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# Severe White Pine Blister Rust Infection in Whitebark Pine Alters Mountain Pine Beetle (Coleoptera: Curculionidae) Attack Density, Emergence Rate, and Body Size

EDITH M. DOOLEY<sup>1,2</sup> AND DIANA L. SIX<sup>1,3</sup>

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**ABSTRACT** Exotic tree pathogens can cause devastating ecological effects on forests that can be exacerbated when infections increase the likelihood of attack by insects. Current high rates of mortality of whitebark pine (*Pinus albicaulis* Engelm.) are due to white pine blister rust caused by the exotic fungus, *Cronartium ribicola* J.C. Fisch, and the native mountain pine beetle (*Dendroctonus ponderosae* Hopkins). These two mortality agents interact in whitebark pine; mountain pine beetle preferentially selects white pine blister rust-infected whitebark pine over healthy trees, and likelihood of attack has been observed to increase with infection severity. We examined attack and emergence rates, and size and sex ratio of mountain pine beetle in whitebark pines exhibiting varying white pine blister rust infection severities. Mountain pine beetle attack density was lowest on the most severely infected trees, but emergence rates and size of beetles from these trees were greater than those from uninfected and less severely infected trees. Low attack rates on severely infected whitebark pine may indicate these trees have lower defenses and that fewer beetle attacks are needed to kill them. Higher beetle emergence rates from severely infected trees may be due to low intraspecific competition resulting from low attack rates or differences in nutrient quality.

**KEY WORDS** *Cronartium ribicola*, *Dendroctonus ponderosae*, *Pinus albicaulis*, bark beetle, exotic pathogen

The invasion and spread of exotic forest pathogens has altered the composition of North American forests. Some invasions have caused serious declines or even the functional extinction of affected tree species (Ellison et al. 2005). An example is chestnut blight, a disease caused by the exotic canker fungus, *Cryphonectria parasitica* (Murril) Barr, which has decimated American chestnut (*Castanea dentata* (Marshall) Borkh.) populations (Ellison et al. 2005). Other examples of rapid, extensive tree mortality caused by exotic fungal pathogens are butternut canker due to infections by *Sirococcus clavigneti-juglandacearum* N.B. Nair, Kostichka & Kuntz on butternut (*Juglans cinerea* (L.)), Port-Orford cedar root rot caused by *Phytophthora lateralis* Tucker & Milbrath in Port-Orford cedar (*Chamaecyparis lawsoniana* (A. Murr bis.) Parl), and white pine blister rust caused by *Cronartium ribicola* J.C. Fisch in North American five-needle pines (Loo 2009).

While these diseases are damaging in their own right, their ecological effects can be exacerbated when they interact with native insects that attack infected host trees. In some cases, infection by exotic pathogens results in an increased likelihood of attack by native insects. For example, in mango plantations infection by

two putative exotic pathogenic fungi increase attack rates of the native bark beetle, *Hypocyphalus mangiferae* Stebbing (Masood et al. 2010). This type of interaction has also been observed in coast live oak (*Quercus agrifolia* Née) where a number of native ambrosia and bark beetles are attracted to trees infected with the exotic Oomycete, *Phytophthora ramorum* S. Werres, A.W.A.M de Cock (McPherson et al. 2008).

An exotic fungus–native insect pair is currently causing high rates of mortality of the western North American subalpine keystone and foundation species, whitebark pine (*Pinus albicaulis* Engelm.). Mortality from white pine blister rust and the native tree-killing bark beetle, mountain pine beetle (*Dendroctonus ponderosae* Hopkins; Tomback and Achuff 2010), have contributed to the decline of this tree to such a degree that it is now recommended for listing as an endangered species (Federal Register 2011). Because of recent warming in high elevations, overwintering mortality of the beetle has decreased and most populations have switched from a maladaptive semivoltine (more than one year) life cycle to a seasonally adaptive univoltine (one year) life cycle (Bentz and Schen-Langenheim 2007). This switch allows the beetle to synchronize its entry into winter as cold-tolerant larvae and to emerge in mid-to-late summer in large enough numbers to support successful mass attacks of new trees (Logan and Powell 2001). This has effectively expanded mountain pine beetle's suitable habitat into the high elevation sites where whitebark pine grows.

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Mountain pine beetle exhibits preferences when choosing trees for attack related to tree species and condition. In mixed stands of whitebark and lodgepole pine (*Pinus contorta* Douglas ex Loudon), mountain pine beetle have been observed in some locations to prefer whitebark pine (Six and Adams 2007) while in others, lodgepole pine (Raffa et al. 2012). The beetles have also been observed to attack whitebark pine at higher densities than lodgepole pine (Six and Adams 2007, Dooley et al. 2014). Furthermore, *C. ribicola*-infected whitebark pines are preferred over healthy whitebark pines, and this preference has been observed to increase as the severity of infection increases (Six and Adams 2007, Bokino and Tinker 2012). However, whether infection of trees by *C. ribicola* affects mountain pine beetle productivity is unknown.

*C. ribicola* is a heterocyclic rust fungus that infects pines through needle stomata and infections grow within the phloem of branches to form cankers which eventually spread to the bole of the tree (Geils et al. 2010). The fungus sporulates around the margin of the expanding canker with the older centers eventually drying and cracking. Branches and entire trees die when cankers expand to the extent that they girdle the branch or the bole (Geils et al. 2010). Larger trees can survive infection for >10 yr (Tomback 2001), but during this time they exhibit increasing damage due to the disease. White pine blister rust often kills trees from the top down, greatly reducing crown volume and cone production as infection progresses (Tomback 2001). Trees in infected stands typically display varying stages of disease progression from low infection severity (a few small branch cankers) to high infection severity (a majority of the crown and often the entire upper bole affected; Six and Newcomb 2005).

