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Mountain Pine Beetle Fecundity and Offspring Size Differ Among Lodgepole Pine and Whitebark Pine Hosts

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MOUNTAIN PINE BEETLE FECUNDITY AND OFFSPRING SIZE DIFFER
AMONG LODGEPOLE PINE AND WHITEBARK PINE HOSTS

by

Donovan H. Gross

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Ecology

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2008

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ABSTRACT

Mountain Pine Beetle Fecundity and Offspring Size Differ
Among Lodgepole Pine and Whitebark Pine Hosts

by

Donovan H. Gross, Master of Science

Utah State University, 2008

Major Professor: Dr. Thomas C. Edwards, Jr.
Program: Ecology

Whitebark pine (*Pinus albicaulis* Engelmann) is a treeline species in the central Rocky Mountains. Its occupation of high elevations previously protected whitebark pine from long-term mountain pine beetle outbreaks. The mountain pine beetle, however, is currently reaching outbreaks of record magnitude in high-elevation whitebark pine. We used a factorial laboratory experiment to compare mountain pine beetle (*Dendroctonus ponderosae* Hopkins) life history characteristics between a typical host, lodgepole pine (*Pinus contorta* Engelmann), and whitebark pine. We tested the effects of natal host and brood host on beetle fecundity, offspring size, and brood sex-ratio. We reared mountain pine beetles from whitebark pine and from lodgepole pine, and infested half of them into their natal host and half into the other host. Fecundity was greater overall in lodgepole pine brood hosts. Among lodgepole brood hosts, beetles from whitebark pine had greater

fecundity. Fecundity was also significantly related to phloem thickness, which was greater in lodgepole pine. Offspring were larger from whitebark brood hosts than from lodgepole, regardless of their parents' natal host. Finally, sex-ratio was closer to 1:1 in lodgepole than in whitebark brood hosts. We conclude that host species affects life history of mountain pine beetle with consequences for individual beetle fitness.

(46 pages)

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This thesis is dedicated to Susan and Ellie Gross.

Donovan H. Gross

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BACKGROUND

Unprecedented native bark beetle (Coleoptera: Curculionidae, Scolytinae) outbreaks are simultaneously occurring from Alaska to the Southwest United States in systems ranging from spruce (*Picea* spp.) forests to pinyon-juniper (*Pinus edulis-Juniperus* spp.) woodlands (Ebata 2004, Breshears et al. 2005, Berg et al. 2006, Logan and Powell 2008). Furthermore, bark beetles are increasingly invasive via novel behavior in their native systems and range expansion into novel habitats. Examples include the spruce beetle, *Dendroctonus rufipennis*, which is considered a “non-aggressive” bark beetle colonizing primarily wind-throw, but has killed millions of hectares of spruce forest from Alaska and the Yukon Territory to southern Utah (Berg et al. 2006). The pinyon ips, *Ips confusus*, is also non-aggressive, but has killed millions of hectares of drought- and heat-stressed pinyon pines throughout the Southwest United States (Breshears et al. 2005). Mountain pine beetle, *D. ponderosae* Hopkins, outbreaks are reaching record magnitudes at higher elevations and latitudes than they previously occurred (Ebata 2004, Taylor et al. 2006, Logan and Powell 2008). All evidence indicates that these dramatic events are due to climatic release of beetle populations combined with highly susceptible forest stand conditions resulting, in many cases, from a century of fire suppression (Logan and Powell 2001, Negrón and Wilson 2003, Carroll et al. 2004, Breshears et al. 2005, Taylor and Carroll 2004, Berg et al. 2006, Taylor et al. 2006, Logan and Powell 2008).

The mountain pine beetle, in particular, is considered the most destructive of the bark beetles (Craighead et al. 1931, Samman and Logan 2000). Mountain pine beetle outbreaks are ongoing in habitats previously considered climatically unsuitable, including

high-elevation whitebark pine (*Pinus albicaulis* Engelmann) communities (Logan and Powell 2008). Current whitebark pine mortality appears far greater than historic outbreaks such as the 1930s outbreaks that created the “ghost forests” (Ciesla and Furniss 1975) of the central Rocky Mountains (J. Logan, personal communication). Further range expansion and persistence of the mountain pine beetle at high elevations and latitudes appears to be limited only by climate (Carroll et al. 2004, Taylor et al. 2006, Logan and Powell 2004). Global warming trends predict that high elevation forests will remain climatically favorable for mountain pine beetle outbreaks (IPCC 2001*a, b*, Logan and Powell 2001, Williams and Liebhold 2002, Logan et al. 2003, Logan and Powell 2004). Long-term persistence of mountain pine beetle in high-elevation whitebark pine means long-term and large-scale consequences for high-elevation forest structure. The nature of these interactions and their consequences are unknown.

The mountain pine beetle is a native polyphagous herbivore, feeding on the phloem of most pines (Pinaceae: *Pinus*) in western North America (Wood 1982). Lodgepole pine, *Pinus contorta* Engelmann, is considered the beetle’s primary host as measured by annual tree mortality (Evensen et al. 1943, Reid 1962*a, b*, McCambridge and Trostle 1972, Wood 1982, Aukema et al. 2006). Mountain pine beetles attack living trees *en masse* in July or August and construct vertical egg galleries in the phloem layer (Wood 1982). Mass attack helps overwhelm host defenses and increases individual fitness (Raffa and Berryman 1983, Berryman et al. 1985, 1989). Constitutive defenses of pines consist largely of resin which provides physical obstruction and mild toxicity (Berryman 1972, Raffa and Berryman 1983, Franceschi et al. 2005). Beetle eggs hatch in

approximately two weeks and larvae feed laterally on the phloem, girdling and killing the tree. Mountain pine beetles also cultivate mutualistic fungi (Six 2003, Six and Klepzig 2004) which may aid in suppressing tree defenses (Berryman et al. 1989) and provide critical nutrition to developing brood (Six and Paine 1998, Bentz and Six 2006).

Mountain pine beetle, which has four larval instars, commonly completes its lifecycle in one year (univoltine), overwintering as second or third instar larvae (Wood 1982).

Populations generally emerge synchronously within a 30-day window (Bentz 2006) from their natal hosts and attack new brood host trees. Synchronous univoltinism is considered necessary for mass attack and, consequently, defines an outbreak (Amman 1973, Safranyik 1978).

Cool weather at high elevations and latitudes prevents the beetle from reaching outbreak populations through delayed development and disruption of synchronous univoltinism (Amman 1973, Safranyik 1978, Logan and Powell 2001). The effect of variable temperature on developmental rate thresholds at different life stages directly determines the degree of developmental synchrony within a population (Bentz et al. 1991, Logan and Bentz 1999, Powell et al. 2000). This results in a range of annual temperatures which synchronize development, outside of which development abruptly becomes asynchronous (Powell et al. 2000, Logan and Powell 2001). Because mass attack maximizes individual fitness and relies on population synchrony, the temperature ranges resulting in synchronized univoltinism at the appropriate time of year are considered adaptive (Powell et al. 2000, Logan and Powell 2001).

High-elevation whitebark pine habitats were historically cooler than the range of adaptive seasonality for the mountain pine beetle. Whitebark pine is the only North American member of the stone pines (Pinaceae: genus *Pinus*, sub-genus *Strobus*, sub-section *Cembrae*) and as such, has indehiscent cones and vertebrate dispersed seeds (Tomback and Linhart 1990). Whitebark pine grows at the highest elevations in the Rocky Mountains, Coast Ranges, and Sierra Nevada (Arno and Hoff 1989). It is a long-lived, slow-growing and slowly maturing pine. Whitebark pine commonly lives over 1,000 years and may take 80 years before reaching reproductive maturity (McCaughey and Tomback 2001). Whitebark pine is less shade-tolerant than many of its high-elevation counterparts (e.g., Engelmann spruce *Picea engelmannii* and subalpine fir *Abies lasiocarpa* in the Rocky Mountains), and accomplishes wide-spread dispersal of mast cone crops to gaps and disturbed sites via a commensalistic interaction with Clark's nutcracker (*Nucifraga columbianna*). The nutcracker harvests and caches whitebark pine seeds and consumes a portion. Red squirrels (*Tamiasciurus hudsonicus* also) cache cones and seeds in middens which are often raided by grizzly bears (*Ursos arctos horribillis*) (Mattson et al. 2001). In addition to providing critical nutrition and habitat to wildlife, whitebark pine provides many other ecosystem services including high-elevation snow retention, soil stabilization, and aesthetic beauty.

