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**Gallery success, brood production and condition of
mountain pine beetles (Coleoptera: Curculionidae) reared in
whitebark and lodgepole pine from Alberta, Canada**

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19 Breeding pairs of mountain pine beetles (*Dendroctonus ponderosa* Hopkins) were
20 introduced into freshly cut bolts of whitebark pine (*Pinus albicaulis* Engelmann) and
21 lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelmann) in the
22 laboratory. Brood adults emerging from the bolts were collected and galleries were dissected
23 to compare reproductive success, brood production and adult condition between the two
24 pines. Beetles were more likely to establish egg galleries that produced brood in lodgepole
25 than in whitebark pine. Larval gallery density/cm egg gallery was significantly higher in
26 whitebark pine than in lodgepole pine; however, egg galleries also tended to be shorter in
27 whitebark pine bolts, and consequently, brood production per gallery did not differ between
28 the two host species. Female body size, female mass and female fat content of brood adults,
29 and survival from larva to adult did not differ between beetles reared in the two hosts.
30 Though this no-choice assay did not simulate the sequence of events occurring during host
31 selection, these data may suggest that beetles could be less likely to attack whitebark pines in
32 southwestern Alberta. Whitebark pines that are attacked will produce brood in similar
33 numbers and condition as those from lodgepole pines.

34

35 **Introduction**

36 The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera:
37 Curculionidae) is considered the most destructive forest insect in western North America
38 (Furniss and Carolin 1977). This beetle infests 22 species of pines in several forest types and
39 eco-regions from Baja Norte, Mexico (31°N) to northern Alberta and British Columbia
40 (58°N) (, Furniss and Schenk 1969, Smith et al. 1981, Wood 1982, Amman and Cole 1983,
41 Safranyik et al. 2010). The biology, population dynamics and ecological roles of mountain
42 pine beetle are best understood in forest types where the species has most commonly caused
43 large-scale outbreaks. These forest types are typified as being even-aged, dominated by
44 lodgepole pine (*Pinus contorta* Douglas ex Loudon var. *latifolia* Engelmann) or ponderosa
45 pine (*Pinus ponderosa* Douglas ex Lawson), > 80 years old and growing between 800 m and
46 1400 m asl (49 °N - 55°N) (Reviewed in Safranyik and Carroll 2006).

47 The recent expansion of the mountain pine beetle into more northern forests, higher
48 elevation forests (Carroll et al. 2004) and jack pine (*P. banksiana* Lamb) containing forests
49 (Cullingham et al. 2011) in western Canada is purportedly related to anthropogenic factors,
50 including fire suppression, which have resulted in huge areas of overmature stands, and
51 winter warming due to climate change (Taylor and Carroll 2004, Safranyik et al. 2010). This
52 expansion into new areas formerly unfavorable for the beetle has generated much discussion
53 and interest (e.g., Cudmore et al. 2010, Safranyik et al. 2010). The mountain pine beetle has a
54 highly adaptable life history (Bentz et al. 1991, 2010) and exhibits relatively consistent
55 features in outbreak dynamics across a broad geographic and host range (Cole and
56 Amman 1980, Amman 1984); however, new research indicates that in these newly invaded
57 forest types key aspects of the beetle's biology (Myrholm and Langor 2015), population
58 dynamics (Bentz and Schen-Langenheim 2007) and ecological influences differ compared to
59 that in the altitudes and latitudes the beetle has typically occupied in the last century

(Safranyik et al. 2010). The dramatic expansion of the mountain pine beetle into northern Alberta and British Columbia and eastward into the boreal forest has garnered most of the attention (e.g., Kurz et al. 2008, Bentz et al. 2010). While sustained outbreaks at high altitudes in other parts of the range are not completely unprecedented (Logan and Powell 2001), they represent a significant deviation from typical patterns of mountain pine beetle activity recorded in the last 125 years (Arno and Hoff 1989), are also thought to be related to climate (Carroll et al. 2004, Logan et al. 2010) and are potentially as devastating as expansion to more northern latitudes (Tomback et al. 2001, ASRD and ACA 2007, Logan et al. 2010).

During the past century mountain pine beetle outbreaks were infrequent in high elevation, subalpine forests of western North America, and were typically associated with prolonged periods of unseasonably warm summer and winter temperatures (Logan and Powell 2001). Several endangered and/or threatened five needle pines, some with current or pending formal conservation listing, thrive in these high-altitude forests (Gibson et al. 2008), including whitebark pine (*Pinus albicaulis* Engelmann), that are sensitive to changes in disturbance regimes because they grow slowly and mature late in life. As whitebark pine is a foundational (Ellison et al. 2005) and keystone (Tomback et al. 2001) species in sub-alpine zones, and is listed as endangered in Canada (COSEWIC 2010), the recent outbreak of mountain pine beetle in high altitudes is a cause for special concern (ASRD and ACA 2007).

