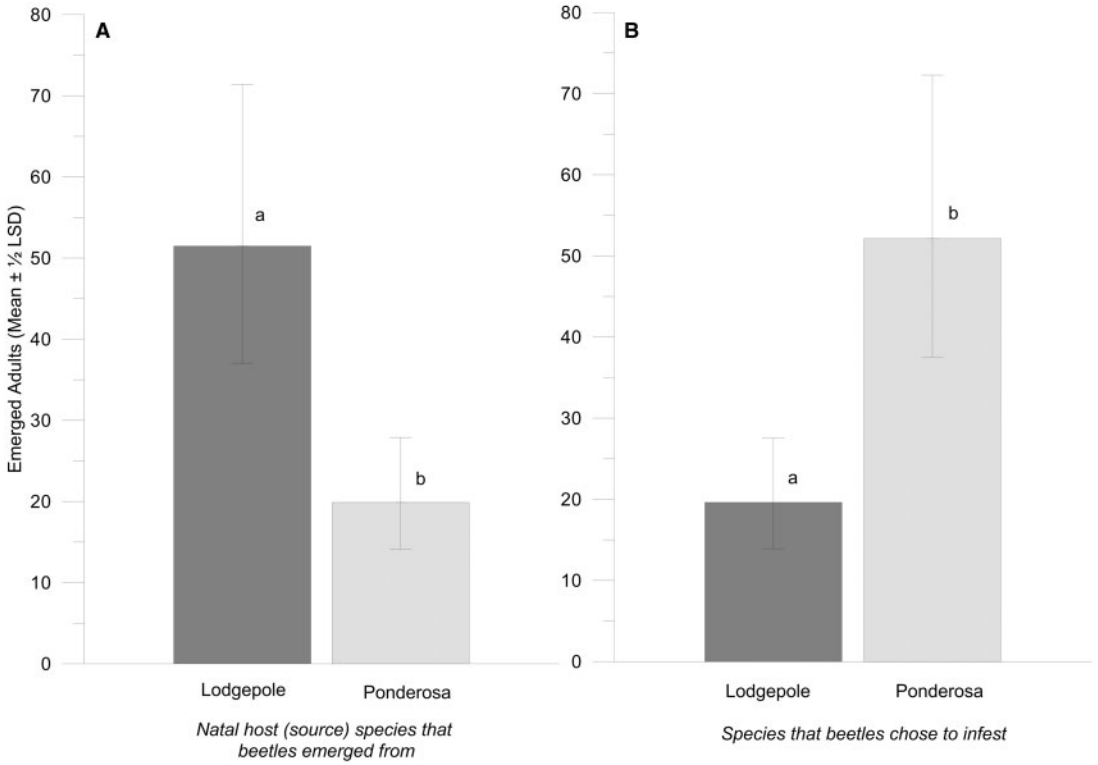

Fig. 7. Mountain pine beetle brood produced from log sections cut from trees in the Arapaho-Roosevelt NF, CO; 2010–2011. A. Beetle source species: Mean number of mountain pine beetle brood produced in log sections that had parental lines of either lodgepole and ponderosa pine host trees (source species). $N = 240$ log sections (120 log sections from arenas with lodgepole as natal source of beetles, 120 log sections from arenas with ponderosa as natal source of beetles). (Mean ± ½ LSD). Differing letters indicate statistical separation of means in a mixed-model analysis ($\alpha = 0.05$). B. Beetle choice species: Mean number of mountain pine beetle brood produced in log sections of lodgepole or ponderosa pine chosen by beetles from both natal tree species. $N = 240$ log sections (120 sections of ponderosa as choice species, 120 sections of lodgepole as choice species) (Mean ± ½ LSD). Differing letters indicate statistical separation of means in a mixed-model analysis ($\alpha = 0.05$).*A significant year effect was detected, though not depicted in the figure. More insects emerged from source trees in 2010 than 2011, though year effect has little ecological relevance.

($F_{1,20} = 0.4$, $P = 0.55$; $F_{1,20} = 0.88$, $P = 0.36$; Table 2). Brood size per female in ponderosa pine chosen host logs was 11.3 (9.5, 13.6; mean ± 1/2 LSD) and in lodgepole pine logs, it was 10.2 (8.8, 11.9). Oviposition gallery length also did not differ between natal host species or choice host species ($F_{1,20} < 0.01$, $P = 0.99$; $F_{1,20} = 1.31$, $P = 0.26$).