Whitebark pine is in sharp decline throughout much of its distribution. White pine blister rust, caused by the exotic fungus *Cronartium ribicola*, and successional replacement are causing significant mortality of whitebark pine throughout its range (Keane and Arno 1993, Keane et al. 1994, Tomback et al. 1995, Campbell and Antos

2000, Zeglen 2002). Blister rust kills seedlings, cone-producing branches and eventually mature trees, with infection rates over 80% in many areas (Keane and Arno 1993, Keane et al. 1994, Campbell and Antos 2000, Tomback et al. 2001, Zeglen 2002, Kinloch 2003, Murray and Rasmussen 2003). Whitebark pine shows the lowest genetic potential for rust-resistant breeding of all the susceptible pines (Kinloch and Dupper 2002).

Furthermore, blister rust increases individual tree susceptibility to mountain pine beetle attack (Kulhavy et al. 1984, Six and Adams 2007). Successional replacement of whitebark pine, primarily by subalpine fir, has been hastened by a century of fire suppression (Keane et al. 1994, Keane et al. 2002). Finally, global warming is projected to result in decreased total available habitat for whitebark pine (Romme and Turner 1991). The combination of these mortality factors makes whitebark pine conservation of greater concern, and understanding the ecology of those mortality factors of greater importance.

Whitebark pine communities have rarely experienced mountain pine beetle outbreaks (Logan and Powell 2001). Exceptions include extensive outbreaks in the 1930's, and outbreaks in the 1980's (Ciesla and Furniss 1975, Despain 1991, Perkins and Swetnam 1996, Bartos and Gibson 1990). Each of these outbreaks was coincident with a period of unusually warm weather, falling within the predicted adaptive range of the pine beetle (Logan and Powell 2001). Logan and Bentz (1999) hypothesized that the climate warming anticipated by IPCC (2001a) would result in high-elevation forests becoming seasonally adaptive for the mountain pine beetle and therefore, more susceptible to outbreaks in the future. By 2003, there were extensive outbreaks in high-elevation

whitebark pine throughout its southern Rocky Mountain distribution (Idaho, Montana, and Wyoming) (Logan and Powell 2008). These ongoing outbreaks commenced with the onset of auspicious temperatures and are proceeding at unexpected speed and intensity (Logan and Powell 2001, 2004). The important difference between current and past outbreaks is that global warming predictions indicate that high-elevations will remain adaptive for beetle outbreaks (IPCC 2001*a, b*, Logan and Powell 2001, Williams and Liebhold 2002, Logan et al. 2003, Carroll et al. 2004, Logan and Powell 2008). Furthermore, the structure of many of these stands is considered highly susceptible to beetle outbreaks (Perkins and Roberts 2003). This scenario makes understanding mountain pine beetle ecology in high-elevation whitebark pine critical if conservation of the pine is to remain a goal.

Observations by J. Logan and colleagues at Railroad Ridge, Idaho, a high-elevation (approx. 3000 m), long-term study site of the Western Bark Beetle Project (Rocky Mountain Research Station, USDA Forest Service, <http://www.usu.edu/beetle>) were that an ongoing mountain pine beetle outbreak began surprisingly quickly with the onset of adaptive seasonal weather. They further noted that whitebark pine mortality from mountain pine beetle was exceptionally rapid and intense, relative to their experience in lodgepole pine systems. Their observations led to the following hypotheses: (1) whitebark pine is more productive of mountain pine beetle brood than lodgepole pine; (2) whitebark pine provides a superior food resource in terms of quality and/or quantity of phloem; and (3) whitebark pine is less defended against the beetle than lodgepole pine.

Host species has been shown to affect mountain pine beetle reproduction in several ways. Amman (1982), using host material of similar phloem thickness, found that mountain pine beetles produced significantly more brood in western white pine (*Pinus monticola*) than in lodgepole pine. Amman (1982) also found beetles produced significantly more egg gallery in whitebark pine than in western white pine, and broods took significantly longer to emerge from whitebark as opposed to ponderosa pine (*Pinus ponderosa*). In this study, whitebark pine had the thickest phloem, although all host material was chosen only if phloem exceeded 2.5-mm, leaving open to question the relevance of these host effects to a natural setting. Although a mean phloem thickness is reported for each host species, it was not included in the analyses and it cannot be said whether it had an effect on beetle reproduction independent of host species. Furthermore, all mountain pine beetles in this study were obtained from lodgepole pine in northwestern Wyoming, again leaving open to question the influence of maternal effects on host use by this generalist herbivore. For example, Langor et al. (1990) found that the host species in which the female parent was reared affected mortality and size of progeny when crossing beetles from lodgepole and limber (*Pinus flexilis*) pine. They found that females from limber pine produced more eggs and smaller offspring than females from lodgepole pine. In addition, Langor (1989) found that beetles had higher fecundity and developed faster in limber pine than in lodgepole pine. Phloem thickness was not investigated in the studies, leaving open to question the significance of host effects versus the well-established effects of phloem thickness. Thus, the effect of host species on mountain pine

beetle reproduction relative to phloem thickness is unknown, especially for whitebark pine.

Phloem thickness has repeatedly been shown to vary within and among species and to directly affect mountain pine beetle life-history parameters. A classic example is Amman's (1972) work, which demonstrated that mountain pine beetle brood production was directly related to phloem thickness of lodgepole pine. To date there are no investigations of the relative effects of phloem thickness and host species; each effect has been investigated separately. Because phloem thickness and host species have each been shown to influence mountain pine beetle life history characteristics, and since they co-vary in nature, a next step is to investigate the relative influence of host species (food quality) and phloem thickness (food quantity). This information, combined with phloem thickness distribution and stand structure, is necessary before an even basic inference about the potential impact of the beetle on whitebark pine stands is possible.

INTRODUCTION

The mountain pine beetle is an aggressive, endophytic herbivore of pines. At outbreak population levels, the mountain pine beetle readily attacks and kills healthy trees, and is considered the most destructive of all the bark beetles (Samman and Logan 2000). Currently, mountain pine beetle outbreaks are reaching record magnitudes at higher elevations and latitudes than previously occurred (Ebata 2004, Taylor et al. 2006, Logan and Powell 2008, Hedgren 2007). Accompanied by this range expansion is the interaction with new host types which have never before been exposed to long-term mountain pine beetle predation.

The mountain pine beetle can persist at low population levels (endemic) under almost any condition, providing there are pines (usually weakened ones) available. It has been long understood that an outbreak requires conditions which allow for a synchronized population; that is, most adult mountain pine beetles emerging from their natal host and attacking brood hosts within an approximate two week time period. Given adequate host material, mountain pine beetle population cycles, and population synchrony, are driven principally by temperature (Logan and Bentz 1999, Powell et al. 2000, Logan and Powell 2001, Powell and Logan 2005). Mountain pine beetle populations require temperature input within a sharply defined range to synchronize (Logan and Bentz 1999, Powell et al. 2000, Logan and Powell 2001), and it has been shown theoretically that temperature alone can result in population synchrony (Powell et al. 2000, Powell and Logan 2005). This relationship historically precluded mountain pine beetle outbreaks from high elevations and latitudes, except during occasional warm

spells. Temperatures at high elevations (2500 – 3000 m) since approximately 2000 have remained within the range for population synchrony, termed “adaptive seasonality” (Logan and Powell 2001), to occur.

