Contrasting Geographic Patterns of Genetic Differentiation in Body Size and Development Time With Reproductive Isolation in *Dendroctonus ponderosae* (Coleoptera: Curculionidae, Scolytinae)

RYAN R. BRACEWELL,[1] MICHAEL E. PFRENDER,[2] KAREN E. MOCK,[3] AND BARBARA J. BENTZ[4,5]

Ann. Entomol. Soc. Am. 106(3): 385–391 (2013); DOI: http://dx.doi.org/10.1603/AN12133

ABSTRACT Body size and development time are two critical phenotypic traits that can be highly adaptive in insects. Recent population genetic analyses and crossing experiments with the mountain pine beetle (*Dendroctonus ponderosae* Hopkins) have described substantial levels of neutral molecular genetic differentiation, genetic differences in phenotypic traits, and reproductive isolation. To determine whether genetic differences in adaptive phenotypic traits exist that correspond to reproductive boundaries, we conducted a common garden experiment with seven *D. ponderosae* populations previously used to identify reproductive incompatibilities. Genetic differences in development time were striking between faster developing, and more synchronized, northern populations and slower developing, and less synchronized, southern populations. Additionally, genetic differences in average body size were found between many populations. Differences in these two traits, however, failed to clearly demarcate populations that exhibit reproductive incompatibilities. Our results suggest that local selection pressures likely drive divergence in these two traits that is largely independent of the evolution of reproductive isolation in *D. ponderosae*.

KEY WORDS mountain pine beetle, speciation, adaptation, life-history, bark beetle

Reproductively isolated populations typically harbor clear phenotypic differences. These differences are due to a combination of divergent selection, genetic drift, and the input of independent mutations. Identifying genetically based phenotypic differences among populations can often help determine whether reproductive isolation is occurring and what role particular factors might play in driving divergence. How populations become reproductively isolated and what ecological and genetic forces impede gene flow is central to understanding the speciation process (Coyne and Orr 2004).

Recently, reproductive isolation in the form of hybrid male sterility has been described in the economically and ecologically important bark beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae, Scolytinae) (Bentz et al. 2011, Bracewell et al. 2011). This beetle is geographically widespread in coniferous forests of western North American (Fig. 1) where it is considered a *Pinus* generalist (Wood 1982, Kelley and Farrell 1998) and is currently in an outbreak phase in many areas (Bentz et al. 2010, Safranyik et al. 2010). Previous population genetic analyses did not find molecular evidence of longstanding reproductive isolation, yet did find substantial population level subdivision, with evidence of gene flow occurring primarily in an isolation-by-distance pattern (Mock et al. 2007). This gene flow appears to occur primarily in a horseshoe shape around the Great Basin Desert such that populations in the southernmost reaches of the species' range (southern California and central Arizona) are the most genetically divergent (Fig. 1).

Experimental crosses in *D. ponderosae* described a complex pattern of reproductive isolation in the form of postmating (specifically postzygotic) isolation (Bracewell et al. 2011). Nearly all hybrid males were sterile when either a male or female from southern California (hereafter CA) was crossed to individuals from populations from Idaho (ID) and Utah (UT) (Fig. 1). However, crosses between CA and populations extending northward through California (CA2, CA3) and Oregon (OR) produced fully fertile offspring. Crosses between OR and ID populations showed a unidirectional incompatibility where hybrid males from the ID female × OR male cross had drastically reduced fecundity (Bracewell et al. 2011). These results suggest a reproductive barrier geographically located between the OR and ID populations, and crosses from populations close to this zone (OR × ID)

[1] Wildland Resources Department, Utah State University, 5230 Old Main Hill, Logan, UT 84322.
[2] Department of Biological Science, Environmental Change Institute, University of Notre Dame, Notre Dame, IN 46556.
[3] Wildland Resources Department, Utah State University, 5230 Old Main Hill, Logan, UT 84322.
[4] Corresponding author: Department of Ecosystem and Conservation Sciences, University of Montana, 32 Campus Drive, Missoula, MT 59812 (e-mail: bbentz@fs.fed.us).
[5] USDA Forest Service Rocky Mountain Research Station, 860 North 1200 East, Logan, UT 84321.