Discussion

The results of our experiments strongly suggest that mountain pine beetle can and does select other hosts during outbreaks. Lodgepole pine and ponderosa pine logs were both infested by beetles that had developed in either natal host, and significantly more beetles infested and bred in ponderosa pine. This lack of natal host-caused preference also indicates host selection from one pine species to another rather than separate populations remaining in their respective natal hosts. In both our controlled-field experiment and our lab assay, mountain pine beetle preferred to infest ponderosa pine almost 2:1 over lodgepole pine, even though twice as many beetles had developed within the source lodgepole pine trees. The similarity of insects' choices in the two tests suggests that secondary host selection based on aggregation pheromones was not a major factor influencing the outcome of the field-choice experiment, as only one beetle was tested at a time in the bioassay experiment. We found similar emergence timing and sex ratios between mountain pine beetles emerging from lodgepole and ponderosa pines growing in sympatry. Had we found differences, further investigations of reproductively isolated populations may have been warranted. Finally, we found similar metrics of reproductive success in both host species. Our findings suggest that ponderosa pine in the Front Range of Colorado may be equally or even more vulnerable as lodgepole pine to elevated levels of mountain pine beetle-caused mortality under conditions in which the trees' defense systems are not effective, and where mountain pine beetle populations develop in adjacent lodgepole pines.

Evidence for Sympatric Host Races

The similar emergence phenology and sex ratios of mountain pine beetle in both pine species did not support the hypothesis of host race separation. Studies conducted by Langor (1989) and Langor et al. (1990) of the emergence, infestation, and reproduction of mountain pine beetle in lodgepole and limber pine from different locations in British Columbia and Alberta also did not detect evidence of reproductive isolation among populations from the two hosts, and found that insects from both tree species interbred and produced fertile offspring. Because our study area contained both host species at the same elevation, it is likely that the mechanisms behind the synchronized temporal emergence from lodgepole and ponderosa pine natal hosts are controlled by the number of degree days required for life stage development (Bentz et al. 1991, Logan and Bentz 1999, Safranyik et al. 2010) which may be influenced by elevation, climate, latitude, and other factors (Bentz et al. 1991). At

sites with mixed lodgepole and limber pine around 2,650 m in WY, Dean (2007) also found overlapping peak emergence periods for the two host species, between late July and early September.

Emergence phenology has not been fully documented for either host species in the Front Range. A recent study, using traps baited with insect attractants, collected mountain pine beetles between June and October, 2009–2010, in mixed lodgepole-limber pine stands in the Front Range, though peak emergence data were not reported for either pine species (Mitton and Ferrenberg 2012). At our sites at ~2,600 m, data from emergence cages on trees showed that peak emergence occurred between late July and mid-August in both lodgepole and ponderosa pine in 2010–2011 (Fig. 4). Other studies with similar methods found peak emergence periods broadly similar to ours, even at different elevations: during the second and third weeks of August for ponderosa pine in the Black Hills, SD, at around 1,750 m (Schmid 1972), and during the first week of August for lodgepole pine at 2,670 m, west of the Continental Divide in Grand County, CO (Tishmack et al. 2005). Our results for Colorado's Front Range, therefore, agree with others in finding little evidence for mountain pine beetle host race separation among sympatric pine species based on emergence timing.

Sex ratios during the 5 wk of greatest emergence in both host species were weighted toward female emergence, which was twice that of males early in the flight period. Ratios subsequently equilibrated as the flight period waned, as found by DeLeon et al. (1934) and Rasmussen (1980), and did not differ between host species. Given that female mountain pine beetles "pioneer" or seek susceptible hosts, then initiate gallery construction, life strategies favoring female emergence early in the flight period might confer a benefit to females by allowing more time for individuals to find and successfully colonize a suitable host (Reid 1962). Earlier infestation could benefit the next generation by allowing larvae a longer period of time to reach cold-tolerant stages of development before winter (Bentz et al. 1991). Cerezke (1995) found significant differences in mountain pine beetle sex ratios among three different hosts in Alberta—ranging from approximately 51% female for jack pine, to 60% female for lodgepole pine across the entire emergence period. However, we did not find any evidence of different female emergence timing among species, supporting the results of similar studies by Dean (2007) and Gross (2008), and suggesting that emergence may be governed by seasonality in this region.