High-elevation whitebark pine has experienced mountain pine beetle outbreaks several times in the past. The most widespread outbreaks were during exceptionally warm periods of the 1930s and again during the 1980s (Ciesla and Furniss 1975, Bartos and Gibson 1990, Despain 1991). Outbreaks during the 1930s created widespread “ghost forests” of standing dead trees (Ciesla and Furniss 1975). The 1930s outbreaks resulted in particularly high mortality rates among whitebark pine (Perkins and Roberts 2003). During the 1980s outbreaks, some authors noted that whitebark pine experienced greater mortality rates than lodgepole pine (Bartos and Gibson 1990, Despain 1991). This result, however, was either mixed (Bartos and Gibson 1990), or anecdotal (Despain 1991). Never answered quantitatively was whether this was due to a characteristic of the host species themselves, or due simply to an exhausted lodgepole resource and an abundant whitebark resource recently made available by warmer temperatures. The important distinction between the current high-elevation mountain pine beetle outbreak and those of the past is that high elevations and latitudes are expected to *remain* within the temperature ranges for an adaptive seasonality.

The focus of this paper is to quantify the relative productivity of mountain pine beetle using lodgepole pine and whitebark pine as hosts. We conducted an experiment to compare mountain pine beetle life history characteristics (fecundity, offspring size, and sex-ratio) between lodgepole pine and whitebark pine hosts from the same stand.

Furthermore, the beetles used in the experiment were from the same stand as the host material, eliminating the influence of regional or population-level genetic differences (e.g., Bentz et al. 2001). The experiment was a full factorial in which we reared beetles from both hosts and then infested half of the beetles into their natal host species and half into the other host. This was intended to: (1) determine if beetles are more successful (i.e., have higher fecundity and larger offspring) if they infest the same host as the one in which they were reared; (2) quantify the relative productivity of mountain pine beetles infesting these two hosts species; and (3) determine if beetles could successfully reproduce in whitebark pine if they were reared in either lodgepole pine or whitebark pine.

MATERIALS AND METHODS

All materials for the laboratory experiment were obtained from Galena Summit, Idaho, USA. Here, lodgepole pine and whitebark pine occur in mixed stands, along with subalpine fir. At the time of materials collection, Galena Summit was experiencing a building mountain pine beetle outbreak. Parent-generation mountain pine beetles were collected from trees naturally infested by mountain pine beetles in the summer of 2005. Infested lodgepole pines and whitebark pines were selected randomly if they were at least 25-cm diameter at breast height and met “mass attack” criteria. Mass attack means that the tree was sufficiently infested with mountain pine beetles that it would have died from the beetle attack, as determined by visual examination of the phloem. Mass attacked trees were chosen because beetles from mass attacked trees constitute the majority of an outbreak population and because these beetles are the focus of the study. It is unknown if there are individual beetle characteristics that contribute to the ability to mass attack and successfully infest a tree.

Three infested trees of each species were cut on 9 and 17 August 2005 and immediately transported to the lab (approximately 430 km, 5 hours) where beetles were reared to emergence at room temperature (~20°C) in rearing cans. Rearing cans consisted of garbage cans with glass jars fitted to the side for collection and a dark cloth over the top. Emerging beetles are attracted to the light in the glass jar and are easily collected. Infested trees from which parent beetles were collected are referred to as “natal hosts.” Beetles emerged from natal hosts over a two week period. Brood beetles were collected daily and placed on moist filter paper in Petri dishes and refrigerated at 8°C until they

were used to inoculate the brood host material. This is a standard technique used at the Rocky Mountain Research Station to keep beetles alive for a period of several days until enough beetles can be collected to begin an experiment (E. M. Hansen, personal communication). Beetles from whitebark and lodgepole were kept separate at all times. Beetles were then sexed under a dissecting scope according to unique anatomy of the seventh tergum (Lyon 1958), after which males and females were kept separate. Just prior to experiment set up, beetles were allowed to warm up to room temperature and only the most vigorous beetles were kept. Beetles that were not moving or were moving very slowly and making no attempts to escape were discarded.

Trees used as brood host material were selected if they were live (green, moist phloem), healthy (no signs of stress in the crown), and uninfested by mountain pine beetles. Selected trees had to be at least 30-cm diameter at 1.4-m height. Trees at least 30-cm diameter represented the typical size of attacked trees at Galena Summit and is near the minimum size in which mountain pine beetles can successfully reproduce under usual circumstances. These trees were termed “green.”

Green trees were cut down on 18 August 2005 and cut into 40-cm long sections (bolts). Bolts were collected from green trees starting with ground surface and going up until 20 bolts had been collected from each tree. Green bolts were transported immediately to the lab where the cut ends were waxed with paraffin and then refrigerated at 0°C until experimental set up. Waxing the cut ends and refrigeration helps prevent drying and fungal infection. Vertical orientation and vertical order of the green bolts was maintained and recorded (bottom bolt, second bolt, etc.). Vertical orientation was

maintained to simulate natural conditions as closely as possible. Beetles are commonly observed to vary in attack density by bole height, so vertical order was recorded as a possible source of variation which could be blocked in the covariance analysis.

The experiment was set up on 1 and 2 September 2005. Green bolts were prepared by removing 2.5-cm wide strips of the bark and phloem every 9 cm around the bolt. This created 9-cm wide “leave strips” of intact bark and phloem, separated by 2.5-cm wide strips of bare wood. Strips of bare wood provided a barrier to infesting beetles between leave strips and allowed us to control the area available to infesting beetles. Each leave strip was caged with nylon mesh with a collection tube attached. Each leave strip was 360 cm². The number of leave-strips per bolt varied by bolt diameter and irregularities, such as branches or knots. Leave-strips ranged from 2 to 6 per bolt, with most bolts having 3 or 4. Phloem thickness has been shown to affect beetle brood production (Amman 1972), so phloem thickness was measured at three locations on each side of each leave strip (6 measurements per leave strip). A mean phloem thickness was calculated from the 6 measurements for each leave strip. Phloem thickness measurements were standardized by subtracting each value from the population mean and using deviation from the population mean for analyses. This was done for each tree species separately.

Experimental units were assigned treatments randomly during the two day set up period. Each leave strip constituted an experimental unit and received one female followed by one male beetle to simulate natural infestation sequence. Each beetle pair was from either lodgepole or whitebark pine natal hosts. An equal number of leave strips

was obtained from each brood host tree species. Half of the lodgepole pine experimental units received beetles reared from lodgepole and half received beetles from whitebark pine. Half of the whitebark pine experimental units received beetles reared from lodgepole pine and half received beetles from whitebark pine. Thus, the experiment was a balanced complete factorial at inception (Table 1). Some experimental units failed, so the final sample sizes shown in Table 1 are not balanced.

Table 1. Factorial experiment sample sizes.

| Natal Host Species | Brood Host Species | |
|--------------------|--------------------|----------------|
| | Lodgepole Pine | Whitebark Pine |
| Lodgepole Pine | 43 | 43 |
| Whitebark Pine | 45 | 44 |

Each leaf strip was caged individually using nylon mesh and monitored daily until near the end of the experiment when brood emergence was very slow, after which they were monitored two times per week. Because each female beetle was infested into one leaf strip, individual caging allowed us to estimate individual fecundity.

The experiment was designed as a two-way nested factorial with two covariates. Factors, with two levels each, were the natal host species from which the parent beetles were reared and the brood host species of the green bolts. Natal host, brood host, and natal host \times brood host were fixed effects in the model. Random (measured but not controlled) covariates were height of the green bolts from the bottom and centered (deviation from the mean) phloem thickness of the leaf strip, both nested within brood host. Response variables were number of brood beetles from each strip (fecundity), sex-

ratio of brood, and brood size measured as width of the pronotum. Fecundity was analyzed from the total population of brood beetles. Analyses of sex-ratio and size of brood individuals were conducted from random samples of brood beetles. Mixed models were used to analyze the data because there were two fixed effects and two nested random covariates (Milliken and Johnson 2002). All analyses were performed using the SAS statistical package, version 9.1 (SAS Institute, Cary, North Carolina, USA).