The severity and nature of mountain pine beetle impact on whitebark pine depends on interactions between the beetle and its host, as moderated by the environment. Important life history features of the mountain pine beetle (e.g., survival, fecundity, condition, development) have been shown to vary among host tree species (Amman 1982, Langor 1989, Cerezke 1995), and such differences ultimately determine host suitability, and directly influence mountain pine beetle population dynamics and success.

There are relatively few empirical data about the quality of whitebark pine as a host for the mountain pine beetle. In laboratory rearings, Amman (1982) found that whitebark pines bolts produced more and larger brood compared to lodgepole pines (though these differences were not statistically significant) while, Gross (2008) found that lodgepole pine bolts produced significantly more brood than whitebark pines while whitebark pines produced larger beetles. Both studies are based on host material from only one or two trees of each host species and did not adequately control for variation in phloem thickness, thus different results could simply reflect natural variation within a tree species. Therefore, to increase understanding of the suitability of whitebark pine as a host for the mountain pine beetle in the northern part of the ranges of both species, we undertook a laboratory rearing study. We compared the life history and reproductive characteristics egg gallery success, brood production and brood adult size, mass and fat content, between mountain pine beetles reared in bolts of whitebark pine and lodgepole pine. We interpreted these responses as indicators of host quality for the beetle. This work compliments studies of mountain pine beetle success in standing trees of each species (Esch 2012) and comparisons of the natural enemies associated with the beetle found in each of these host trees (Esch et al. 2015).

Materials and Methods

Collection and Preparation of Host Material and Beetles. Mountain pine beetles used as parental stock for rearings were collected from six naturally infested lodgepole pines near Eureka River, in northern Alberta (56.4799° N, 118.5177° W) on 4 September 2008. Infested bolts were sealed with paraffin wax to prevent desiccation, held at 5° C until 20 October 2008 and then moved to a greenhouse for larvae to complete development. Bolts were placed in large ventilated plastic rearing containers (modified 110-litre black garbage cans) in the greenhouse, and held at 18 to 22°C under a 12L:12D photoperiod. Emerging beetles were collected daily from the rearing containers, placed in Petri plates lined with fresh

110 pine phloem [sexes separated according to Lyon (1958)], and stored in the dark in a cooler at
111 8°C until used.

112 Host material for rearing mountain pine beetles was collected near Vickary Creek in
113 southern Alberta (49.7757° N, 114.5282° W). These trees were located on an east-facing
114 slope, at 1 950 m elevation, situated in a stand dominated by Engelmann spruce, *Picea*
115 *engelmannii* Parry ex Engelmann, and subalpine fir, *Abies lasiocarpa* (Hooker) Nuttall, and
116 with approximately equal parts of whitebark pine and lodgepole pine representing minor
117 components (ca., 30%) of the canopy. Although exact composition was not recorded, the
118 stand was similar to a *minor seral* whitebark pine community described by Arno and Hoff
119 (1989). Ten whitebark pines [diameter at breast height (DBH) 20-31 cm] and 10 lodgepole
120 pines (DBH 19-29 cm) with no visible signs of insect damage or disease were felled on 22
121 and 23 September 2008, and each felled tree was used as a source of 2-3 bolts (each 1.1 m in
122 length) for rearing beetles as described below. Bolts were transported to the Canadian Forest
123 Service, Northern Forestry Centre in Edmonton, Alberta, and held in a greenhouse at 18 to
124 22°C under 12L:12D photoperiod for the duration of this experiment.

125 **Gallery Initiation and Beetle Collection.** The bark surface of each bolt used for
126 rearing was divided into 1-3 strips, each 1.1 m long and ≥ 30 cm wide, depending on bolt
127 circumference, by cutting longitudinal grooves with a chainsaw through the bark ca. 1 cm
128 into the sapwood. Previous experience suggested that this allowed the beetles to feed *ad*
129 *libitum* while having their area of activity constrained (Langor, unpublished). Paraffin wax
130 was used to seal the ends and grooves of each bolt to slow desiccation and reduce infection
131 by saprophytic fungi.