Our objective was to determine if *C. ribicola*-infected trees affect resource suitability for mountain pine beetle, particularly as infection severity increases. To determine whether white pine blister rust affects beetle fitness and productivity, we examined attack density and emergence rates of beetles infesting whitebark pines of differing infection severities and compared responses from increasingly infected trees to those of healthy trees to determine, what, if any, level of blister rust infection severity impacted beetle fitness and productivity. We also determined size and sex ratios of mountain pine beetle emerging from these trees the following year. Beetle size is a useful proxy for fitness, as larger beetles produce more and larger eggs (McGhehey 1971), show increased flight capability (Thompson and Bennett 1971), and have higher survival rates in cold temperatures (Atkins 1967). Sex ratio, in addition to affecting numbers of progeny produced, can be an indicator of host tree quality, with stressful developmental conditions causing sex ratios to become skewed toward greater numbers of females per male (Amman and Cole 1983, Lachowsky and Reid 2014).

## Materials and Methods

**Study Site.** This study was conducted in Tom Miner Basin, Gallatin National Forest, MT. This

location was chosen because it had mountain pine beetle activity as well as extensive white pine blister rust infection. The site (45° 08'04" N, 111° 08'04" W) was situated in a north-south drainage at an elevation of ~2,507 m. The forest was composed of whitebark and lodgepole pine with smaller components of Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco).

**Stand-Level White Pine Blister Rust Infection Severity and Mortality.** We established three 10- by 50-m belt transects following the 2011 Greater Yellowstone Network Whitebark Pine Monitoring Working Group (2011) protocol to quantify overall incidence and severity of white pine blister rust as well as the cause of mortality of dead trees. Each whitebark pine greater than 1.4 m in height was included in assessments within each transect and rated for infection severity. To assess blister rust, we substituted the rapid rating system (Six and Newcomb 2005) which uses percentage area of the tree affected, for the one used in the Greater Yellowstone Network protocol, which uses counts of cankers. The Six and Newcomb method gives comparable results to those of the canker counting method but is much faster and provides greater overall information including the distribution of the disease within the tree. This rating system divides the tree's bole and crown individually into thirds (top, middle, and bottom). The tree is examined from all sides to evaluate the percentage of each third that displays rust signs and symptoms such as cankers, flagged branches, and bark chewed by rodents. Each of the six sections (three bole thirds + three crown thirds) is rated from 0–3 depending on the percent area affected by disease. Total ratings for a tree can range from 0 (no signs of infection) to 18 (complete infection) based on the sum of scores for independent assessments of the crown and the bole. However, trees usually die of infection by the time they achieve a score of 12 to 14, and trees with higher scores are seldom seen (Six and Newcomb 2005).

**Effects of White Pine Blister Rust Infection Severity on Mountain Pine Beetle.** Whitebark pines large enough to support mountain pine beetle development (>19 cm in diameter; Cole and Amman 1969) spanning a broad range of white pine blister rust infection severities were located within the study site. Trees were chosen to span infection severity ratings from 0 to 12. We stratified these trees into bins of two rating scores that, as a pair, were separated by one severity value to ensure that each category represented a substantially different level of infection severity. The rust rating bins used in this study were 0, 2–3, 5–6, 8–9, and 11–12, which we hereafter refer to as rust infection categories 0, 1, 2, 3, and 4, respectively. We included six whitebark pine in each rust infection category for a total of 30 trees.

Study trees were baited with *trans*-verbenol and e-brevicomin mountain pine beetle tree baits (attractant pheromone; Synergy Semiochemicals Corp., Burnaby, BC, Canada) on 4 August 2010. On this date, two of the preselected study trees (one category 1 tree and

one category 4 tree) were not baited because they were being mass attacked by mountain pine beetle. Because phloem and bark thickness may influence beetle attack density and productivity (Amman and Cole 1983), we also measured these variables at the time baits were placed on the trees. We took these measurements by inserting a ruler into small cuts on the east and west sides of each tree at 1.4 m. We averaged the east and west measurements for both phloem thickness and bark thickness. On 14 October 2010, baits were removed from trees.

From 6 to 9 July the following year (2011), prior to brood adult emergence, we marked two 25- by 55-cm rectangles on the bark of each tree to delineate two subsampling areas. These were centered on the bole at 1.4 m above the ground on the north and south sides. Within these sampling areas, we counted and marked the number of mountain pine beetle entrance holes with paint. Each entrance hole with pitch, frass, or a combination of the two, was considered to represent an entrance hole produced by a single male and female pair (Safranyik and Linton 1985). Other holes without pitch or frass were counted as ventilation holes (produced by tunneling parents) or re-emergence holes (from parents that survive winter and re-emerge the following spring or summer; Safranyik and Linton 1985).

After counting beetle entrance and re-emergence or ventilation holes, cages were stapled over each sampling area. Cages consisted of vinyl screen with the bottom folded into a funnel that was attached to the neck of a plastic soda bottle with the screw-cap attached. A hole was made in the cap into which was inserted a piece of plastic tubing with screen secured over the bottom of the tube. The cap and tube assembly could be easily removed to collect insects that fell into the tube upon emergence from the tree. A piece of No Pest Strip (Hot Shot, Madison, WI) was placed in each tube to kill insects that emerged into the cage. A Lindgren 12-unit multiple funnel trap baited with a mountain pine beetle attractant lure (*trans*-verbenol, exobrevicomin, and the tree monoterpene synergist myrcene; Synergy Semiochemicals Corp., Burnaby, BC, Canada) was installed at the site on 7 July to track general emergence and the flight period at the site.

Mountain pine beetle were collected from cages (Fig. 2A) and the trap (Fig. 2B) approximately every 2 wk on the following dates: 28 July, 12 August, 24 August, 3 September, and 17 September, 2011 (Fig. 2). Beetles collected from cages were placed in 70% ethanol in separate vials for the north and south sides of each tree for each collection date. The study was concluded on 17 September 2011 when beetle emergence and trap captures had dropped to near zero (Fig. 2A,B).