Fecundity was analyzed using PROC GLIMMIX and the full model described above. Fecundity count data was Poisson distributed, so a Poisson error distribution with a log link function was used in PROC GLIMMIX rather than transforming the data. Sex-ratio was analyzed using PROC GLIMMIX with a binomial distribution and logit link function to estimate the binomial probability of the brood being female or male. Brood size data were distributed normally, so PROC MIXED was used with the default normal error distribution. Size data was blocked by sex, since females are known to be larger than males. Sex-ratio and size data were analyzed using only natal host, brood host, and the interaction of natal host \times brood host as fixed effects. Phloem thickness of the brood host material was also analyzed with PROC MIXED using brood host and the interaction of height \times brood host as fixed effects. Quantile-quantile plots, quantile-normal plots, symmetry (distance above versus distance below median) plots, and predicted versus residual plots were used to confirm that the appropriate error distributions were used (Hamilton 1992). For each model, Tukey-Kramer probability was used to compare treatment means. For all analyses, significance was measured at the $\alpha=0.10$ level. Data

are expressed as mean \pm 1 standard error. PROC GLIMMIX is an iterative analysis using maximum likelihood to estimate probabilities, rather than type I or type III sums of squares. Only degrees of freedom, an F-statistic, and probability are provided.

RESULTS

Fecundity

Phloem of green bolts was thicker in lodgepole pine (3.81 ± 0.1 mm) than in whitebark pine (2.85 ± 0.12 mm). This difference was highly significant ($F=68.17$, $df=135$, $P<0.0001$). Phloem thickness varied significantly by the interaction of height \times brood host species ($F=8.53$, $df=135$, $P=0.004$).

Fecundity estimates from the four main treatment combinations are summarized in Figure 1. Statistics for fecundity are summarized in Table 2. Mean (± 1 standard error) mountain pine beetle fecundity was greater in lodgepole brood hosts (20.3 ± 1.55) than in whitebark brood hosts (13.6 ± 1.35). This difference was significant ($F=6.57$, $df=66.1$, $P=0.01$, Figure 1). The interaction of natal host \times brood host was highly significant ($F=12.94$, $df=50.4$, $P<0.001$). Mean (± 1 standard error) fecundity of beetles from lodgepole infested into lodgepole was highest (20.5 ± 2.31), followed by beetles from whitebark infested into lodgepole (20.0 ± 2.11), then by beetles from lodgepole infested into whitebark (14.5 ± 2.02), and last by beetles from whitebark infested into whitebark (12.7 ± 1.82) (Figure 1). The random nested covariates of height and centered phloem thickness were not significant (Table 2). Tukey-Kramer probabilities revealed that beetles from whitebark infested into lodgepole differed significantly from all three other treatment combinations (Table 3). No other pairwise comparisons were significant.

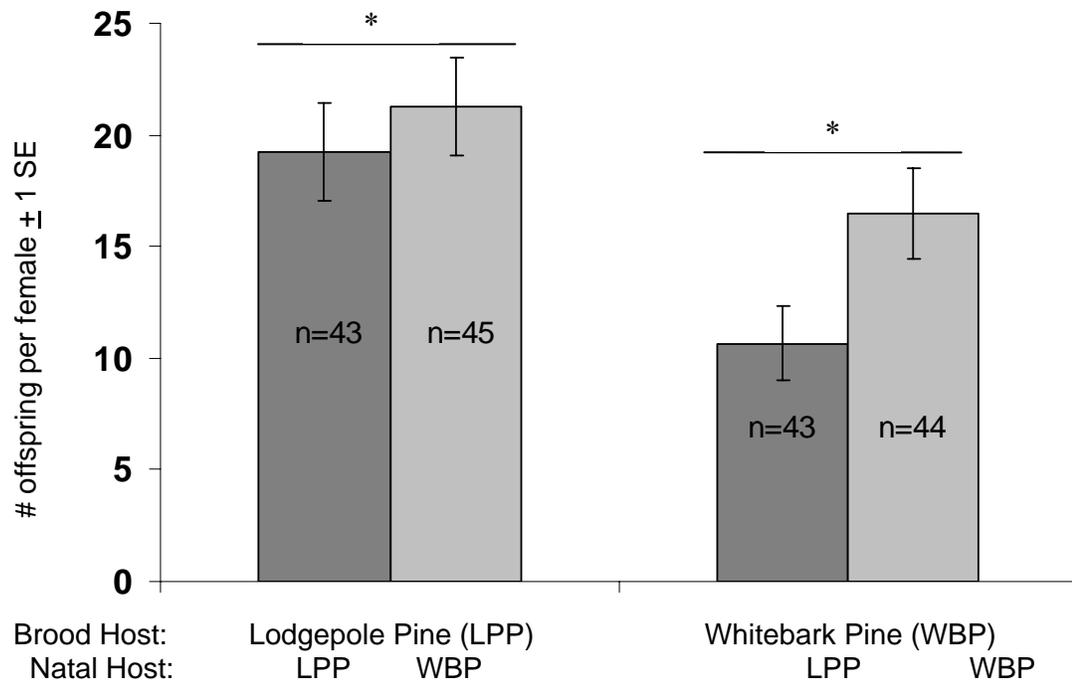


Fig. 1. Mean fecundity (± 1 standard error) of mountain pine beetles obtained from lodgepole and whitebark pine (natal host) and infested into both brood hosts. An “*” above the main bar groups indicates the significant effect of brood host on fecundity at the $\alpha=0.10$ level. Natal host was also a significant main effect at the $\alpha=0.10$ level.

Emergence time varied by treatment (Table 4). Beetles were infested randomly among the four treatments over a two day period. Beetles emerged about 10 days later from whitebark than from lodgepole regardless of their parents’ natal host.

Table 2. Type III tests of fixed effects from mixed-model analysis of fecundity (cumulative brood * female⁻¹) from lab rearing experiments, using Poisson error distribution and untransformed data.

| Effect | df ^a | F | P |
|--------------------------|-----------------|-------|--------|
| Brood host ^b | 66.1 | 6.57 | 0.013 |
| Natal host ^c | 48.7 | 3.65 | 0.062 |
| BH x NH | 50.4 | 12.94 | <0.001 |
| Height ^d (BH) | 145 | 0.01 | 0.92 |
| Phloem(BH) | 53.5 | 1.57 | 0.22 |

^a Denominator degrees of freedom (Kenward-Roger method).

^b Brood host (BH), *P. contorta* or *P. albicaulis*, into which beetles were infested.

^c Natal host (NH), *P. contorta* or *P. albicaulis*, host from which parent beetles were collected.

^d Height on bole from where experimental bolts were obtained.

Table 3. Tukey-Kramer comparison probabilities of mean fecundity from the four main treatment combinations in the lab experiment.

| Brood/Natal Host | Brood/Natal Host | | | |
|------------------|------------------|---------|--------------|--------------|
| | LPP/LPP | LPP/WBP | WBP/LPP | WBP/WBP |
| LPP/LPP | . | 0.620 | 0.013 | 0.490 |
| LPP/WBP | 0.620 | . | 0.007 | 0.310 |
| WBP/LPP | 0.013 | 0.007 | . | 0.045 |
| WBP/WBP | 0.490 | 0.310 | 0.045 | . |

Lodgepole pine = LPP; whitebark pine = WBP

Table 4. Time to 50% emergence for mountain pine beetle offspring of parents obtained from lodgepole pine and whitebark pine and infested into both host species.

| Brood Host | Natal Host | N | Mean | Standard Error |
|------------|------------|----|------|----------------|
| Lodgepole | Lodgepole | 43 | 17 | 1.2 |
| | Whitebark | 45 | 16 | 1.8 |
| Whitebark | Lodgepole | 43 | 18 | 2.6 |
| | Whitebark | 44 | 16 | 2.3 |

Size and Sex-Ratio of Brood Individuals

Offspring were larger when reared in whitebark pine regardless of the parents' natal host (Figure 2). Statistics for size are summarized in Table 5. For females, only the main effect of brood host was significant in determining size ($F=20.2$, $df=569$, $P<0.0001$), with mean (± 1 standard error) size of females from whitebark larger (2.08 ± 0.0067) than females from lodgepole (2.04 ± 0.0088). For males, the interaction of brood host \times natal host was significant ($F=3.40$, $df=445$, $P=0.07$). Mean (± 1 standard error) size of males was largest in the brood from beetles from whitebark infested into whitebark (1.94 ± 0.010), followed by beetles from lodgepole infested into whitebark (1.90 ± 0.015), followed by beetles from whitebark infested into lodgepole (1.87 ± 0.009), and the smallest brood was of beetles from lodgepole infested into lodgepole (1.85 ± 0.010).