132 We attempted to establish one mountain pine beetle gallery in each bark strip on each
133 bolt as follows. A newly emerged female beetle of average size (conspicuously small and
134 large beetles were discarded) and good condition (actively moving about the Petri plate) was

placed in a small hole scored into the bark and phloem ca. 30 cm from the base of the bolt. The hole was then sealed with one half of a large gelatin capsule attached to the bolt with a pin to prevent female escape. After 24 h, each hole was checked for gallery initiation, as indicated by boring dust in the gelatin capsule. Females failing to initiate a gallery after 24 h were re-inserted into their hole, while dead females were replaced with fresh females.

After gallery construction proceeded to the point where females were no longer visible at the entrance of their gallery, a male was inserted into the gallery entrance and the gelatin capsule was replaced to prevent escape. Capsules were checked again after 24 h and dead or rejected males were replaced by new males. This procedure was repeated daily for seven days, after which we stopped attempting to initiate galleries in those bark sections where galleries were apparently not established. In total, we attempted to establish 36 galleries in 18 lodgepole pine bolts and 46 galleries in 20 whitebark pine bolts.

After gallery initiation was complete, each bark strip was individually caged with 1 mm² nylon screen. To accomplish this, wooden slats (ca. 1 cm thick, 3 cm high, and the length of the bolt) were inserted into the chainsaw grooves on each bolt, thereby providing 'sides' to each bark strip. Then nylon screen was glued and stapled to the top and ends of each slat and to the top end of the bolt. The screen at the bottom end of each cage was formed into a funnel-shape, fit with a collecting jar and then sealed to the bolt with glue and staples to prevent beetle escape. F₁ adults (hereafter called 'brood adults') began emerging 47 days after the end of the gallery initiation period and continued emerging for 36 days. Brood adults were collected daily, placed in individual 1.5 ml microcentrifuge tubes, and stored at -20°C for subsequent analysis. Parent beetles emerging during this 36 day period could not be distinguished from brood adults.

Gallery Dissection and Beetle Condition. After brood adults stopped emerging, the total number of emergence holes was recorded for each gallery. Differences in the number of

emergence holes and captured beetles indicate as many as 26% of brood adults may have escaped the cages by chewing through the mesh, despite our best efforts to seal the bark strips. Because of this discrepancy, we used the number of emergence holes as a measure of brood production, knowing that this number likely underestimates emergence (Amman and Cole 1983). A piece of unconsumed phloem was excised from each bolt and its thickness was measured with calipers (0.01 ± 0.005 cm) and the size of each bolt was measured using a DBH tape (0.1 ± 0.05 cm). We measured phloem thickness at the end of the experiment to limit infection by saprophytic fungi. Although it may have introduced some experimental error, we assumed that phloem desiccated similarly between the two species. The bark was then peeled so that egg gallery length and number of larval galleries could be recorded. Unfortunately, number of eggs laid per gallery (fecundity) could not be reliably assessed because it was impossible to accurately tally dead eggs or identify egg niches in phloem degraded by saprophytic fungal activity. Consequently, oviposition could not be used reliably as the criterion for successful gallery initiation; instead we used presence of at least one larval gallery. The larval gallery density was determined from the number of larval galleries per cm of egg gallery assessed over the entire egg gallery. Larval survival was estimated from the number of emergence holes per bark strip divided by the number of larval galleries per egg gallery.

Nine hundred and forty six brood adults were collected. From these, the 466 females beetles were retained to assess brood adult condition. Pronotum width was measured to the nearest 0.1 ± 0.05 mm, using a dissecting microscope (K series, Motic, Xaimen, China) fitted with an ocular micrometer. Beetles were dried at 75°C for 24 h and then weighed to the nearest microgram using a balance (Sartorius model CP2P, Elk Grove, IL). Fat content was determined as the difference in dry mass before and after fat extraction in a Soxhlet apparatus. To accomplish this, beetles were individually placed in perforated 1.5 ml

microcentrifuge tubes that were then heated in a Soxhlet apparatus (45/50 Pyrex, Fischer Scientific, Toronto, ON, Canada) while immersed in petroleum ether for 8 h at 35-60°C. Beetles were returned to the drying oven a second time for 24 h at 75°C and re-weighed to determine fat loss.