Mountain pine beetles collected from the Lindgren trap and the emergence cages were counted in the lab. Broken beetles were counted by locating pronota. All mountain pine beetles from emergence cages with intact thorax and abdomen were sexed using a microscope at 30 $\times$  magnification using the gender distinct anatomy of the seventh abdominal tergite (Lyon 1958). To determine size, the pronotum of each beetle that

was sexed was photographed at 30 $\times$  magnification using a Leica EZ4D microscope camera (Heerbrugg, Switzerland) and the Leica Application Suite v. 2.0.0, 2010. All photographs were calibrated by photographing a 1-mm slide ruler to set the measurement scale in Image J software (Rasband 2011). A line was then drawn on the image between the lateral edges of the pronotum using Image J's calibrated measurement tool.

**Statistical Analysis.** All analyses were conducted using R statistical software (R Development Core Team 2011). Data from the three transects were pooled to develop site estimates of white pine blister rust infection severity and mortality. Distributions of phloem thickness, bark thickness, beetle attack density, beetle emergence rate, and beetle size were checked for normality using the Holmes Shapiro–Wilk Normality Test. Variance inflation factors were calculated to detect covariance between factors. We tested for differences in bark and phloem thickness by rust infection category using analysis of variance tests. To test for interactions between time of beetle emergence and rust infection category, we produced a running graph of the number of beetles emerging from trees in each rust infection category (Fig. 2). We found no difference in timing of emergence of beetles in different categories, so we performed all further analyses based on total number of beetles collected throughout the season in each category rather than by collection date.

To test for differences in numbers of mountain pine beetle entrance holes, numbers of emerged beetles, and beetle size between the north and south subsampling areas, we used a t-test for entrance holes, and a Mann–Whitney rank sum test for the number of emerged beetles (emergence data did not meet the assumptions of a parametric test). We found no differences in numbers of beetle entrance holes or numbers of emerged beetles between the north and south subsampling areas, so we pooled values for each tree, and converted counts to a per m<sup>2</sup> basis for further analysis.

A generalized linear model (GLM) with a Poisson distribution and logarithmic link function was fit with maximum likelihood estimation to test for differences in attack density (entrance holes/m<sup>2</sup>) between rust infection severity categories. The tree covariates DBH, bark thickness, phloem thickness, and the interaction of these factors with rust infection category were included during model fitting to test for significant effects on mountain pine beetle attack rate. The residuals of the Poisson model were over dispersed, so to correct the reported standard errors, we recalculated the variance as the mean times the dispersion parameter (Zuur et al. 2009). Attack model estimates were converted to the normal scale by exponentiation, and estimated standard errors were calculated using the delta method. To determine if beetle attack density was influenced more by crown or bole infection, or crown and bole infections in different thirds of the tree, we calculated Pearson correlation coefficients between attack density and the rust infection scores of the following divisions: total crown, total bole, top crown, middle crown, bottom crown, top bole, middle bole, and bottom bole.

**Table 1. Summary statistics (means  $\pm$  SEM) for whitebark pine characteristics, white pine blister rust (WPBR) severity rating scores, mountain pine beetle entrance holes, mountain pine beetle parent re-emergence or ventilation holes, and adult mountain pine beetle collected from emergence cages presented by WPBR infection category**

	WPBR infection category				
	0	1	2	3	4
DBH (cm)	25.92(0.69)	28.83(1.40)	28.33(1.61)	27.17(2.65)	27.00(0.71)
Phloem (mm)	2.50(0.25)	2.42(0.15)	2.29(0.28)	2.21(0.33)	2.06(0.16)
Bark (mm)	3.67(0.33)	3.54(0.44)	4.04(0.56)	4.75(0.46)	5.19(0.19)
WPBR crown rating	0(0)	1.67(0.33)	2.83(0.17)	4.83(0.48)	6.75(0.85)
WPBR bole rating	0(0)	0.83(0.17)	2.67(0.21)	3.50(0.50)	4.75(0.63)
WPBR total rating	0(0)	2.50(0.22)	5.5(0.22)	8.33(0.21)	11.5(0.29)
Entrance holes/m <sup>2</sup>	146.17(17.18)	179.33(18.01)	173.33(30.57)	136.33(25.33)	51.00(20.83)
Parent re-emergence/ventilation holes/m <sup>2</sup>	3.67(2.94)	3.17(2.46)	3.00(1.97)	5.50(2.67)	5.50(3.50)
No. beetles collected from cages/m <sup>2</sup>	45.00(23.02)	175.83(51.51)	173.83(42.05)	143.00(26.92)	42.33(56.48)

Infection categories range from 0 (not infected) to 4 (highly infected) (see text for description of how trees were binned by infection severity).  $N = 6$  trees for all categories.

To analyze the total number of beetles emerging from trees in each category of rust infection severity, we modeled this value as emergence rate (number of beetles emerging per m<sup>2</sup> divided by number of entrance holes per m<sup>2</sup>). The distribution of emergence rate best approximated a negative binomial distribution, so we used a GLM with a negative binomial distribution and a logarithmic link. We modeled emergence rate in relation to rust infection severity category by predicting number of beetles emerging per m<sup>2</sup> with number of entrance holes per m<sup>2</sup> entered as an offset variable. Additional covariates entered into the model during model fitting to check for their significant effects on emergence rate were: bark thickness, phloem thickness, tree DBH, entrance holes per m<sup>2</sup>, and number of parent re-emergence holes or ventilation holes per m<sup>2</sup>. Emergence model estimates were converted to the normal scale by exponentiation, and estimate standard errors were calculated using the delta method. We tested for differences in modeled attack density and emergence rate estimates between each rust infection category using Tukey's test for multiple comparisons.

To test for differences in beetle size between rust infection categories, we used a linear mixed effects model with individual host tree as a random factor. Additional covariates entered into the model to check for their respective effects on beetle size were: phloem thickness, bark thickness and DBH of the beetle's host tree, beetle sex, subsampling location (north or south), date on which the beetle was collected, and the number of entrance holes in the subsampling area.