Host Selection

The results of both the field-choice experiment and the laboratory bioassay with individual beetles identified an overall mountain pine beetle preference (almost 2:1) for ponderosa pine over lodgepole pine logs regardless of the natal host species in which the beetles had developed. The behavior of individual beetles in our bioassays mirrored that of the selection preference in our controlled-field experiments, adding support to the notion that host selection in the controlled arenas was primarily based on olfactory recognition of pine terpenes and/or on gustatory acceptance.

Overall, our host selection results agree with those of other controlled experiments. Richmond (1933) found that in five trials of each natal host species over 2 yr, on average 63% of the beetles that emerged from ponderosa pine cut-logs subsequently infested ponderosa cut-logs, whereas 75% of beetles emerging from lodgepole pine cut-logs subsequently infested ponderosa rather than lodgepole cut-logs. Wood (1963) investigated host selection behavior of serial populations of *Ips paraconfusus* in ponderosa pine, sugar pine (*P. lambertiana* Dougl.), and Jeffrey pine (*P. jeffreyi* Grev.; 22, 19, 31 generations, respectively). Insects were offered ten homogenized phloem discs prepared from the three alternate hosts and they did not consistently prefer phloem discs from their natal host species, even when multiple generations had developed within that host. However, three field studies found the opposite results: greater proportions of attacks occurred over time on the initial hosts of mountain pine beetle in mixed stands in which more than one host species was available (Baker et al. 1971, Dean 2007, Raffa et al. 2013).

The mixed results of previous research addressing Hopkins' Host Selection Principle have contributed to a long-running debate regarding its validity and relevance (van Emden *et al.*, 1996, Barron 2001). Several insect groups other than bark beetles display behaviors akin to host preference, particularly parasitoids (van Emden 1996), flies (Tulley et al. 1994, Barron and Corbet 1999, Ray 1999), ants (Jaisson 1980), and bees (Breed et al. 1998). Hopkins' principle has been addressed in studies of these groups, but not fully tested or confirmed, and some researchers state that it has limited utility in predicting insect behavior if host availability changes (van Emden et al. 1996). In 1916–1917, Hopkins reported that mountain pine beetle become "adapted" to their hosts over time, and speculated that it may take several generations of breeding in an alternate host to develop future host selection preference for the alternate species. However, he did not discuss the possible underlying mechanisms behind these behaviors. Neurological studies many decades later identified a complete reorganization of the brain during insect metamorphosis, which decreases the probability that host preference could simply be transferred from larval insect stages to adults (Barron 2001). Other entomologists have suggested that either a chemical legacy from the host plant material (Corbet 1985) and (or) learning by adult beetles may elicit behavior consistent with Hopkins' Host Selection Principle (van Emden et al. 1996). The debate over mechanisms has not been entirely resolved (Barron 2001) and was not directly addressed by our study. However, the fact that previous field studies of mountain pine beetle have tended to support Hopkins (Baker et al. 1971, Dean 2007, Raffa et al. 2013), but studies like ours that used cut or processed sections of trees have not (Richmond, 1933, Wood, 1963, Raffa et al. 2013; this study), suggests that defenses of live trees may play an important role in insects' selection of hosts (see Host Defenses section below).

Reproductive Success

Tree species often vary in their quality as suitable hosts for successful reproduction of mountain pine beetle (Langor et al. 1990, Raffa et al. 2013), which may significantly affect insects' selection behavior when choices are available (Amman 1982). However, in answer to our final study question, we found that mountain pine beetle fecundity and oviposition gallery lengths did not differ between lodgepole and ponderosa pine hosts. This suggests the nutrient requirements for acceptance of host material by the breeding parents and the development of their offspring were similar between lodgepole and ponderosa. Consequently, these two species may represent hosts of similar quality, under the conditions examined in this study. In contrast, Langor et al. (1990) and Dean (2007) both found higher fecundity of mountain pine beetle in limber versus lodgepole pine, and Gross (2008) and Raffa et al. (2013) found higher rates of reproduction of mountain pine beetle in whitebark pine than lodgepole pine. Few studies to our knowledge have directly compared ponderosa and lodgepole pine; Amman (1982) found no significant differences in brood production between these species, but reported other evidence suggesting that ponderosa was a higher-quality host. Although we found that the number of brood per female was not

different between the two hosts, a separate investigation showed that body size of individual mountain pine beetles was larger in insects that developed in ponderosa pine natal and choice logs (West 2013). The ecological relevance of larger body size in individuals has not been fully resolved, though larger size may reflect a greater cache of lipids available for use against host defenses, may aid females in initiating a breeding site (Reid and Baruch, 2010), or may contribute to greater dispersal distances for pioneering adults (Graf et al. 2012).