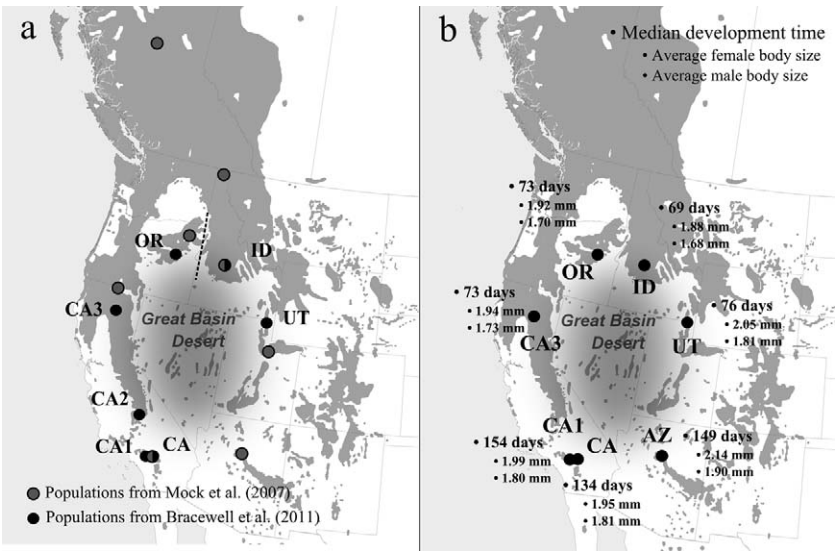

Fig. 1. (a) *Dendroctonus ponderosae* distribution and populations previously investigated for reproductive incompatibilities (Bracewell et al. 2011) and neutral molecular genetic differentiation (Mock et al. 2007). *Dendroctonus ponderosae* distribution generally follows its primary host pine distribution (shown) although boundaries in British Columbia and Alberta Canada are currently expanding and the southern range limit in southern California and central Arizona/southern Colorado is hard to determine because of low densities. Previous research from Mock et al. (2007) suggests that gene flow occurs in an isolation by distance gene flow pattern around the Great Basin Desert, with the two most southern populations sampled being the most genetically divergent. Reproductive isolation in the form of hybrid male sterility has been described by Bracewell et al. (2011) when CA is crossed to ID and UT, although CA is compatible with populations extending northward to OR. Crosses between OR and ID produce partially reproductively compromised hybrid males in one direction of the cross (Bracewell et al. 2011) and it has been suggested that a reproductive boundary exists geographically between the OR and ID populations. (b) Populations used in this study to investigate genetic divergence in body size and development time and trait measurements after two generations in a common garden environment.

showed lower levels of reproductive incompatibility than did more geographically distant crosses (CA × ID and CA × UT). Comparable levels of hybrid sterility are most often observed between organisms with marked phenotypic and genetic differentiation (e.g., Coyne and Orr 1989, Presgraves 2002). The observed pattern of reproductive isolation in *D. ponderosae* raises the question of whether genetic differences in adaptive phenotypic traits correspond to observed patterns of reproductive incompatibility.