For all three models (attack density, emergence rate, and body size), all variables and interactions between variables were entered into the model during model fitting. Only variables or interactions which were significant and meaningful in the context of the study (DBH, phloem thickness), and whose inclusion in the model improved model fit, were included in the final model. Overall significance of predictors in the final model was assessed by comparing changes in deviance that occur when adding predictors to the null model with a  $\chi^2$  distribution or by using F-tests.

For each tree, we calculated beetle sex ratio (number of females per male) and tested for difference in

sex ratio between rust infection categories using a one-way analysis of variance (ANOVA).

## Results

**Stand-Level Whitebark Pine Rust Infection Severity and Mortality.** Overall, 77% ( $n = 119$ ) of the 154 whitebark pines that were surveyed in transects were dead of rust infection, mountain pine beetle, or both. Of all living trees surveyed ( $n = 35$ ; greater than 1.4 m in height), mean rust infection severity rating was 5.6 ( $\pm 0.70$ ). Seventy-one percent ( $n = 25$ ) of the trees exhibited evidence of rust infection, while 29% ( $n = 10$ ) exhibited no blister rust signs or symptoms. The mean DBH of living whitebark pines in the transects was 10.90 ( $\pm 1.62$ ) cm, whereas the mean DBH of infected trees was 11.58 ( $\pm 1.77$ ) cm. The mean DBH of live whitebark pine large enough for mountain pine beetle attack ( $>15$  cm DBH) was 25.52 ( $\pm 2.00$ ) cm with a mean rust infection severity of 6.7 ( $\pm 1.5$ ).

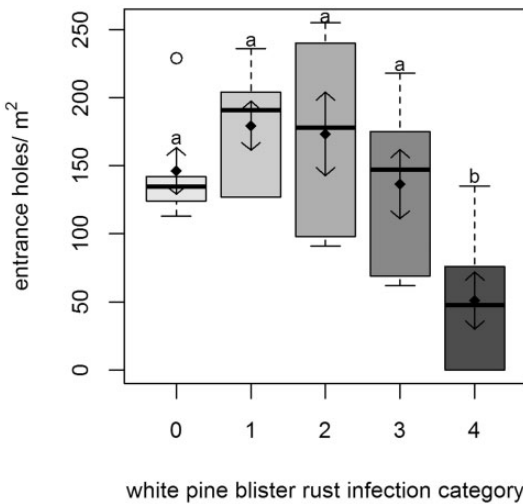
**Bark and Phloem Thickness.** Bark thickness did not vary by rust infection category ( $F = 1.225$ ,  $df = 4$ ,  $P = 0.711$ ) nor did phloem thickness ( $F = 0.536$ ,  $df = 4$ ,  $P = 0.325$ ).

**Mountain Pine Beetle Attack Density.** Two category 4 (high infection severity) trees were not successfully attacked even though they were baited with attractant pheromones. We found no difference in the number of entrance holes between the north and south sampling areas (Table 1, south  $\bar{x} = 20.14$ , north  $\bar{x} = 20.29$ ,  $t = -0.056$ ,  $df = 64$ ,  $P = 0.96$ ), so we pooled these values and calculated attack density (entrance holes per m<sup>2</sup>) per tree for further analysis. We modeled attack density of all trees ( $n = 30$ ), including the two nonattacked trees, as their values likely indicate mountain pine beetle rejected these trees even in the presence of an attractive pheromone signal. Results of the generalized linear model predicting attack density (all trees included, Table 2) indicated that when compared with category 0 trees, only category 4 trees differed significantly in attack density (Table 2; Fig. 1). There were 58 ( $\pm 13$ )% fewer attacks on category 4 trees than on category 0 trees. The model also found that phloem thickness was a significant predictor of attack density

**Table 2. Predictors and statistics for generalized linear models predicting mountain pine beetle attack density and emergence rate, and generalized linear mixed effects model predicting adult mountain pine beetle pronotum width (size) in relation to white pine blister rust infection category**

Model	Predictors	Coeff.β	SE	df	t-value	P-value
Attack density	Category 0 (intercept)	4.06	1.49	24	10.93	<0.0001
	Category 1	0.25	0.21	24	1.18	0.2510
	Category 2	0.24	0.21	24	1.14	0.2659
	Category 3	0.02	0.23	24	0.09	0.9300
	Category 4	-0.87	0.31	24	-2.78	0.0103
Emergence rate	Phloem thickness	0.36	0.13	24	2.80	0.0099
	Category 0 (intercept)	3.19	1.49	22	2.14	0.0327
	Category 1	0.39	0.34	22	1.12	1.2614
	Category 2	0.33	0.34	22	0.95	0.3399
	Category 3	0.17	0.34	22	0.50	0.6189
Size	Category 4	0.85	0.44	22	1.95	0.0518
	Log(ent. holes/m <sup>2</sup> )	-0.68	0.30	22	-2.30	0.0214
	Category 0 (intercept)	2.53	0.09	1024	29.70	0.0000
	Category 1	0.03	0.02	22	1.11	0.2783
	Category 2	0.01	0.02	22	0.51	0.6176
	Category 3	0.01	0.02	22	0.51	0.6180
	Category 4	0.62	0.03	22	2.45	0.0229
	Julian emergence date	-0.003	0.00	1024	-8.44	0.0000
Sex, male	-0.15	0.01	1024	-15.39	0.0000	
	Phloem thickness	0.03	0.01	22	1.82	0.0830

Infection categories range from 0 (not infected) to 4 (highly infected) (see text for description of how trees were binned by infection severity).  $N = 6$  trees for all categories in the entrance model,  $N = 6$  for all categories in the emergence and size models except for category 4 with  $N = 4$



**Fig. 1.** Attack density of mountain pine beetle in whitebark pine by white pine blister rust infection category. Boxplots of beetle attack density (entrance holes/m<sup>2</sup>) in five white pine blister rust infection categories. Infection categories range from 0 (not infected) to 4 (highly infected) (see text for description of how trees were binned by infection severity).  $N = 6$  trees for all categories. Diamonds indicate means, arrows indicate standard errors, and circles represent outliers (1.5 times the interquartile range). Different letters denote significantly different means as estimated by the Poisson GLM attack density model.