Tukey-Kramer probabilities for pairwise comparisons of size data are summarized in Table 6. Pairwise comparisons of the four treatments combinations indicated that

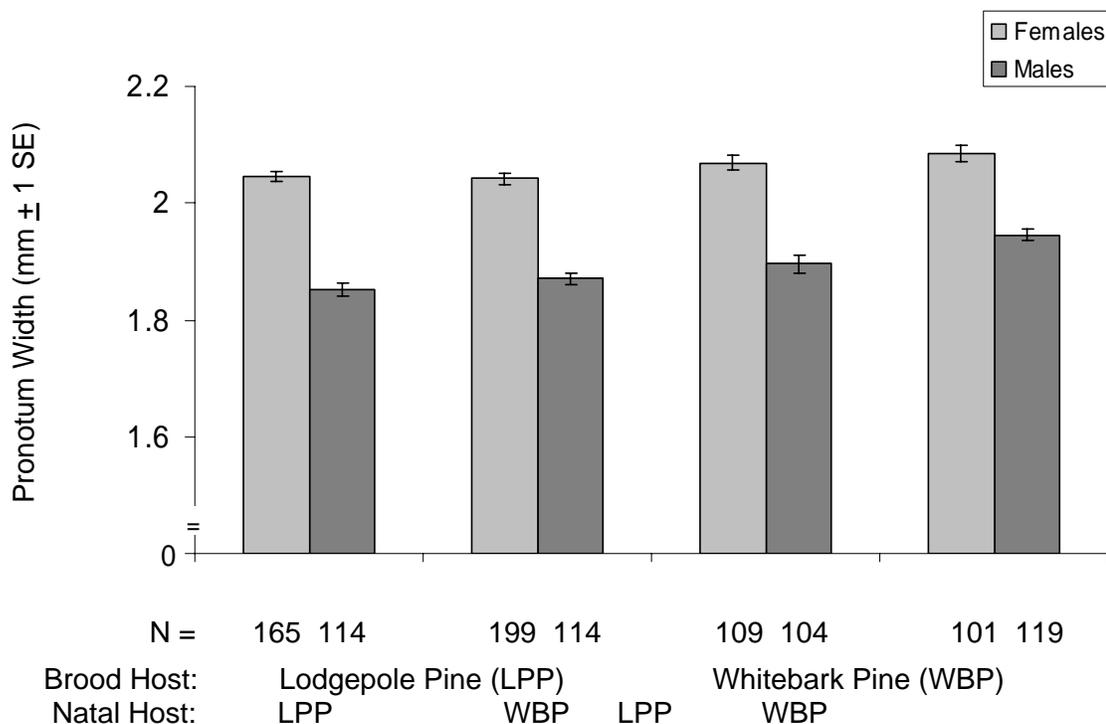


Fig. 2. Mean pronotum width (± 1 standard error) of female and male mountain pine beetles emerging from four experimental natal host/brood host treatment combinations. Natal host species is the species that parent beetles were obtained from and brood host is the species in which their brood was reared.

female offspring of beetles from whitebark infested into whitebark were significantly larger than offspring of beetles from lodgepole infested into lodgepole ($P=0.004$) and offspring of beetles from lodgepole infested into whitebark ($P=0.006$). Female offspring of beetles from whitebark infested into lodgepole were significantly smaller than those of beetles from lodgepole infested into whitebark ($P=0.02$) and smaller than those of beetles from lodgepole infested into lodgepole ($P=0.06$). No other treatment comparisons of female size were significant (Table 6).

Table 5. Type III tests of fixed effects from analysis of variance of pronotum width (mm), males and females analyzed separately.

| Effect | df | SS | F | P |
|----------------|-----|--------|-------|---------|
| Females | | | | |
| Brood host | 569 | 0.3024 | 20.20 | <0.0001 |
| Natal host | 569 | 0.0031 | 0.21 | 0.64 |
| BH x NH | 569 | 0.0143 | 0.96 | 0.33 |
| Males | | | | |
| Brood host | 445 | 0.4429 | 32.77 | <0.0001 |
| Natal host | 445 | 0.1098 | 8.22 | 0.004 |
| BH x NH | 445 | 0.0467 | 3.40 | 0.07 |

Abbreviations are brood host (BH), natal host (NH), denominator degrees of freedom (df), sums of squares (SS).

Pairwise comparisons of male offspring size indicate that offspring of beetles from whitebark infested into whitebark were the largest and significantly different from offspring of beetles from lodgepole infested into lodgepole ($P < 0.0001$), and from lodgepole infested into whitebark ($P < 0.001$), and from whitebark infested into lodgepole ($P = 0.005$). Male offspring of beetles from whitebark infested into lodgepole were larger than offspring of beetles from lodgepole infested into lodgepole ($P = 0.04$). No other treatment comparisons of male size were significant (Table 6).

Sex-ratios, as percent female, are shown in Figure 3. ANOVA statistics of sex-ratio are summarized in Table 7. Mixed-model analysis of sex-ratio indicated that percent sex-ratio differed significantly among brood hosts ($F = 16.58$, $df = 1021$, $P < 0.0001$). Sex-ratio of offspring did not differ among natal hosts ($F = 0.01$, $df = 1021$, $P = 0.93$) or by the

interaction of brood host \times natal host ($F=2.41$, $df=1021$, $P=0.12$). Mean (± 1 standard error) proportion female beetles was closest to 0.50 in whitebark brood hosts (0.49 ± 0.02) than in lodgepole (0.62 ± 0.02) (Figure 3).

Table 6. Tukey-Kramer adjusted probabilities for comparison of mean pronotum width (mm) from the four main treatment combinations from the lab experiment, for females and males separately.

| Brood/Natal Host | Brood/Natal Host | | | |
|------------------|------------------|----------------------|---------|---------|
| | LPP/LPP | LPP/WBP ⁴ | WBP/LPP | WBP/WBP |
| Females | | | | |
| LPP/LPP | . | 0.97 | 0.06 | 0.004 |
| LPP/WBP | 0.97 | . | 0.02 | 0.006 |
| WBP/LPP | 0.06 | 0.02 | . | 0.80 |
| WBP/WBP | 0.004 | 0.006 | 0.80 | . |
| Males | | | | |
| LPP/LPP | . | 0.88 | 0.036 | <0.0001 |
| LPP/WBP | 0.88 | . | 0.19 | <0.0001 |
| WBP/LPP | 0.036 | 0.19 | . | 0.005 |
| WBP/WBP | <0.0001 | <0.0001 | 0.005 | . |

Abbreviation are lodgepole pine (LPP) and whitebark pine (WBP).

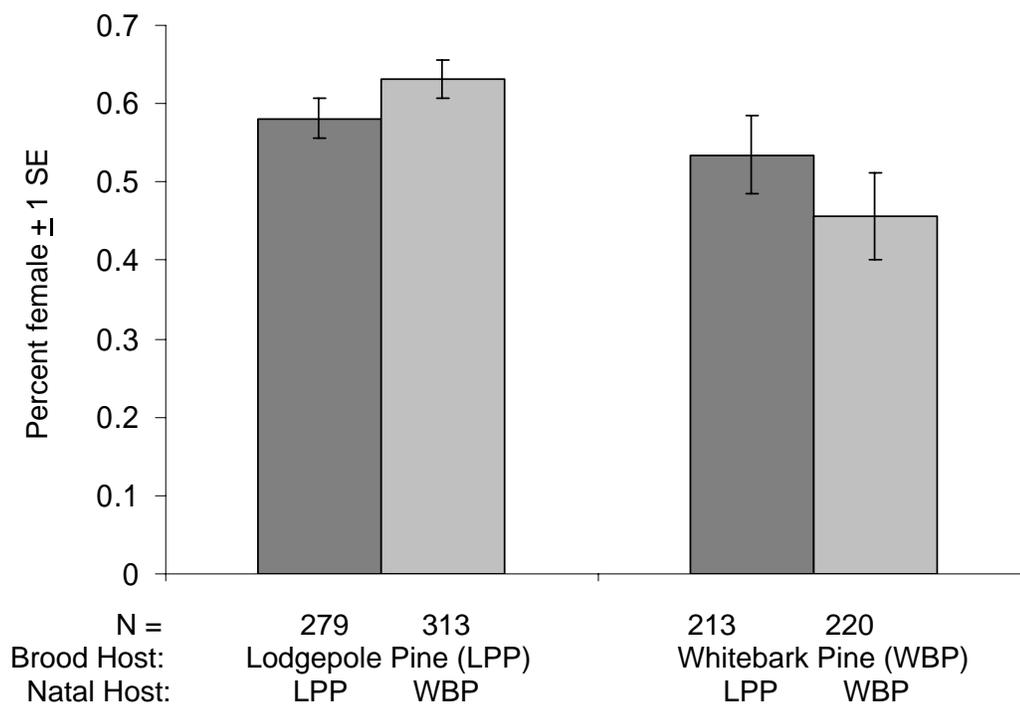


Fig. 3. Mean percent female (± 1 standard error) of brood from laboratory rearing experiments. Natal hosts were the species from which parent beetles were obtained and brood hosts were the species in which their brood was reared.