Body size and development time are generally considered to be environment-specific adaptations in insects (Roff 1980, Fairbairn 1984, Mousseau and Roff 1989, Nylin and Gotthard 1998), and can differ among geographically separated populations. Studies of these two traits in *D. ponderosae* indicate that substantial geographic variation exists among some populations (Bentz et al. 2001, Bentz et al. 2011). These phenotypic differences have both genetic (involving complex gene interactions) and environmental (plasticity in response to temperature) components (Bentz et al. 2011). Population-level differentiation in temperature-dependent traits is thought to be driven by strong selection in *D. ponderosae.* Development time is under direct temperature control, and lifestage-specific thresholds synchronize individuals within a population (Bentz et al. 1991, Powell and Logan 2005). *D. ponderosae* use a coordinated attack strategy whereby hundreds to thousands of individuals are needed to synchronously attack and overcome host tree defenses during colonization (Raffa and Berryman 1983), thereby making emergence synchrony a crucial component to an adaptive life cycle (Logan and Bentz 1999). Appropriate developmental timing that results in a univoltine life cycle is also considered important to population success (Amman 1973, Safranyik 1978). Therefore, development has to be finely tuned to local climatic conditions that vary substantially across the broad latitudinal and elevational range of this insect, and be flexible enough to accommodate local and seasonal variation. Linked to development time is body size (Bentz et al. 2011), which is known to have a strong influence on *D. ponderosae* fitness (Reid 1962, McGhehey 1971, Pureswaran and Borden 2003, Elkin and Reid 2005) and also has been used to aid in species identification in *Dendroctonus* as it generally varies among species (Wood 1982).

Here, we determine whether genetically based divergence in *D. ponderosae* body size and development time corresponds to patterns of reproductive isolation among populations (Bracewell et al. 2011). Our results will help discern whether there is shared spatial structuring of reproductive isolation and phenotypic divergence and whether the same geographic or environmental forces that act to differentiate populations with respect to adaptive traits also influence the evo-

Table 1. Collection location and host tree species of *Dendroctonus ponderosae* populations sampled for body size and development time comparisons

Identifier	Locality (nearest city)	Elevation (m)	Latitude and longitude	Host tree
CA	Big Bear Lake, CA	2092	34° 15′ N, 116° 54′ W	*Pinus monophylla*
CA1	Arrowbear Lake, CA	2029	34° 12′ N, 117° 03′ W	*Pinus lambertiana*
CA3	Old Station, CA	1487	40° 37′ N, 121° 29′ W	*Pinus contorta*
OR	Prairie City, OR	1601	44° 17′ N, 118° 24′ W	*Pinus contorta*
ID	Stanley, ID	2008	44° 17′ N, 115° 02′ W	*Pinus contorta*
UT	Garden City, UT	2183	41° 58′ N, 111° 31′ W	*Pinus contorta*
AZ	Flagstaff, AZ	2813	35° 19′ N, 111° 42′ W	*Pinus flexilis*

lution of reproductive isolation in this system. If little to no correspondence between phenotypic divergence and reproductive isolation is observed, our results would suggest that local population processes and selective forces are driving genetically based differences in the phenotype that are independent of the underlying reproductive incompatibilities indicative of the early stages of speciation.

Materials and Methods

Insect Collection. Seven *D. ponderosae* populations were sampled from coniferous forests bounding the Great Basin Desert in the spring of 2007 by felling trees infested with larvae (Table 1; Fig. 1). Six of the seven populations used in our study correspond directly to samples collected in Bracewell et al. (2011), and three of the seven populations (CA, ID, and AZ) were collected in geographic proximity to samples from Mock et al. (2007) (Fig. 1). Sections from the bole of each tree (≈40 cm) were collected and the cut ends were sealed with paraffin wax to reduce desiccation. The sections were then transported to the USDA Forest Service in Logan, UT, and placed in refrigeration (≈3°C). After all populations were collected, the tree sections were placed in rearing containers at room temperature (≈21°C) to allow larval development to the adult stage. Emerging adults were collected from each population daily and placed in petri dishes with moistened filter paper and then returned to ≈3°C for storage. Individuals used for matings were randomly chosen from the peak emergence period (≈15 d with highest total of emerged adults) each population. Gender was determined using characters on the seventh abdominal tergite (Lyon 1958).