(Table 2). Both blister rust category and phloem thickness were found to be significant in the model (Table 3).

Holding rust infection category constant, attack density increased by 43 ( $\pm 18$ )% with each 1 mm increase in phloem thickness. Multiple comparison tests

indicated that category 4 trees had significantly lower attack rates than each of the other three categories, while attack rates on trees in categories 0, 1, 2, and 3 did not differ from one another (Fig. 1). Attack density was more closely related to total rust infection bole score (Pearson correlation coefficient = -0.29,  $N = 30$ ) than to total rust infection crown score (Pearson correlation coefficient = -0.19,  $N = 30$ ). Pearson correlation coefficients indicate that within each crown third, attack densities were weakly negatively correlated to rust infection score (crown top = -0.13, crown middle = -0.16, crown bottom = -0.20,  $N = 30$ ). Within bole thirds, there was no correlation between mountain pine beetle attack density and rust infection score for the bottom bole third (Pearson correlation coefficient = -0.01,  $N = 30$ ) and only a weak correlation for the middle bole third (Pearson correlation coefficient = -0.06,  $N = 30$ ). The top bole third showed the strongest negative correlation between attack density and rust infection score (Pearson correlation coefficient = -0.36,  $N = 30$ ) indicating that as infection severity score of the top third of the bole increased, beetle attack density decreased.

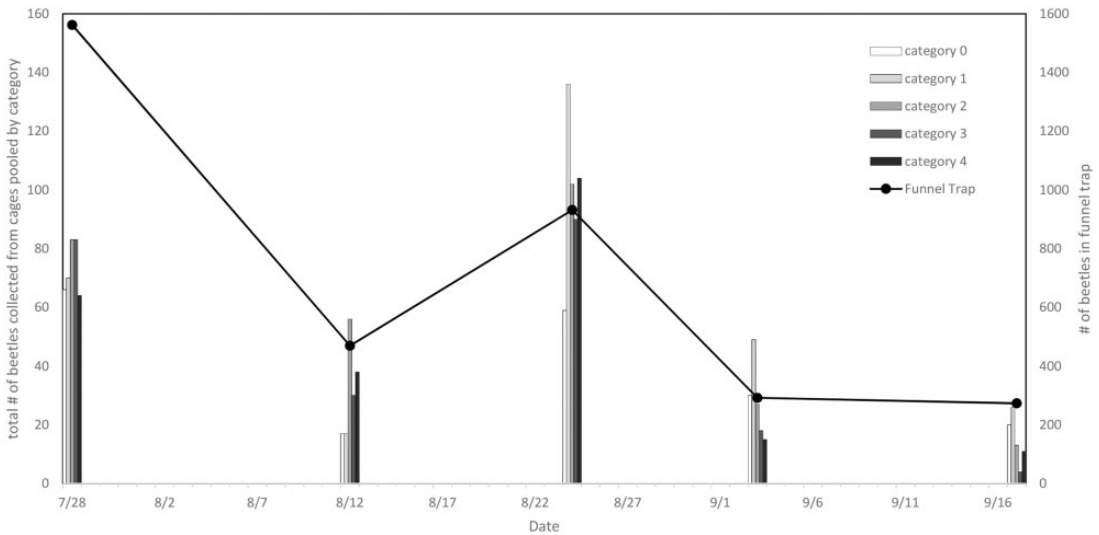
**Emergence of Mountain Pine Beetle.** A total of 1,234 beetles were collected from cages on the 28 attacked trees. The temporal pattern of emergence of mountain pine beetle throughout the season did not differ between rust infection categories (Fig. 2). All rust infection categories show two peaks of beetle emergence: one between 9 July and 28 July (July 28th collection) and one between 12 August and 24 August (24 August collection; Fig. 2). These emergence peaks matched peaks of beetles captured in the Lindgren funnel trap (Fig. 2).

The numbers of beetles collected from each sampling area per tree, averaged for all trees within each rust infection category, are shown in Table 1. Beetle

**Table 3.** Statistics for  $\chi^2$  tests of reduction in residual deviance with the addition of successive predictors into generalized linear models predicting mountain pine beetle attack density (entrance) and emergence rate, and  $F$ -test statistics for significance of model terms in the generalized linear mixed-effects model predicting adult mountain pine beetle pronotum width (size) in relation to white pine blister rust infection category

Model	Predictors	df	Deviance	Residual df	Residual deviance	$P$ -value
Entrance	NULL	29	1296.58	—	—	—
	Category	4	555.61	25	740.97	<0.0001
	Phloem	1	168.57	24	572.40	0.0050
Emergence	NULL	27	55.64	—	—	—
	Category	4	20.65	23	34.99	0.0004
	log(av.ent)	1	5.46	22	29.52	0.0194
Size	Predictors	df Numerator	df Denominator	$F$ -value	$P$ -value	
	(Intercept)	1	1024	70552.08	<.0001	
	Category	4	22	2.38	0.0825	
	Julian emergence date	1	1024	74.65	<.0001	
	Sex	1	1024	239.03	<.0001	
	Phloem thickness	1	22	3.30	0.0830	

Infection categories range from 0 (not infected) to 4 (highly infected) (see text for description of how trees were binned by infection severity).