Table 7. Type III tests of fixed effects from mixed-model analysis of sex-ratios from the lab experiment.

| Effect | df | F | P |
|----------------|------|-------|---------|
| Brood host | 1021 | 16.58 | <0.0001 |
| Natal host | 1021 | 0.01 | 0.93 |
| BH \times NH | 1021 | 2.41 | 0.12 |

Abbreviations are brood host (BH), natal host (NH), and degrees of freedom (df).

DISCUSSION

Three fundamental questions were addressed. The first was whether beetles are more successful in terms of fecundity and offspring size if they infest the same host in which they were reared. Our results indicate that beetles do not necessarily have greater fecundity when they infest the same host from which they came (Figure 1). In our experiment, beetles reared from lodgepole pine had greater fecundity than those reared from whitebark pine when infested into either host. This is not consistent with the limited data in the literature. Amman (1982) reared mountain pine beetles from lodgepole pine and infested them into four pine species. Mountain pine beetles infesting ponderosa pine, western white pine, and whitebark pine, had greater fecundity than in lodgepole. Amman (1982) did not perform the converse experiment, but his data show that mountain pine beetles do not necessarily do better when infesting their natal host.

Offspring size was not influenced by natal host versus brood host. In this case, whitebark pine produced larger beetles (Figure 2). This suggests that there could be a nutritional component of whitebark, either in the phloem itself or the fungal community which it supports, that confers greater size to the offspring. Beetles emerging from whitebark pine, however, emerged about 10 days later than their lodgepole counterparts (Table 4), which tends to lead to larger offspring. Previous work by Bentz et al. (2001) documented latitudinal variation in the development time and offspring size of mountain pine beetles reared in lodgepole pine and ponderosa pine. They attributed these observed differences to genetics, given that they reared their beetles for two generations in a

common environment. They ruled out the influence of host species on these two traits. In contrast, our experiment clearly shows a direct effect of host species on offspring size and development time.

Langor (1989) found host effects on mountain pine beetle life history when comparing lodgepole to another less commonly used host, limber pine. He found that mountain pine beetles from limber pine had greater fecundity and shorter development times than mountain pine beetles from lodgepole. This is contrary to our results, even though limber pine and whitebark pine are closely related and can even hybridize. Langor's (1989) study, however, was conducted in the field at separate locations and environment may have affected his results. Langor (1989) also noted that phloem was thicker among limber pines than lodgepole pine, although he did not measure or analyze phloem thickness. In our experiment lodgepole had thicker phloem, but phloem thickness nested in host species was not a significant effect.

The second question was whether the productivity of mountain pine beetle infesting lodgepole and whitebark pine differed. Our data indicate that lodgepole pine is a superior host for mountain pine beetle in terms of fecundity. Among either host species, beetles from lodgepole had greater fecundity.

The final question we addressed was whether mountain pine beetles could successfully reproduce in whitebark pine if they were from whitebark pine or lodgepole pine. They can successfully reproduce in whitebark pine when they come from either whitebark pine or lodgepole pine, an important subtlety which had not been previously resolved. One shortcoming of this experiment that deserves further research is whether

the F₂ generation reared in whitebark pine would be fertile. This was not evaluated in our work. It has been found, though, that the second generation is not always fertile, often producing sterile males.

There are several alternatives consistent with the patterns observed in our data that cannot be eliminated. Some research has attributed differences in life history characteristics of mountain pine beetles to fungal symbionts. Bentz and Six (2006) compared the ergosterol content of fungi from the mycangia of mountain pine beetles from lodgepole pine. They found that the fungal symbionts of mountain pine beetle did not differ in their ergosterol content, but that they did contain more ergosterol than uninoculated lodgepole pine phloem and that it was a critical nutrient. Furthermore, Six and Paine (1998) found a significant effect of fungal symbiont species on development time in the mountain pine beetle. Finally, Six and Bentz (2007) found that temperature affects the relative abundance of the two primary fungal symbionts carried by the mountain pine beetle. These three findings together, that fungi provide a necessary nutrient lacking in host tissue, that fungi affect development time, and that temperature affect relative abundances of the mutualistic fungi, could explain much of the variation in population size, reproductive rates, and individual size that is commonly observed when comparing lodgepole and whitebark hosts. The mountain pine beetle exploits several host species and at least a few fungal species with varying results from each combination. Information on how temperature, host species, and fungal symbiont species interact could shed light on the differences we observed in our experiment.

A final mechanistic hypothesis that can be inferred from our data and cannot be excluded in preference of another is that many of the characteristics that mountain pine beetles exhibit when reared in whitebark pine lend themselves to expeditionary activities and low-level endemic population survival and may be an evolved relationship. Stated another way, whitebark pine appears to directly or indirectly (e.g., through fungal symbiont selection) confer attributes to a mountain pine beetle that makes whitebark a good “reservoir” host. Among these attributes is lower fecundity in favor of larger offspring. Adult beetles do not feed while exploring for host material and a larger beetle with more lipid storage is more capable of extended host finding expeditions.

Another attribute of whitebark pine that adds to the reservoir host hypothesis is its apparent lack of defenses. Mass attacked whitebark pines are commonly found with no pitch tubes and appear unattacked until closer inspection. Lodgepole pine is well defended and consequently requires a synchronous mass attack to succumb. Whitebark pine’s limited defenses combined with larger beetles emerging from whitebark makes whitebark an appealing host when populations are low. This scenario is further perpetuated by the effect of temperature on beetle development. Consideration of temperature has been traditionally limited to the thermal input necessary for synchronous emergence, termed “adaptive seasonality” (Logan and Powell, 2001). The reverse of this relationship is that temperatures cooler than the adaptive range result in asynchronous emergence and maladaptive seasonality (emerging at the wrong time of year) (Powell and Logan 2005). This fits very well within the lodgepole-mountain pine beetle relationship due to the necessity for synchronous mass attack. Whitebark pine, however, may not

require mass attack to be overwhelmed. Furthermore, because it lacks significant defenses, it may support strip attacks and partial attacks. In other words, it may not be so maladaptive for a beetle to emerge with only a few cohorts in a whitebark pine system. This could be thought of as a bet-hedging strategy: put out large, strong beetles across the full range of potential attack dates in a forest of susceptible and plentiful hosts to survive the hard times after lodgepole has been depleted. Of course many beetles will enter life stages inappropriate for the season, but the overall result may be better than a population emerging synchronously and competing for severely depleted lodgepole material.

Once temperatures at the high elevations become suitable, populations can very rapidly synchronize (Powell et al. 2000, Powell and Logan 2005). If at the same time lodgepole host material becomes more abundant, beetle populations would rapidly build in the lodgepole hosts where higher fecundity output is possible. This scenario directly challenges prevailing notions of the beetle's life history, but it does not challenge the data. In fact, it is very consistent with the current data set and warrants a closer look.