Limitations of Our Study

Several limitations of our study design are worthy of discussion. First, the use of cut-logs in our field-choice experiments may have altered the phloem terpene blend encountered by foraging beetles, compared with that present in live trees. Monoterpenes that were released from cutting the logs potentially oxidized rather quickly, and insects' host acceptance behavior may have been affected by the changes as some of the terpenes were oxidized over the 7 d of each trial. We attempted to address this possible shortcoming by using cut-logs large enough to reduce the oxidation effect throughout the logs, and by supplying fresh logs every 7 d. A 7-d period also appeared to be short enough that beetles' selection of logs was not constrained by lack of space; i.e., most logs were not "full" of galleries by the seventh day. Second, flight of adult mountain pine beetles may increase responsiveness to host stimuli (Shepherd 1965). Our field-choice arenas provided a limited opportunity for the recently emerged beetles to fly once they entered the arenas, but the proportion that actually flew prior to host selection is unknown. However, nearly all beetles infested the logs, so we inferred that under the conditions of our experiment, flight was not an issue.

Third, our tests with sections of logs, bark, and phloem could not fully account for the variation within and between individual trees in variables that might influence host selection, such as chemical composition and bark structure (i.e., the flakes and fissures beetles use when entering the tree). In an attempt to represent as much variation as possible, we used bark/phloem units derived from multiple trees (24) located at two locations within the lodgepole–ponderosa pine ecotone. Finally, in our rearing studies, each infested cut-log was placed in a temperature-controlled environment, which may have selected for various microbial symbionts. Optimal growth temperatures vary between blue staining fungi carried by the mountain pine beetle (Six and Bentz, 2007, Moore and Six 2015). We reared the brood in temperature-controlled environments that overlap with optimal fungal growth temperatures, so as to not favor one symbiont over another, though we did not attempt to quantitatively or qualitatively monitor these symbionts. These conditions should not have affected comparisons between the brood rearings, though they may be different from the conditions encountered by beetles developing in a montane or subalpine environment. However, the symbiont community in each beetle–host combination should be considered in future studies when comparing host selection in different environmental conditions and host tree species.

Host Defenses

The most significant, but inevitable, limitation of host selection studies in controlled conditions involves the use of cut sections of trees rather than intact live trees. Under natural conditions, trees initiate complex systems of defense that have both quantitative and qualitative components—the amount and chemical composition of oleoresin, respectively (Raffa and Berryman 1983). In pine trees, oleoresin flow is considered a primary defense mechanism against bark beetle attack, and occurs when beetles sever the resin canals. The flow often serves to trap beetles ("pitching" them out of the tree) and is followed by triggered histological (auto-necrosis) mechanisms to contain the penetration of attack (Franceschi et al. 2005, Raffa and Berryman 1983). In our host selection experiments and those of other researchers (Richmond 1933, Wood 1963, Amman 1982, Cerezke 1995, Raffa et al. 2013), the use of cut sections of trees prohibited these quantitative defenses, as well as other interactions that occur between the beetles and live hosts, as turgor pressure that is related to resin flow was eliminated by cutting of the stem into sections. However, compounds associated with host defense within the oleoresins were likely still present, and these have been found to vary significantly among tree species in their toxicity to different species of bark beetles (Raffa et al. 2005). Deterrents to host selection via secondary host defenses may be the single most important factor in insect host selection (Schoonhoven et al. 1992). If that is the case, our results suggest that under the conditions of our study, either these two species of trees in the southern Rocky Mountains have similar concentrations of defensive compounds that attacking beetles can tolerate, or the beetles were not strongly affected by any chemical differences that may exist. These hypotheses are being tested in ongoing work (West 2013).