Statistical Analysis. All parameters measured from each attempted or successful gallery were averaged to give a single value for each tree and values were compared between host species. Differences in tree diameter (average of all bolts) and phloem thickness of each tree (average of all bolts) was tested using a Welch's *t*-test. The effect of host species on proportion of successful egg galleries was tested using a Generalized Linear Mixed Model (GLMM) that included phloem thickness as a random effect (random intercept) and normally distributed errors $N(\mu, \sigma^2)$. Relationships between gallery success and phloem thickness were investigated with Pearson's correlations. Since not all bark strips contained successful galleries, sample size was too small (nine lodgepole pine trees and six whitebark pine trees) to include phloem thickness as a random effect for models of the other parameters measured in this experiment. The effects of host species on egg gallery length, number of larval galleries per egg gallery, larval gallery density, brood survival, sex ratio, brood adult emergence, as well as female brood adult size, mass and fat content were tested by General Linear Models (GLM). GLMs were fit by restricted maximum likelihood estimates, while the GLMM was fit by penalized quasi-likelihood estimates (see Bolker et al. 2009). Wald's *t*-values were used to assess significance of model parameters. All analyses were performed in R version 2.15.3 (R Development Core Team 2013) using the *nlme* (Pinheiro et al. 2008) and *MASS* (Venables and Ripley 2002) packages following procedures outlined by Zuur et al. (2009).

Results

Host Material. Diameter of bolts used in this study ranged from 15 to 31 cm. There was no difference between host species in tree diameter (lodgepole pine: 22 ± 0.7 cm (mean $\pm$ SE); whitebark pine: 26 ± 1.7 cm; $t=1.79$, $df=15.3$, $p=0.098$) or phloem thickness (lodgepole pine bolts: 1.1 ± 0.09 mm; whitebark pine bolts: 1.3 ± 0.15 mm; $t=0.585$, $df=15.3$, $p=0.567$).

Gallery Success. Egg gallery success varied between host species. Of the 82 attempted egg galleries, 21 pairings from nine lodgepole pine trees and 13 pairings from six whitebark pine trees produced brood. The proportion of successful egg galleries on lodgepole pines was significantly higher than on whitebark pines ($t=2.11$ $df=17$, $p=0.049$; Fig. 1A). Overall, the proportion of successful egg galleries tended to increase with phloem thickness ($\rho=0.535$, $df=18$, $p=0.015$). This correlation was statistically significant in whitebark pine bolts ($\rho=0.898$, $df=8$, $p<0.001$) but not in lodgepole pine bolts ($\rho=0.416$, $df=8$, $p=0.231$). For 17 of the 48 unsuccessful pairings (35%, 12 pairings in whitebark and five in lodgepole), no egg galleries were excavated into the phloem or sapwood. In the remaining 31 unsuccessful pairings, egg galleries were initiated but were short (1-15 cm) with either one parent (eight pairs in whitebark and six in lodgepole) or both parents dead in the gallery (one pair in lodgepole), or seemingly abandoned by both parents (12 in whitebark and five in lodgepole).

Gallery Characteristics. Egg gallery lengths were not statistically different between lodgepole pine (41.0 ± 2.74 cm) and whitebark pine (32.2 ± 6.90 cm) ($t=1.00$ $df=14$, $p=0.334$; Fig. 1B). The total number of larval galleries per egg gallery in lodgepole pine (63.9 ± 11.31) was not significantly different ($t=0.28$ $df=14$, $p=0.785$) from that in whitebark pine bolts (68.9 ± 13.22). Larval gallery density was significantly greater in whitebark pine (3.1 ± 0.44 galleries/cm) than in lodgepole pine (1.8 ± 0.19) ($t=2.818$ $df=14$, $p=0.015$; Fig. 1C).

Brood Adult Production. Brood adult emergence was a function of both parental fecundity and larval survival. Brood adults emerged from all successful galleries except one (in lodgepole pine) where all larvae died as early instars. There was no significant host effect on successful larval development from L1 to adulthood ($t=1.11$ $df=14$, $p=0.287$; Fig. 1D), although there was a trend for higher success in lodgepole pine, $66.1 \pm 8.29\%$ (SE), than in whitebark pine, $54.1 \pm 4.01\%$. Brood adult emergence did not differ significantly between hosts ($t=0.322$, $df=14$, $p=0.752$, Fig. 1E) and averaged 39.5 ± 7.75 brood per gallery in lodgepole pine and 35.9 ± 6.71 in whitebark pine. Sex ratio (50% females in lodgepole pines; 48% females in whitebark pine) did not differ between the two host species ($t=0.31$ $df=14$, $p=0.761$).