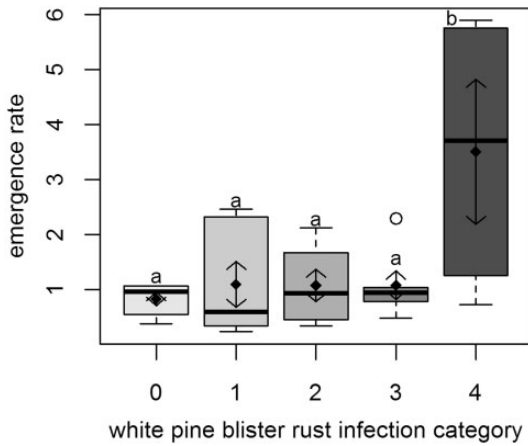


**Fig. 2.** Numbers of mountain pine beetles collected during emergence period. (A) Numbers of beetles collected from emergence cages on whitebark pine averaged by white pine blister rust infection category, and (B) number of beetles collected from a pheromone-baited Lindgren funnel trap at the study site, over five collections dates ranging from 28 July to 17 September 2011. Infection categories range from 0 (not infected) to 4 (highly infected) (see text for description of how trees were binned by infection severity).  $N = 6$  trees for all categories.

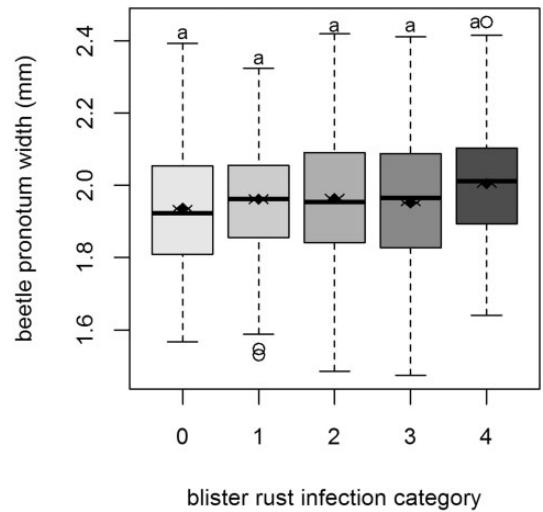
emergence rates within a rust infection category indicate that category 4 trees had higher emergence rates than trees in all other categories. The variance of emergence rates among trees in category 4 was also much greater (Fig. 3). These findings were confirmed by the GLM, which used two significant terms, rust infection category and log (attack density) to predict beetle emergence rate (Table 3). Emergence rate was significantly related to log (attack density) in a negative exponential ( $x^{-0.68(\pm 0.30)}$ ) manner. Rust infection category 4 was the only level of this variable that exhibited significance in this model (Table 2). The estimated emergence rate of mountain pine beetle from category 4 trees was 233 ( $\pm 101$ )% higher than from category 0 trees. Multiple comparison tests also found that

emergence rates from category 4 trees were significantly higher than that from trees in all other categories (Fig. 3). Estimated beetle emergence rates in categories 0 through 3 did not differ from one another (Fig. 3).

**Beetle Size.** Of the 1,234 beetles collected from emergence cages, 1,054 beetles were intact and could be sexed and measured for pronotum width. The average widths of pronota of male and female beetles emerging from the north and south sides of trees of each rust infection category are shown in Table 4. Widths of beetles collected from the north sides of trees (mean = 1.98 mm) were significantly larger than those from south sides of trees (mean = 1.95 mm;  $t = 2.37$ ,  $df = 1051.56$ ,  $P = 0.02$ ). In addition to rust



**Fig. 3.** Mountain pine beetle emergence rate by white pine blister rust infection category. Boxplots of emergence rate (no. entrance holes/m<sup>2</sup>/no. beetles collected/m<sup>2</sup>) for 28 whitebark pine in five white pine blister rust categories representing trees ranging from no infection (category 0) to high infection severity (category 4). Diamonds indicate means, arrows indicate standard errors, and circles represent outliers (1.5 times the interquartile range). Different letters denote significantly different means as estimated by the negative binomial GLM emergence model. Categories 0–3, *N* = 6, category 4, *N* = 4 (two category 4 trees were not attacked).



**Fig. 4.** Mountain pine beetle size by white pine blister rust infection category. Boxplots of pronotum widths of beetles emerging from 28 whitebark pine in five white pine blister rust categories representing trees ranging from no infection (category 0) to high infection severity (category 4). Diamonds indicate means, arrows indicate standard errors, and circles represent outliers (1.5 times the interquartile range). *N* for each category: 0 = 163, 1 = 240, 2 = 242, 3 = 192, 4 = 217.

**Table 4.** Mean ( $\pm$  SEM) of pronotum widths for adult males and female mountain pine beetles emerging from north and south sampling areas on 28 whitebark pine presented by white pine blister rust infection severity category

	Infection Category				
	0	1	2	3	4
<b>Females:</b>					
North	2.00 (0.02)	2.01 (0.02)	2.02(0.02)	2.03(0.02)	2.06(0.01)
(N)	57	58	66	75	103
South	1.97 (0.02)	2.00 (0.01)	2.01(0.01)	1.99(0.03)	2.00(0.02)
(N)	48	103	103	46	53
<b>Males:</b>					
North	1.89 (0.02)	1.90 (0.03)	1.83(0.02)	1.83(0.03)	1.94(0.02)
(N)	38	27	42	38	37
South	1.75 (0.03)	1.86 (0.02)	1.86(0.02)	1.85(0.03)	1.90(0.03)
(N)	20	52	31	33	24

Infection categories range from 0 (not infected) to 4 (highly infected) (see text for description of how trees were binned by infection severity). *N* = 6 trees for all categories except category 4 where *N* = 4 because two trees were not successfully attacked.

infection category, other variables that were significant predictors of beetle size in the linear mixed effects models were date on which the beetle was collected and sex. Phloem thickness bordered on significance (Tables 2 and 3). The only rust infection category that was a significant predictor of beetle size was category 4 (Table 2), and overall, the rust infection category term bordered on significance (Table 3). Holding sex, collection date, and phloem thickness constant, beetles in category 4 trees were on average 0.06 ( $\pm$  0.03) mm larger than beetles emerging from category 0 trees (Fig. 4). Holding all other variables constant, male

mountain pine beetle were estimated to be on average 0.15 ( $\pm$  0.01) mm smaller than female beetles. Each additional day into the emergence season, beetles were on average 0.01 ( $\pm$  0.01) mm smaller holding rust infection category, phloem thickness, and sex constant. Each additional 1 mm increase in phloem thickness related to a 0.03 ( $\pm$  0.01) mm increase in pronotum width holding all other predictors constant.