Assessing Population Level Genetic Differences. To characterize relative differences in development time and body size across *D. ponderosae* populations, we conducted intrapopulation matings in a common garden environment and compared individuals from the F_2 generation. Two generations of matings were conducted to minimize maternal effects originating from the initial collection environment (e.g., prior host use). The common garden environment consisted of a constant temperature (22.5°C) with constant light (24:0 L:D), and used a single rearing tree species, lodgepole pine (*Pinus contorta* variety *latifolia*) collected from the Wasatch–Cache NF, UT, just before each generation of mating. Similar rearing protocols have been used previously and are described in detail elsewhere (e.g., Bracewell et al. 2011, Bentz et al. 2011). For each generation of laboratory matings, two randomly selected bolts (≈40 cm tree sections in length, and ≈28–33 cm in diameter) were used to rear each population. Matings were performed by inserting a female, and then a male, into a predrilled hole in the phloem of each bolt. Each male or female pair was spaced 3 cm from its neighbor around the circumference of the bolt to homogenize infestation density and brood competition. After inserting each pair into the end of a bolt, a small piece of screen was fixed over the entrance hole to prevent escape. After all pairs were in place, the infested bolts were individually enclosed in screen so that the resulting emergence of progeny could be monitored and beetles collected for size measurements.

Infested bolts were placed in two separate temperature-controlled rearing chambers at 22.5°C. Twenty-four pairs per population (12 pairs per bolt) were used to produce the F_1 generation. For each population, adult beetles from the peak emergence period (≈15 d with highest total of emerged adults) from both bolts were pooled and 20 pairs (10 pairs per bolt) randomly selected to produce the F_2 generation. Previous laboratory experiments using this approach indicate that >80% of matings contribute offspring to the brood adult pool (Bracewell et al. 2011) Total development time (i.e., the time from introduction of male/female pair to brood adult emergence) of the F_2 generation was determined by recording the number of adults emerging from a bolt, by population, every other day, until emergence ceased (≈10 d without an individual). Pronotum width, which is a proxy measure for overall size (Bentz et al. 2001, 2011), was measured on up to 50 F_2 beetles per gender per population. Measurements were taken from randomly selected beetles pooled from replicate bolts.

Statistical Analysis. Differences among populations in body size (pronotum width) and development time were analyzed using SAS (SAS Institute, Cary, NC, version 9.1.3). The pronotum data were found to be normally distributed and analyzed using a general linear model in PROC GLM with population as the main fixed effect. Post hoc pairwise comparisons of size differences between all populations were conducted using Tukey–Kramer honestly significant difference (HSD) tests. Females of *D. ponderosae* are known to be on average significantly larger than the males (e.g., Sturgeon and Mitton 1986, Bentz et al. 2001) and therefore the sexes were analyzed separately.

Table 2. Mean size (pronotum width) and parameter estimates (±SEM) from a logistic growth model fit to emergence data of *Dendroctonus ponderosae* from seven populations reared in a common garden environment

Population	*n*	Male pronotum (mm)	*n*	Female pronotum (mm)	Median development time (t_m) (days)	Time interval for 10- 90% emergence (Δt) (days)
CA	44	1.81 (0.01)b	50	1.95 (0.02)c	133.95 (6.09)a	74.99 (5.73)a
CA1	29	1.80 (0.02)b	48	1.99 (0.01)bc	154.21 (6.09)a	87.25 (5.73)a
CA3	50	1.73 (0.01)c	50	1.94 (0.01)cd	73.08 (6.09)b	26.05 (5.73)b
OR	50	1.70 (0.01)c	50	1.92 (0.02)cd	73.01 (6.09)b	27.02 (5.73)b
ID	50	1.68 (0.01)c	50	1.88 (0.01)d	69.33 (6.09)b	25.97 (5.73)b
UT	49	1.81 (0.01)b	50	2.05 (0.01)b	75.99 (6.09)b	27.10 (5.73)b
AZ	50	1.90 (0.02)a	50	2.14 (0.02)a	149.05 (6.09)a	82.85 (5.73)a

Pairwise differences in size and development parameter estimates were tested using a Tukey–Kramer HSD test. Values followed by the same letter within a column are not significantly different.