Our results indicate that lodgepole pine is a superior host to whitebark pine in terms of number of offspring that can be produced from trees of the same size. Whitebark pine in our study, however, had thinner phloem than typically found in lodgepole pine (Amman 1982). Beetles did reproduce effectively in whitebark pine and had larger offspring. Larger size and more energy reserves could be an advantage to exploring beetles at the leading edge of range expansion or during an incipient outbreak. A prevailing notion is that outbreaks in adjacent lodgepole pine stands "spill-over" into whitebark stands as lodgepole resources are depleted or when temperatures are warm

enough. Instead it could be that whitebark pine forests have been refugia for the beetle between outbreak cycles at lower elevations, and that warmer temperatures have altered that relationship, resulting in the vast outbreaks currently seen in whitebark systems.

In conclusion, our research suggests that host species can have significant effects on the life history of mountain pine beetles, including fecundity and offspring size. It is not clear whether the host effects are indirect effects via fungal symbionts, or direct effects of host chemistry. Because whitebark pine appears to affect the life history in ways that other hosts do not (e.g., Langor 1989, Bentz et al. 2001), more research is needed on the interactions of whitebark pine with mountain pine beetle life history, genetics, physiology, and fungal symbionts.

LITERATURE CITED

- Amman, G. D. 1972. Mountain pine beetle brood production in relation to thickness of lodgepole pine phloem. *Journal of Economic Entomology* 65(1): 138-140.
- Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. *Environmental Entomology* 2:541-547.
- Amman, G. D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. *Environmental Entomology* 11:590-593.
- Arno, S. F., and R. J. Hoff. 1989. Silvics of whitebark pine (*Pinus albicaulis*). USDA Forest Service General Technical Report INT-253. Intermountain Research Station, Ogden, Utah, USA.
- Aukema, B. H., A. L. Carroll, J. Zhu, K. F. Raffa, T. A. Sickley, S. W. Taylor. 2006. Landscape level analysis of mountain pine beetle in British Columbia, Canada: Spatiotemporal development and spatial synchrony within the present outbreak. *Ecography* 29(3): 427-441.
- Bartos, D. E., and K. E. Gibson. 1990. Insects of whitebark pine with emphasis on mountain pine beetle. Pages 171-178 in W. C. Schmidt and K. J. McDonald, editors. Symposium on whitebark pine ecosystems: ecology and management of a high-mountain resource. 29-31 March 1989, Bozeman, MT. USDA Forest Service Proceedings GTR-INT-270. USDA Forest Service, Washington, D.C., USA.
- Bentz, B. J. 2006. Mountain pine beetle population sampling: inferences from Lindgren pheromone traps and tree emergence cages. *Canadian Journal of Forest Research* 36: 351-360.
- Bentz, B. J., and D. L. Six. 2006. Ergosterol content of fungi associated with *Dendroctonus ponderosae* and *Dendroctonus rufipennis* (Coleoptera: Curculionidae, Scolytinae). *Annals of the Entomological Society of America* 99(2): 189-194.
- Bentz, B. J., J. A. Logan, and G. D. Amman. 1991. Temperature-dependent development of the mountain pine beetle (Coleoptera: Scolytidae) and simulation of its phenology. *Canadian Entomologist* 123:1083-1094.
- Bentz, B. J., J. A. Logan, and J. C. Vandygriff. 2001. Latitudinal life history variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and size. *Canadian Entomologist* 133: 375-387.

- Berg, E. E., J. D. Henry, C. L. Fastie, A. D. De Volder, and S. M. Matsuoka. 2006. Spruce beetle outbreaks on the Kenai Peninsula, Alaska, and Kluane National Park and Reserve, Yukon Territory: relationship to summer temperatures and regional differences in disturbance regimes. *Forest Ecology and Management* 227(3): 219-232.
- Berryman, A. A. 1972. Resistance of conifers to invasion by bark beetle—fungal associations. *BioScience* 22:598-602.
- Berryman, A. A., B. Dennis, K. F. Raffa, and N. C. Stenseth. 1985. Evolution of optimal group attack, with particular reference to bark beetles (Coleoptera: Scolytidae). *Ecology* 66: 898-903.
- Berryman, A. A., K. F. Raffa, J. A. Millstein, N. C. Stenseth. 1989. Interaction dynamics of bark beetle aggregation and conifer defense rates. *Oikos* 56(2): 256-263.
- Breshears, D. D., N. S. Cobb, P. M. Rich, K. P. Price, C. D. Allen, R. G. Balice, W. H. Romme, J. H. Kastens, M. L. Floyd, J. Belnap, J. L. Anderson, O. B. Myers, and C. W. Meyer. 2005. Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences* 102(42): 15144-15148.
- Campbell, E. M., and J. A. Antos. 2000. Distribution and severity of white pine blister rust and mountain pine beetle on whitebark pine in British Columbia. *Canadian Journal of Forest Research* 30:1051-1059.
- Carroll, A. L., S. W. Taylor, J. Régnière, and L. Safranyik. 2004. Effects of climate change on range expansion by the mountain pine beetle in British Columbia. Pages 223-232 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. *Mountain pine beetle symposium: challenges and solutions*. 30-31 October 2003, Kelowna, B. C. Natural Resources Canada, Canadian Forest Service Information Report BC-X-399. Pacific Forestry Centre, Victoria, B.C., Canada.
- Ciesla, W. M., and M. M. Furniss. 1975. Idaho's ghost forest. *American Forests* 81:32-35.
- Craighead, F. C., J. M. Miller, J. C. Evenden, and F. P. Keen. 1931. Control work against bark beetles in western forests and an appraisal of its results. *Journal of Forestry* 29: 1001-1018.
- Despain, D. G. 1991. *Yellowstone vegetation: consequences of environment and history in a natural setting*. Roberts Rinehart Publ., Boulder, Colorado, USA.

- Ebata, T. 2004. Current status of mountain pine beetle in British Columbia. Pages 52-56 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Mountain pine beetle symposium: challenges and solutions. 30-31 October 2003, Kelowna, B. C. Natural Resources Canada, Canadian Forest Service Information Report BC-X-399. Pacific Forestry Centre, Victoria, B.C., Canada.
- Evenden, J. C., W. D. Bedard, and G. R. Struble. 1943. The mountain pine beetle, an important enemy of western pines. USDA Circular 664. USDA, Washington, D.C., USA.
- Franceschi, V. R., P. Krokene, E. Christiansen, and T. Krekling. 2005. Tansley review: anatomical and chemical defenses of conifer bark against bark beetles and other pests. *New Phytologist* 167(2): 353-376.
- Hamilton, L. C. 1992. Regression with graphics: a second course in applied statistics. Duxbury Press, Belmont.
- Hedgren, O. 2007. Massive outbreak of mountain pine beetle in Canadian pine forests. *Entomologisk Tidskrift* 128: 1-8.
- Intergovernmental Panel on Climate Change (IPCC). 2001*a*. Climate change 2001: the scientific basis. Contribution of working group I to the third assessment report of the IPCC. J. T. Houghton, Y. Ding, D. J. Griggs, M. Noguer, P. J. van der Linden, X. Dai, K. Maskell, and C. A. Johnson, editors. Cambridge University Press, Cambridge, UK.
- Intergovernmental Panel on Climate Change (IPCC). 2001*b*. Climate change 2001: impacts, adaptation, and vulnerability. Contribution of working group II to the third assessment report of the IPCC. J. J. McCarthy, O. F. Canziani, N. A. Leary, D. J. Dokken, and K. S. White, editors. Cambridge University Press, Cambridge, UK.
- Keane, R. E., and S. F. Arno. 1993. Rapid decline of whitebark pine in western Montana: Evidence from 20-year remeasurements. *Western Journal of Applied Forestry* 8:44-47.
- Keane, R. E., P. Morgan, and J. P. Menakis. 1994. Landscape assessment of the decline of whitebark pine (*Pinus albicaulis*) in the Bob Marshall Wilderness Complex, Montana, USA. *Northwest Science* 68:213-229.
- Keane, R. E., K. C. Ryan, T. T. Veblen, C. D. Allen, J. Logan, and B. Hawkes. 2002. Cascading effects of fire exclusion in Rocky Mountain Ecosystems: A literature review. USDA Forest Service General Technical Report RMRS-GTR-91. Rocky

Mountain Research Station, Fort Collins, Colorado, USA.