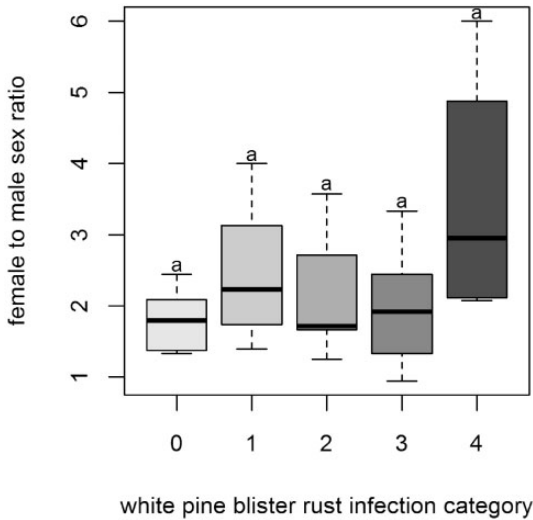
**Sex Ratio.** Female to male sex ratios calculated for beetles from each tree by rust infection category are shown in Fig. 5. No significant difference among sex ratios of beetles emerging from the five categories of rust infection severity (*F* = 2.3, *df* = 4, *P* = 0.13) was found.

**Discussion**

The stands at our study site were heavily affected by both white pine blister rust and mountain pine beetle. Many trees were already dead, and in the remaining living trees, blister rust infections were common and exhibited a broad distribution in severity ratings ranging from zero to 14. Such conditions are broadly representative of most whitebark pine forests across the northern Rocky Mountains.

Two previous studies found that mountain pine beetle preferentially attacks white pine blister rust-infected trees and that the beetle’s preference for infected trees increases in a linear fashion as infection severity increases (Six and Adams 2005, Bockino and Tinker 2012). These studies surveyed trees naturally selected by the beetle at a number of relatively mesic sites in





**Fig. 5.** Mountain pine beetle sex ratio by white pine blister rust infection category. Boxplots of sex ratio (female/male, calculated for each tree) of mountain pine beetle emerging from 28 whitebark pine in five white pine blister rust categories representing trees ranging from no infection (category 0) to high infection severity (category 4). Diamonds indicate means, arrows indicate standard errors, and circles represent outliers (1.5 times the interquartile range). Different letters denote significantly different means. Categories 0–3,  $N = 6$ , category 4,  $N = 4$  (two category 4 trees were not attacked).

Montana (Six and Adams 2005) and more xeric sites in Wyoming (Bockino and Tinker 2012). The two studies produced similar results indicating that a preference by the beetle for trees with greater levels of infection may be a general phenomenon in whitebark pine. However, in our study, highly infected trees were not consistently preferred, and in fact, appeared to be relatively unattractive. Even when baited with attractant pheromones, two category 4 trees were not attacked. The baited category 4 trees that were attacked were attacked at very low densities. However, one category 4 tree was in the process of being attacked as pheromone baits were deployed, indicating highly infected trees are not necessarily rejected.

Our study necessitated the use of pheromone baits to ensure successful attack, control for infection severity, and to synchronize attack timing. The baits likely overrode some of the natural attack dynamics that would have otherwise occurred. In the case of category 4 trees, baits may have increased the likelihood of attack above that which would have occurred naturally. However, the lack of colonization of two trees in category 4 and low rates of attacks on others in this category indicate that the positive response to increasing infection severity may not be a simple linear relationship, but rather a curvilinear response, with attraction increasing with increasing infection severity only to a point, after which it may switch to a negative response. Bockino and Tinker (2012) used an aggregated rating system that cannot be compared to the system used in

Adams and Six (2005) and in this study, and so it is unclear if any of their “high severity” trees were equivalent to our category 4 trees. Of the four sites included in Six and Adams (2005), two had mean severity scores (9.4 and 10.4) substantially higher than the mean infection severity score for trees at the site used in this study (6.7), indicating that category 4 trees were likely present at those sites and were being attacked by mountain pine beetle. The variable results among studies indicate that further investigation of the relationship between mountain pine beetle preference and white pine blister rust infection severity is needed.

Tree diameter did not appear to play a role in the lower attraction by beetles to category 4 trees. It is possible that severely infected trees produce different chemical profiles affecting host recognition by the beetles. It is known that severely diseased trees can emit different monoterpene profiles than healthy trees which may influence host selection. For example, lodgepole pines infected with *Comandra* rust (*Cronartium comandrae* Pk.) contain significantly lower concentrations of myrcene compared with healthy lodgepole pines (Nebeker et al. 1995). If trees severely infected by white pine blister rust also produce low levels of myrcene, this may affect their attractiveness to mountain pine beetle. Myrcene synergizes attraction to the beetle’s aggregation pheromone and is typically added to lures that are used with traps to enhance trap captures. The attractant baits placed on trees in this study released only the mountain pine beetle attractant pheromone blend and did not include myrcene because the volatile is typically released by the host tree (Borden et al. 2008). If trees with high rust infection severity ratings differ appreciably in the volatile profile they emit, attraction to these trees may be reduced even in the presence of pheromone baits.