Development time data were analyzed using a three parameter logistic growth model (Meyer 1994) that describes the total number of adults emerged (k), number of days from 10 to 90% adult emergence (Δt), and median emergence day (t_m). Models were fit and parameter estimates determined using PROC NLMIXED, and calculated using brood adult emergence data from each population (i.e., pair of bolts) from replicate incubators. Model fit was evaluated by comparing predicted development time with observed development time data and by inspecting residual plots. Differences among the populations were analyzed by comparing parameter estimates (k, Δt, and t_m) for each population using a mixed effects model in PROC MIXED. Temperature chamber was included as a fixed effect (Bolker et al. 2009) to test for any influence of slight temperature deviations between chambers. Post hoc pairwise comparisons of differences in development time parameters between populations were conducted using Tukey–Kramer HSD tests. The k parameter, an estimate of the total number of beetles that emerged from a bolt, was not of interest in our study. Large quantities of beetles emerged from all bolts (mean = 132 ± 23). Our focus was on the parameters that describe development time: Δt and t_m.

Results

Adult Size. Size (pronotum width) was significantly different among populations in both males ($F_{6,315}$ = 35.56; $P < 0.0001$) and females ($F_{6,341}$ = 31.08; $P < 0.0001$) and genetic divergence among some populations in this trait was substantial. For example, female beetles with the largest average body size (AZ) were nearly 14% larger than female beetles from the smallest population (ID). A general trend of decreasing size with increasing latitude, consistent with the "converse of Bergmann's Rule" (Mousseau 1997) was observed in latitudinal clines on either side of the Great Basin Desert (Fig. 1). Populations at similar latitudes and separated by the Great Basin Desert (e.g., UT - CA3 and AZ - CA), however, were significantly different in size, and eastern populations were larger than their western counterpart (Table 2).

Males. Males from the AZ population were found to be on average significantly larger than males from all other populations (Table 2). UT, CA, and CA1 males were of intermediate size and not significantly different from one another, yet they were significantly larger than males from more northern populations, CA3, OR, and ID, which were on average the smallest (Table 2).

Females. Patterns were generally similar to those observed in males. Females from the AZ population were significantly larger than females from all other populations (Table 2). The UT population was the second largest on average, and was significantly different from all other populations except CA1. Females from the northern latitude populations, ID, OR, and CA3 were the smallest; however, CA and CA1 were somewhat smaller than expected given the size of the males from those same populations (Table 2).

Development Time. Significant genetic differences among populations were found in median development time (t_m) at a constant 22.5°C ($F_{6,6}$ = 42.05; $P < 0.0001$) and there was no significant temperature chamber effect ($F_{1,6}$ = 1.33; P = 0.2929). Populations from northern latitudes (CA3, OR, ID, and UT), developed significantly faster (nearly half the time) compared with populations from the most southern latitudes (CA, CA1, and AZ) (Fig. 1; Table 2). Within these two latitudinal groups, no significant differences in development time were detected (Table 2). Median development time for the three southern populations was nearly double the time observed for individuals from northern populations (Fig. 2; Table 2). Populations from the southern latitudes also required a significantly greater number of days to progress from 10 to 90% emergence (Δt) ($F_{6,6}$ = 26.88; $P < 0.0004$) (Table 2) and there was no significant temperature chamber effect ($F_{1,6}$ = 0.19; P = 0.6776).

Discussion

We found clear genetic differences in *D. ponderosae* development time and adult size among geographically separated populations. These traits are widely considered adaptively significant (Nylin and Gotthard 1998) and can strongly affect *D. ponderosae* reproductive success (Logan and Bentz 1999, Pureswaran and Borden 2003, Elkin and Reid 2005). The genetic variation within *D. ponderosae* highlights substantial population level differentiation suggestive of local adaptation. Most striking was the clear biogeographical