Our finding that many more mountain pine beetles entered the arenas from lodgepole pine natal hosts than ponderosa hosts, but ponderosa pine logs were subsequently selected significantly more than lodgepole pine logs, suggests that mountain pine beetles have a greater affinity for ponderosa pine over lodgepole pine when the resin flow component of host defenses is disabled. Fewer beetles emerged from the naturally infested ponderosa pine trees (vs. lodgepole pine trees) at our sites that we included in our experiments. However, in the trials, significantly more brood developed from ponderosa pine logs than lodgepole pine as a result of the emerging beetles' selection preference for ponderosa pine. In some respects, our findings align with those of Raffa et al. (2013), who documented that whitebark pine, a high-elevation species seldom infested by mountain pine beetle before the current (1990s–2000s) epidemic, has a less effective suite of defenses than lodgepole pine, the insect's historic natal host. In the laboratory, reproductive success of mountain pine beetle in cut sections of whitebark pine was much greater than in lodgepole pine, suggesting that if mountain pine beetle populations continue to expand into higher-elevation sites containing whitebark pine, this formerly "naïve" host may be particularly vulnerable to attack; this may facilitate the development of increasing populations of beetles if climate conditions are favorable (Raffa et al. 2013). Our results also emphasize that the qualitative (chemical) as well as quantitative defenses of alternate hosts should be fully investigated and compared, to determine if changing environmental conditions might similarly increase the susceptibility of either host.

Implications for the Ongoing Mountain Pine Beetle Epidemic

Based on our findings, the current mountain pine beetle epidemic in the Front Range of Colorado will most likely impact both lodgepole and ponderosa pine, rather than dwindling as the availability of lodgepole pine hosts decreases. In support of our experimental results, a complementary field survey in the Front Range recently documented similar proportions of attacks on both species in mixed stands, although the relative success of the insects in each host could not be directly assessed (West et al. 2014). In Colorado, ponderosa pine forests occupy 1.3 times the acreage of lodgepole pine forests, and the Front Range offers near contiguous stands of susceptible

ponderosa pine hosts in addition to the mixed pine stands we examined. Epidemic levels of beetle-caused mortality occurred in ponderosa-dominated stands within approximately 5–50 km of our sites in the northern Front Range in 2010 and 2011 (Briggs et al. unpublished data; USFS 2011, 2012). Even-aged ponderosa pine stands with tree diameters greater than 25 cm and basal area of more than 34 m^2/ha are considered at high risk to beetle mortality (Stevens et al. 1980), and stands with basal areas greater than 17 m^2 ha in the Front Range have also experienced significant infestation in recent decades (Negron and Popp 2004). Impacts of mountain pine beetle in ponderosa pine stands could be widespread and locally intense where mean diameters and stand basal areas meet or exceed these stocking levels, during conditions in which the quantitative host defenses have been weakened or compromised. Water stress—caused by drought, crowded stand conditions, or both—can limit many aspects of tree defenses, such as the flow and/or toxicity of resin in response to beetle attacks (Franchesi et al. 2005, Lindgren and Raffa 2013). An analysis of recent outbreak locations in Colorado found that warm temperatures coupled with low precipitation had caused regional synchrony in mountain pine beetle habitat susceptibility and facilitated spread of the epidemic (Chapman et al. 2012).

Our study used a novel combination of controlled experiments in both the field and the laboratory to demonstrate that infestation and reproduction by MPB were high in both lodgepole and ponderosa pine host species when the resin flow component of their defense systems was disabled. Instead of demonstrating a preference for their natal hosts, insects freely infested both hosts and showed no signs that populations were separated among species. The strong overall preference for ponderosa pine, but equal reproductive success of insects in both hosts, suggests that development in ponderosa pine may confer a benefit to insects' offspring in this host that has yet to be fully identified. If this possibility were tested and confirmed in the field, and the susceptibility of ponderosa pine to infestation was increased by drought, forest managers could expect to observe rapid expansion of mountain pine beetle populations from one host to another in a single epidemic. Previously undocumented mortality of naïve host species such as jack pine (Safranyik et al. 2010, Cullingham et al. 2011), whitebark pine (Millar et al. 2012, Raffa et al. 2013), and interior hybrid spruce (McKee et al. 2013) has been predicted and reported from diverse latitudes and elevations, as warming temperatures enable the mountain pine beetle to expand its prior range (Safranyik et al. 2010, Bentz et al. 2010, de la Giroday et al. 2012). Assessments of the ways in which host–insect interactions are affected by changes in temperature, precipitation, and other abiotic variables are becoming increasingly important in efforts to predict the effects of altered climate regimes on forested ecosystems (Raffa et al. 2013, Six et al. 2014).

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