Attack rate was not only affected by overall tree infection score, but also by the location within the tree where infection occurred. We found attack rate to be most negatively correlated with high bole severity scores for the top third of the tree. This may be due to the common occurrence of “top kill” in trees with severe infections. The general progression of the disease in rust-infected trees begins with the death of small terminal branches, followed by mortality of larger branches, and then the eventual girdling of the bole. Once the bole is girdled, all portions of the tree above the girdled area die. As cankering spreads on the mainstem, the entire tree eventually dies. Because of this progression, category 1 and 2 trees generally have higher crown scores than bole scores, while bole scores increase in trees in categories 3 and 4. White pine blister rust infections that have extended into the bole may alter tree defenses against mountain pine beetle because a majority of the photosynthetic engine producing energy for making defensive compounds (the crown) has been killed (Christiansen et al. 1987). Lower attack rates on trees with extensive bole cankers may, at least in part, be due to reduced defenses.

The lower attack density on severely infected trees supports the hypothesis that diseased trees with weak vigor have lower defenses, thus requiring a smaller

threshold number of beetles for a successful attack (Paine et al. 1997). If highly infected trees have lower defenses, it should take fewer beetles to execute a successful attack, thereby decreasing the potential for intraspecific competition. In lodgepole pine, attack densities above 75 per m<sup>2</sup> (Raffa and Berryman 1983) or 97 per m<sup>2</sup> (Cole 1962) resulted in intraspecific competition among brood, which reduced the number of emerging brood per parental pair. In this study, the significant negative effect of attack density on emergence rate suggests that intraspecific competition affected brood success. Trees in categories 0–3 all had mean attack densities greater than 100 per m<sup>2</sup>. This density is at the high end for mountain pine beetle in lodgepole pine (Reid 1963, Raffa and Berryman 1983) and falls within the range where mortality from intraspecific competition is expected (Raffa and Berryman 1983). In contrast, beetle attack densities on category 4 trees were slightly lower than the optimal attack density in lodgepole pine that results in the greatest emergence rate of brood beetles (Raffa and Berryman 1983).

The relatively high attack densities on trees in categories 0–3 may have been due to the presence of the pheromone baits; however, one tree in category 2 and one tree in category 4 that were not baited because they were undergoing mass attack at the initiation of the study had similar attack densities to other trees in their category. This may indicate that the pheromone baits may not have artificially inflated attack densities. In any case, our results show that highly infected trees can be killed with low attack densities and can provide suitable resources for the insect. In fact, mountain pine beetles not only emerged at greater rates from highly infected trees but, beetles emerging from highly infected whitebark pine were larger than those emerging from trees in other infection categories. Based on the relationship between beetle size and fecundity in lodgepole pine (McGhehey 1971), the increase in mean female size of beetles emerging from category 4 trees compared to category 1 trees could result in the production of ~15 more eggs per female. The larger size of beetles emerging from category 4 trees may be due to a number of factors. One possibility is that decreased intraspecific competition allowed for more resources for individual brood. Amman and Pace (1976) found that at lower attack densities in lodgepole pine, mountain pine beetle adult size was larger due to decreased intraspecific competition. However, when we included attack density in our GLM, we found it had no significant effect on beetle size. Therefore, it is unclear if beetles emerging out of category 4 trees were larger because of decreased competition or due to some other variable.

One such variable is nutrient quality. Beetle size and emergence rate may have been greater in category 4 trees because of increased nutrition due to the presence of *C. ribicola* mycelium in the phloem. Tissues of *Pinus monticola* Douglas ex D. Don, a tree closely related to *P. albicaulis*, infected with *C. ribicola* contained increased concentrations of starches (Hudgins et al. 2005). If an increase in starch in response to infection by this fungus also occurs in whitebark pine,

mountain pine beetle may benefit nutritionally from ingesting fungus-colonized phloem. White pine blister rust cankers are surrounded by living swollen, reddened bark that contains mycelia of the fungus. The mycelia extend ~3 cm beyond the margin of the swollen area (Ehrlich and Opie 1940). If feeding on phloem colonized by *C. ribicola* mycelium has positive effects on beetles, this is most likely to occur in severely infected whitebark pine with large bole cankers. Any increase in phloem nutrients contributed by *C. ribicola* mycelium would be limited to areas near cankers which would lead to high variability in beetle productivity within a tree as well as among trees. This may be a possible explanation for the high variance we observed in attack density, emergence rate, and sex ratios in highly infected trees relative to trees that were uninfected or infected at lower levels or only in the crown. It is unknown how *C. ribicola* may interact with the beetle's nutritional fungal symbionts, *Grosmannia clavigera* (Robinson-Jeffery and Davidson) Zipfel, de Beer & Wingfield and *Ophiostoma montium* (Rumbold) von Arx, when sharing a common phloem substrate.

While we found no significant difference in mountain pine beetle sex ratio between rust infection categories, category 4 trees tended to produce higher female to male sex ratios ( $\bar{x} = 3.5$ , Fig. 5) and exhibited a much greater variance in sex ratios than other infection categories. Female-skewed sex ratios in *Dendroctonus* are due to differential survival between males and females, often due to stressful conditions. For example, male mountain pine beetles exhibit higher mortality rates than females in response to overwintering (Lachowsky and Reid 2014) and in trees with thin, dry phloem. Sapwood moisture content in white pine blister rust-infected whitebark pine has been shown to decrease as infection severity increases (Six and Adams 2007), potentially increasing stress on developing larvae.

Overall, our study indicates that the preference of mountain pine beetle for white pine blister rust-infected trees may not be a simple linear response, but potentially a curvilinear one, with beetles initially responding positively to increasing infection severity, but at some point when severity becomes high, switching to a negative response. Regardless, when beetles do enter highly infected trees, the trees appear to be adequate for development. Low rates of attack translate to high emergence rates relative to the numbers of beetles that enter and greater overall size, which may increase individual beetle fitness through effects on fecundity. However, from a population perspective, attack densities and numbers of brood produced were highest in category 1 and 2 trees (Table 1), indicating these trees may not only be the most preferred by the beetle, but also those most likely to contribute to beetle persistence or spread within stands of whitebark pine.

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