Brood Adult Condition. Host species did not significantly influence brood adult size ($t=0.598$, $df=14$, $p=0.201$, Fig. 1F), mass ($t=1.035$, $df=14$, $p=0.318$, Fig. 1G) or fat content ($t=1.41$ $df=14$, $p=0.181$, Fig. 1H). Average female brood adult pronotal width was 2.1 ± 0.05 mm in beetles from lodgepole pine and 2.0 ± 0.05 mm in brood from whitebark pine. Nonetheless, brood adults tended to be slightly heavier in whitebark pine (4.80 ± 0.362 mg) than in lodgepole pines (4.44 ± 0.150 mg) while brood adults from lodgepole pine tended to have slightly higher fat content ($37 \pm 2.3\%$) than did those from whitebark pine ($33 \pm 1.2\%$).

Discussion

Drawing inferences about host quality from results based on rearings in cut bolts requires caution because the host environment is undoubtedly very different in cut bolts compared to trees attacked naturally, especially insofar as host defences are concerned. Host material was collected for this experiment at the end of September, and although it is not unusual for mountain pine beetles to initiate attacks in September in Alberta (D.W. Langor, unpublished data), these bolts were collected nearly a month after the peak of mountain pine beetle attack at these altitudes and latitudes (Safranyik and Carroll 2006). Consequently,

phloem hardening, the process whereby sieve and associated cells in the phloem die and are replaced by callose, would have been more advanced in these bolts than in naturally attacked trees (Alfiere and Evert 1968). Although phloem hardening has not been explicitly compared between whitebark and lodgepole pines, this process is essentially similar between hard and soft pines (Alfiere and Evert 1968). Bolts were sealed with wax to reduce moisture loss associated with this hardening, as well as to offset the accelerated drying caused by experimental conditions. Starch, nitrogen, lipid and mineral levels do not decrease as phloem hardens (Haack and Slansky 1987); however, carbohydrate levels, and potentially other nutrient levels maybe be reduced in sub-corticle tissues in cut bolts compared to live trees (Dunn and Lorio 1992). Nonetheless, such rearing experiments can provide useful insights concerning host effects on beetles (e.g. Langor and Spence 1991).

Bolts were collected for our study from only ten trees of each species from a single stand, although the number of trees used is relatively large compared to other mountain pine beetle rearing studies (e.g. Bentz et al. 2001). Nonetheless, it is possible that these results were influenced by host conditions specific to a single stand, and it would be inappropriate to assert that they reflect what occurs across the broad geographic ranges of whitebark pine or lodgepole pine. This is particularly true for lodgepole pine, which exhibits enormous variability in ‘chemotype’ across its distribution (Clark et al. 2010). Thus, while the results of our localized study cannot be extrapolated broadly, they do highlight real host-associated patterns in beetle success that are valuable for designing future research and are part of a larger scale study of mountain pine beetle survival, phenology and natural enemy abundance in whitebark pines in Alberta (Esch 2012).

Observing mountain pine beetle behavior led Hopkins (1916) to formulate his famous host-selection principle, which states that “a species which breeds in two or more hosts will prefer to continue to breed in the host to which it has become adapted.” This theory has

existed in many incarnations and has been vigorously debated over the past century (Reviewed in, Barron 2001). From this, we might expect that beetles would prefer and be better adapted to develop in lodgepole pines in this study, because it was the host tree for all parental beetles. Though a number of studies failed to validate this principle amongst the bark beetles (See Barron 2001), it is evident that rapid, genetic isolation of mountain pine beetles can occur within one host species over a few generations (Langor and Spence 1991). It is likely that the beetles higher gallery success in lodgepole pine was due to a combination of conditioned, genetic, and host quality related effects (Barron 2001), though untangling these factors was not possible in this study. Data presented here lends support to Hopkin's host-selection principle, as it is formulated above. However, it should also be noted that brood production and brood adult condition were not better in lodgepole pines, the host from which the parents originated. This suggests that host quality, regardless of parental origin, may also play an important role in beetle reproductive output and condition.