- Kinloch, B. B., Jr. 2003. White pine blister rust in North America: past and prognosis. *Phytopathology* 93:1044-1047.
- Kinloch, B.B., Jr., and G. E. Dupper. 2002. Genetic specificity in the white pine blister rust pathosystem. *Phytopathology* 92:278-280.
- Kulhavy, D. L., A. D. Partridge, and R. W. Stark. 1984. Root disease and blister rust associated with bark beetles (Coleoptera: Scolytidae) in western white pine in Idaho. *Environmental Entomology* 13: 813-817.
- Langor, D. W. 1989. Host effects on the phenology, development, and mortality of field populations of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Canadian Entomologist* 121:149-157.
- Langor, D. W., J. R. Spence, and G. R. Pohl. 1990. Host effects on fertility and reproductive success of *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). *Evolution* 44:609-618.
- Logan, J. A., and B. J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera: Scolytidae) seasonality. *Environmental Entomology* 28:924-934.
- Logan, J. A., and J. A. Powell. 2001. Ghost forests, global warming, and the mountain pine beetle (Coleoptera: Scolytidae). *American Entomologist* 47:160-172.
- Logan, J. A., and J. A. Powell. 2004. Modeling mountain pine beetle phenological response to temperature. Pages 210-222 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. Mountain pine beetle symposium: challenges and solutions. 30-31 October 2003, Kelowna, B.C. Natural Resources Canada, Canadian Forest Service Information Report BC-X-399. Pacific Forestry Centre, Victoria, B.C., Canada.
- Logan, J. A., and J. A. Powell. 2008. Ecological consequences of climate change altered forest insect disturbance regimes. In F. H. Wagner (ed.), *Climate change in western North America: evidence and environmental effects*. University of Utah Press (in press). <http://www.usu.edu/beetle/documents/Logan-Powell2005.pdf>
- Logan, J. A., J. Régnière, and J. A. Powell. 2003. Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment* 1: 130-137.
- Lyon, R. L. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. *Canadian Entomologist* 90: 582-584.

- Mattson, D. J., K. C. Kendall, and D. P. Reinhart. 2001. Whitebark pine, grizzly bears, and red squirrels. Pages 121-136 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities. Island Press, Washington.
- McCambridge, W. F., and G. C. Trostle. 1972. The mountain pine beetle. USDA Forest Service, Forest Pest Leaflet 2.
- McCaughey, W. W. and D. F. Tomback. 2001. The natural regeneration process. Pages 105-120 *in* D. F. Tomback, S. F. Arno, and R. E. Keane, editors. Whitebark pine communities: ecology and restoration. Island Press, Washington, D.C., USA.
- Milliken, G. A., and D. E. Johnson. 2002. Analysis of messy data, Volume III: Analysis of covariance. Chapman and Hall/CRC, New York.
- Murray, M. P., and M. C. Rasmussen. 2003. Non-native blister rust disease on whitebark pine at Crater Lake National Park. *Northwest Science* 77(1): 87-91.
- Negrón, J. F., and J. L. Wilson. 2003. Attributes associated with probability of infestation by the piñon ips, *Ips confusus* (Coleoptera: Scolytidae), in piñon pine, *Pinus edulis*. *Western North American Naturalist* 63(4): 440-451.
- Perkins, D. L., and D. W. Roberts. 2003. Predictive models of whitebark pine mortality from mountain pine beetle. *Forest Ecology and Management* 174:495-510.
- Perkins, D. L., and T. W. Swetnam. 1996. A dendroecological assessment of whitebark pine in the Sawtooth – Salmon River region, Idaho. *Canadian Journal of Forest Research* 26:2123-2133.
- Powell, J. A., J. L. Jenkins, J. A. Logan, and B. J. Bentz. 2000. Seasonal temperature alone can synchronize life cycles. *Bulletin of Mathematical Biology* 62:977-998.
- Powell, J. A., and J. A. Logan. 2005. Insect seasonality: circle map analysis of temperature-driven life cycles. *Theoretical Population Biology* 67:161-179.
- Raffa, K. F., and A. A. Berryman. 1983. The role of host plant resistance in the colonization behavior and ecology of bark beetles (Coleoptera: Scolytidae). *Ecological Monographs* 53:27-49.
- Reid, R. W. 1962a. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia I. Life cycle, brood development, and flight periods. *Canadian Entomologist* 94: 531-538.

- Reid, R. W. 1962*b*. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the East Kootenay region of British Columbia II. Behaviour in the host, fecundity and internal changes in the female. *Canadian Entomologist* 94: 605-613.
- Romme, W. H., and M. G. Turner. 1991. Implications of global climate change for biogeographic patterns in the Greater Yellowstone Ecosystem. *Conservation Biology* 5:373-386.
- Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. Pages 77-84 in A. A. Berryman, G. D. Amman, and R. W. Stark, editors. Symposium proceedings: theory and practice of mountain pine beetle management in lodgepole pine forests. 25-27 April 1978, Moscow, Idaho, USA. University of Idaho Forest, Wildlife and Range Experiment Station, Moscow, Idaho, USA.
- Samman, S., and J. A. Logan, editors. 2000. Assessment and response to bark beetle outbreaks in the Rocky Mountain area: a report to Congress from Forest Health Protection, Washington Office. USDA Forest Service General Technical Report RMRS-GTR-62. Rocky Mountain Research Station, Ogden, Utah, USA.
- Six, D. L. 2003. Bark beetle—fungal symbioses. Pages 97-114 in K. Bourtzis and T. A. Miller, editors. *Insect symbiosis*. CRC Press, New York.
- Six, D. L., and J. Adams. 2007. White pine blister rust severity and selection of individual whitebark pine by the mountain pine beetle (Coleoptera: Curculionidae, Scolytinae). *Journal of Entomological Science* 42(3): 345-353.
- Six, D. L., and B. J. Bentz. 2007. Temperature determines symbiont abundance in a multipartite bark beetle-fungal ectosymbiosis. *Microbial Ecology* 54(1): 112-118.
- Six, D. L., and K. D. Klepzig. 2004. Bark beetle-fungal symbiosis: Context dependency in complex associations. *Symbiosis* 37: 189-205.
- Six, D. L. and T. D. Paine. 1998. Effects of mycangial fungi and host tree species on progeny survival and emergence of *Dendroctonus ponderosae* (Coleoptera: Scolytidae). *Environmental Entomology* 27(6): 1393-1401.
- Taylor, S. W., and A. L. Carroll. 2004. Disturbance, forest age, and mountain pine beetle outbreak dynamics in BC: a historical perspective. Pages 41-51 in T. L. Shore, J. E. Brooks, and J. E. Stone, editors. *Mountain pine beetle symposium: challenges and solutions*. Natural Resources Canada, Canadian Forest Service Information Report BC-X-399.

- Taylor, S. W., A. L. Carroll, R. I. Alfaro, and L. Safranyik. 2006. Forest, climate and mountain pine beetle outbreak dynamics in western Canada. Pages 67-94 *in* L. Safranyik and B. Wilson, editors. The mountain pine beetle: a synthesis of biology, management, and impacts in lodgepole pine. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, B.C., Canada.
- Tomback, D. F., S. F. Arno, and R. E. Keane, editors. 2001. Whitebark pine communities. Island Press, Washington, D.C., USA.
- Tomback, D. F., J. K. Clary, J. Koehler, R. J. Hoff, and S. F. Arno. 1995. The effects of blister rust on post-fire regeneration of whitebark pine: the Sundance burn of northern Idaho. *Conservation Biology* 9:654-664.
- Tomback, D. F., and Y. B. Linhart. 1990. The evolution of bird-dispersed pines. *Evolutionary Ecology* 4:185-219.
- Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. *Great Basin Naturalist Memoirs* 6: 1-1359.
- Williams, D. W., and A. M. Liebhold. 2002. Climate change and the outbreak ranges of two North American bark beetles. *Agricultural and Forest Entomology* 4:87-99.
- Zeglen, S. 2002. Whitebark pine and white pine blister rust in British Columbia, Canada. *Canadian Journal of Forest Research* 32:1265-1274.