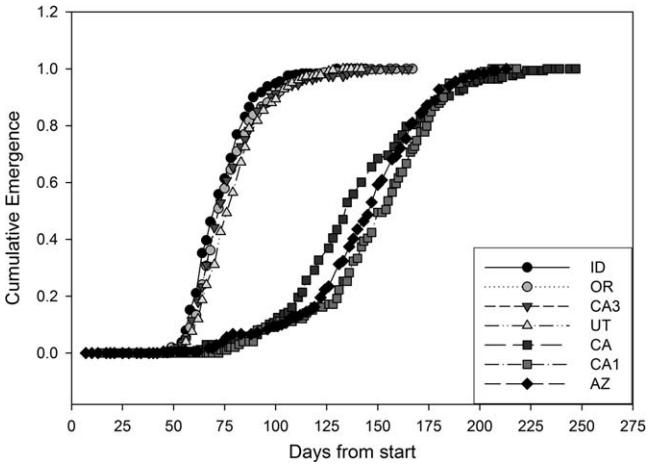

Fig. 2. Cumulative development time of *Dendroctonus ponderosae* from seven populations reared in a common garden environment. Populations from northern latitudes (CA3, OR, ID, and UT) had a significantly faster median development time, and were significantly more synchronized (time from 10 to 90% emergence) than individuals from southern populations (CA, CA1, and AZ). Curves based on average of 263 (SE = 62.31) beetles per population.

difference seen in development time. Beetles collected from northern latitudes emerged earlier and more synchronously than beetles from southern latitudes. The finding of a less synchronized emergence in these populations corroborates and expands on work from Bentz et al. (2011) and has significant implications for understanding outbreak dynamics and potential range expansion in this widely distributed species.

Adult size was highly variable among populations. A clear biogeographical break consistent with differences in development time was not evident, suggesting different selection pressures on body size and development time among populations (Kingsolver and Huey 2008). Thus, differences in developmental rate exist within *D. ponderosae*, and some populations achieve the same body size as other populations in less time (Bentz et al. 2011). Currently, it is unknown during what stage(s) developmental differences occur because in our experiment development time includes the entire sequence from parent beetle insertion into the bolt through brood adult emergence.

We found no significant differences in either development time or body size between partially reproductively isolated populations on either side of the geographic-reproductive boundary (OR and ID) found in Bracewell et al. (2011). Development time was found to differ significantly between populations that show the highest levels of hybrid male sterility (CA compared with ID and UT) although body size differences varied in their significance depending on the gender and population (Table 2). However, development time was also significantly different between populations found to be fully reproductively compatible (i.e., CA compared with CA3 and OR) (Bracewell et al. 2011). Neutral molecular markers have identified CA and AZ as the most genetically divergent populations (Mock et al. 2007), yet these populations did not differ significantly in development time. In addition, geographically distant populations often had very similar body size measures. Our results show that patterns of *D. ponderosae* body size and development time, two important life-history traits, are not wholly consistent with an isolation by distance gene flow pattern around the Great Basin Desert (Mock et al. 2007). Additionally, no differences in these traits were clearly associated with the proposed reproductive boundary (Bracewell et al. 2011). Our results suggest that body size and development time are likely influenced by local forces, primarily climatic in the case of development time, that appear to be independent of reproductive isolation and only loosely associated with genetic drift at neutral molecular markers.

The slower developmental rates in southern populations are likely an adaptation to the increased thermal input encountered in lower latitudes. Although the physiological mechanism is unclear, inter-population variation in developmental rate could be an adaptation to maintain univoltinism and emergence synchrony (Bentz et al. 2001), which are both considered crucial to *D. ponderosae* reproductive success (Amman 1973, Safranyik 1978). Such striking differences in developmental rate between northern and southern populations could potentially lead to allochronic isolation if divergent populations were to occur in sympatry. However, molecular evidence suggests that gene flow occurs between northern and southern populations (Mock et al. 2007) and fertile offspring are produced when individuals from some northern and southern populations are crossed (Bracewell et al. 2011). Our sampling strategy leaves many geographical gaps and it is likely that populations located between the distinct northern and southern populations might have intermediate development times, thereby forming a latitudinal gradient of differences in developmental rate. There is some support for this scenario, as Bentz et al. (2001) found that the F_2 generation of a southern Utah population (geographically interme-

diate between AZ and UT), reached 50% emergence in ≈100–110 d when reared at ≈21°C.