Egg gallery success was greater in lodgepole pine, with a tendency to increase with phloem thickness in both hosts. These patterns could in part be explained by the parental effects described above and/or by differences between host species. Pioneer females are more likely to construct egg galleries on larger trees that tend to have thicker phloem (Roe and Amman 1970). Gallery initiation is also partially controlled by gustatory and olfactory feedback from chemical properties of host tissues, with particular compounds known to attract or repel beetles (Raffa and Berryman 1982). Differences in composition of monoterpenes, a dominant class of insect-related defensive compounds found in the sub-cortical tissues of pines, have been found between whitebark and lodgepole pines (Raffa et al. 2013, Bentz et al. 2015). In no-choice assays, Raffa et al. (2013) found beetles entered whitebark pine and lodgepole pine equally readily. Under natural conditions, mountain pine beetles preferentially attack lodgepole pines over whitebark pines (Raffa et al. 2013, Bentz et

al. 2015) while other studies failed to find significant differences in host preferences (Baker et al. 1971, Six and Adams 2007). Though the no choice assays conducted in this study do not replicate the full series of events occurring during natural attack, our data support the consensus of the most robust data that mountain pine beetles may show some preference for lodgepole pine over whitebark pine.

Brood production, brood adult condition and gallery characteristics, except larval gallery density, did not differ significantly between the two host species. Other studies show no significant difference in mountain pine beetle brood production between these two hosts in the field (Esch 2012, Bentz et al. 2014, 2015, Dooley et al. 2014) or laboratory experiments (Amman 1982) while one laboratory rearing study showed greater brood production in lodgepole pine compared to whitebark pine (Gross 2008). Some field (Bentz et al. 2015) and laboratory experiments (Gross 2008) showed brood adults were significantly larger when they developed in whitebark pine compared to lodgepole pine, while Amman (1982) showed similar results, however, the differences were not statistically significant. Mountain pine beetle larval galleries are more densely spaced in trees with thicker phloem (Amman and Cole 1983). The greater larval gallery density observed may have simply reflected the greater proportion of successful egg galleries in whitebark pines in bolts with thick phloem. The absence of large differences in brood production and survival, brood adult condition and sex ratio measured in this study suggest that the sub-cortical environment of these two hosts differed little in terms of nutritional properties, or that any such differences had little effect on the developing brood.

Mountain pine beetle nutrition is also mediated by symbiotic ophiostomatean fungi and other microorganisms (Ayres et al. 2000, Myrholm and Langor 2015). Though these relationships are beyond the scope of this paper, it may be worth noting that in a separate study, performance of three fungal species did not vary significantly in live lodgepole pine

versus whitebark pine trees (E. D. Esch and A. V. Rice unpublished data). It is unlikely that the limited host effects on mountain pine beetle in this experiment can be explained by differences in fungal performance.

Conclusions. Mountain pine beetles were less successful at initiating egg galleries on whitebark pine bolts than on lodgepole pine bolts in our study. Though data presented here are limited, and do not simulate the conditions whereby host selection occurs naturally, they lend support to observations the beetle prefers lodgepole pines over whitebark pines, and suggest that this pattern may hold true in the east slopes of the Rocky Mountains of southern Alberta. However, the limited influence of host species on the majority of parameters measured in this study and observed elsewhere indicates that host tree species is not the most important factor affecting reproductive output or brood adult condition. In studies that show significant influence of host species on reproductive output or brood adult condition, these differences may be due to the confounding effects of phloem thickness (e.g. Amman 1982, Langor 1989). Data presented here and elsewhere show no difference in phloem thickness between the two host species (Baker et al. 1971, Esch 2012, Bentz et al. 2015) while others show some thicker phloem in whitebark pines (Dooley et al. 2014). Given this, it is likely that factors such as stand density, tree size (Perkins and Roberts 2003), white pine blister rust (*Cronartium ribicola* Fischer) infection severity (Six and Adams 2007, Dooley and Six 2015) and climate (Logan and Powel 2001) will be more important in predicting growth and spread of mountain pine beetle populations in subalpine forests than host tree species. Interaction among these factors with respect to mountain pine beetle success in whitebark pine is yet to be investigated fully and should be a priority for future research.

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357 **Figure Captions**

Fig. 1: Boxplots (horizontal bar indicating the median, bottom and top of boxes indicating the 2nd and 3rd quartiles, respectively, lower and upper whiskers indicating 1st and 4th quartiles, respectively, points indicating outliers) of life history characteristics of mountain pine beetles reared in lodgepole pine and whitebark pines bolts. Panels show: A) the average proportion of attempted egg galleries that were successfully established per tree, B) the average length of egg galleries (cm) per tree, C) the average density of larval galleries per cm of egg gallery length per tree, D) the average proportion of brood surviving from first larval instar to emerging adult per tree, E) the average number of brood emerging per tree, F) the average pronotal width (mm) of female brood adults per tree, G) the average mass (mg) of female brood adults per tree and H) the average fat content (percent of mass) of female brood adults per tree. A * indicates a statistically significant difference between host species ($p < 0.05$).

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