Populations used in our study were collected from a variety of latitudes, altitudes, and host species, thereby confounding any one effect (Table 1). In addition to the influence of climate (Bentz et al. 2011), long-term selection imposed by different host tree species may also impact *D. ponderosae* in a variety of ways (Sturgeon and Mitton 1986, Langor and Spence 1991). We suspect long-term host specificity could be a contributing factor to the variation in adult size, but host specificity seems less likely to be a contributing factor in the development time differences found in this study. The three southern populations in our study were collected from three distinct *Pinus* species (*P. monophylla*, *P. lambertiana*, and *P. flexilis*), of which two populations were sympatric (CA and CA1). However, development time did not significantly differ across these three populations. In addition, studies have shown that when a population is lab-reared in a variety of tree species, there is comparatively little impact on development time (Amman et al. 1982, Bentz et al. 2001). Our results also show that prior host use is not the only factor influencing size. Adults from the UT population, collected from lodgepole pine, were significantly larger than adults from all other populations also collected from lodgepole pine (ID, CA3, and OR).

In conclusion, we find clear evidence of substantial genetic differentiation between many populations in development time and body size. Some of these differences did not clearly coincide with patterns of genetic divergence at neutral molecular markers (Mock et al. 2007). Importantly, there were no clear genetic differences in body size and development time that corresponded strongly with patterns of postzygotic reproductive isolation (Bracewell et al. 2011). Therefore, it appears that local population processes and selection pressures can act as major drivers of divergence in *D. ponderosae*, overwhelming the signature of drift, mutation, and migration in spatially structured and reproductively isolated populations.

Acknowledgments

We thank J. Vandgriff for assisting with various aspects of this research. We would also like to recognize the many U.S. Forest Service personnel who helped locate beetle populations, including L. Merrill, D. Cluck, L. Spiegel, J. McMillan, and J. Goldberg. We would also like to thank D. Turner for help with statistical analyses and D. Six and three anonymous reviewers for comments on an earlier draft of this paper. This research was funded by The UDSA Forest Service, Rocky Mountain Research Station.

References Cited

Amman, G. D. 1973. Population changes of the mountain pine beetle in relation to elevation. Environ. Entomol. 2: 541–547.

Amman, G. D. 1982. Characteristics of mountain pine beetles reared in four pine hosts. Environ. Entomol. 11: 590–593.

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. Can. Entomol. 123: 1083–1094.

Bentz, B. J., J. A. Logan, and J. C. Vandygriff. 2001. Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size. Can. Entomol. 133: 375–387.

Bentz, B. J., J. Regniere, C. J. Fettig, E. M. Hansen, J. L. Hayes, J. A. Hicke, R. G. Kelsey, J. F. Negron, and S. J. Seybold. 2010. Climate change and bark beetles of the western United States and Canada: direct and indirect effects. Bioscience 60: 602–613.

Bentz, B. J., R. R. Bracewell, K. E. Mock, and M. E. Pfrender. 2011. Genetic architecture and phenotypic plasticity of thermally-regulated traits in an eruptive species, *Dendroctonus ponderosae.* Evol. Ecol. 25: 1269–1288.

Bolker, B. M., M. E. Brooks, C. J. Clark, S. W. Geange, J. R. Poulsen, M.H.H. Stevens, and J.-S.S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol. Evol. 24: 127–135.

Bracewell, R. R., M. E. Pfrender, K. E. Mock, and B. J. Bentz. 2011. Cryptic postzygotic isolation in an eruptive species of bark beetle (*Dendroctonus ponderosae*). Evolution 65: 961–975.

Coyne, J. A., and H. A. Orr. 1989. Patterns of speciation in Drosophila. Evolution 43: 362–381.

Coyne, J. A., and H. A. Orr. 2004. Speciation. Sinauer, Sunderland, MA.

Elkin, C. M., and M. L. Reid. 2005. Low energy reserves and energy allocation decisions affect reproduction by Mountain Pine Beetles, *Dendroctonus ponderosae.* Funct. Ecol. 19: 102–109.

Fairbairn, D. J. 1984. Microgeographic variation in body size and development time in the waterstrider, *Limnoporus notabilis.* Oecologia 61: 126–133.

Kelley, S. T., and B. D. Farrell. 1998. Is specialization a dead end? The phylogeny of host use in *Dendroctonus* bark beetles (Scolytidae). Evolution 52: 1731–1743.

Kingsolver, J. G., and R. B. Huey. 2008. Size, temperature, and fitness: three rules. Evol. Ecol. Res. 10: 251–268.

Langor, D. W., and J. R. Spence. 1991. Host effects on allozyme and morphological variation of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). Can. Entomol. 123: 395–410.

Logan, J. A., and B. J. Bentz. 1999. Model analysis of mountain pine beetle (Coleoptera : Scolytidae) seasonality. Environ. Entomol. 28: 924–934.

Lyon, R. L. 1958. A useful secondary sex character in *Dendroctonus* bark beetles. Can. Entomol. 90: 582–584.

McGhehey, J. H. 1971. Female size and egg production of the mountain pine beetle *Dendroctonus ponderosae* Hopkins. Nor. For. Res. Cen., Edmonton, Alberta, Inform. Rep. NOR-X-9.

Meyer, P. 1994. Bi-logistic growth. Technol. Forecast. Soc. Change 47: 89–102.

Mock, K. E., B. J. Bentz, E. M. O'Neill, J. P. Chong, J. Orwin, and M. E. Pfrender. 2007. Landscape-scale genetic variation in a forest outbreak species, the mountain pine beetle (*Dendroctonus ponderosae*). Mol. Ecol. 16: 553–568.

Mousseau, T. A., and D. A. Roff. 1989. Adaptation to seasonality in a cricket: patterns of phenotypic and genotypic variation in body size and diapause expression along a cline in season length. Evolution 43: 1483–1496.

Mousseau, T. A. 1997. Ectotherms follow the converse to Bergmann's rule. Evolution 51: 630–632.

Nylin, S., and K. Gotthard. 1998. Plasticity in life-history traits. Annu. Rev. Entomol. 43: 63–83.

Powell, J. A., and J. A. Logan. 2005. Insect seasonality: circle map analysis of temperature- driven life cycles. Theor. Popul. Biol. 67: 161–179.

Presgraves, D. C. 2002. Patterns of postzygotic isolation in Lepidoptera. Evolution 56: 1168–1183.

Pureswaran, D. S., and J. H. Borden. 2003. Is bigger better? Size and pheromone production in the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae). J. Insect Behav. 16: 765–782.

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). Ecol. Monogr. 53: 27–49.

Reid, R. W. 1962. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of Br. Columbia. II. Behaviour in the host, fecundity, and internal changes in the female. Can. Entomol. 94: 605–613.

Roff, D. 1980. Optimizing development time in a seasonal environment: the ups and downs of clinal variation. Oecologia 45: 202–208.

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations, pp. 77–84. *In* A. A. Berryman, G. D. Amman, and R. W. Stark (eds.), Symposium Proceedings: Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. 25–27 April 1978, Moscow, ID, University of Idaho Forest, Wildlife and Range Experiment Station, Moscow, ID.

Safranyik, L., A. L. Carroll, J. Regniere, D. W. Langor, W. G. Riel, T. L. Shore, B. Peter, B. J. Cooke, V. G. Nealis, and S. W. Taylor. 2010. Potential for range expansion of mountain pine beetle into the boreal forest of North America. Can. Entomol. 142: 415–442.

Sturgeon, K. B., and J. B. Mitton. 1986. Allozyme and morphological differentiation of mountain pine beetles *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae) associated with host tree. Evolution 40: 290–302.

Wood, S. L. 1982. The bark and ambrosia beetles of North and Central America (Coleoptera: Scolytidae), a taxonomic monograph. Great Basin Nat. 6: 1–1359.

Received 30 October 2012; accepted 25 February 2013.