Evol Ecol
DOI 10.1007/s10682-011-9474-x

ORIGINAL PAPER

Genetic architecture and phenotypic plasticity of thermally-regulated traits in an eruptive species, *Dendroctonus ponderosae*

Barbara J. Bentz · Ryan R. Bracewell · Karen E. Mock · Michael E. Pfrender

Received: 20 August 2010 / Accepted: 14 March 2011

Abstract Phenotypic plasticity in thermally-regulated traits enables close tracking of changing environmental conditions, and can thereby enhance the potential for rapid population increase, a hallmark of outbreak insect species. In a changing climate, exposure to conditions that exceed the capacity of existing phenotypic plasticity may occur. Combining information on genetic architecture and trait plasticity among populations that are distributed along a latitudinal cline can provide insight into how thermally-regulated traits evolve in divergent environments and the potential for adaptation. *Dendroctonus ponderosae* feed on *Pinus* species in diverse climatic regimes throughout western North America, and show eruptive population dynamics. We describe geographical patterns of plasticity in *D. ponderosae* development time and adult size by examining reaction norms of populations from multiple latitudes. The relative influence of additive and non-additive genetic effects on population differences in the two phenotypic traits at a single temperature is quantified using line-cross experiments and joint-scaling tests. We found significant genetic and phenotypic variation among *D. ponderosae* populations. Simple additive

B. J. Bentz (✉)
US Forest Service, Rocky Mountain Research Station, 860 N. 1200 E., Logan, UT 84321, USA
e-mail: bbentz@fs.fed.us

R. R. Bracewell
Department of Ecosystem and Conservation Sciences, University of Montana, 32 Campus Drive, Missoula, MT 59812, USA
e-mail: ryan.bracewell@umontana.edu

K. E. Mock
Wildland Resources Department, Utah State University, 5230 Old Main Hill, Logan, UT 84322, USA
e-mail: karen.mock@usu.edu

M. E. Pfrender
Department of Biology, Utah State University, 5305 Old Main Hill Road, Logan, UT 84322-5305, USA
e-mail: michael.pfrender.1@nd.edu

M. E. Pfrender
Department of Biological Sciences, 109B Galvin Life Science Center, Notre Dame, IN 46556, USA

Published online: 27 March 2011

genetic variance was not the primary source of the observed variation, and dominance and epistasis contributed greatly to the genetic divergence of the two thermally-regulated traits. Hybrid breakdown was also observed in F_2 hybrid crosses between northern and southern populations, further indication of substantial genetic differences among clinal populations and potential reproductive isolation within *D. ponderosae*. Although it is unclear what maintains variation in the life-history traits, observed plasticity in thermally-regulated traits that are directly linked to rapid numerical change may contribute to the outbreak nature of *D. ponderosae*, particularly in a changing climate.

Keywords Adult size · Bark beetle · Climate change · Development time · Mountain pine beetle · Reaction norm

Introduction

Latitudinal clines in phenotypic traits within and among insect species are widespread (Nylin et al. 1989; Gilchrist and Partridge 1999; Fox et al. 2004; Gibert et al. 2004). Because critical physiological processes in insects are thermally regulated (Taylor 1981), temperature is considered a major environmental factor influencing variability in morphological and life history traits along clines. Temperature effects on individual fitness traits such as development time can have significant population-level consequences by influencing synchrony among individuals, and between individuals and their environment. For example, synchrony of individual development time with the seasonal rhythm of the thermal environment can increase population survival by ensuring that cold-tolerant life-stages are present during winter (Danilevskii 1965), and by synchronizing emergence time among individuals, which ultimately affects mate-finding efficiency (Calabrese and Fagan 2004). Furthermore, nutrition acquisition in many insect herbivores relies on thermally-regulated synchrony between insects and their host plant phenology (Hunter and Elkinton 2000; van Asch and Visser 2007). Selection pressures that maintain appropriate synchronization of individuals under varying environmental conditions may therefore influence observed patterns of thermally-regulated fitness traits among latitudinally-separated populations (Roff 1992; Stearns 1992).

Variability in fitness-related traits among populations, including developmental timing, can be due to genetic differences, variation in environmental conditions among populations, or a combination of the two. Genetic sources of variation include simple additive components whereby the contributions of allelic effects to the final phenotype are independent. However, genetic effects may also include non-additive effects resulting from allelic and genic interactions. These non-additive genetic effects include dominance and epistatic interactions, and along with additive effects they can influence the magnitude and rate of evolutionary change in response to selection (Lair et al. 1997; Bradshaw and Holzapfel 2000). Strong selection on non-additive traits reduces the overall additive component of the genetic variance (Roff and Emerson 2006). Further, dominance and epistasis increase the risk of inbreeding depression, which can reduce fitness and increase the probability of local extinction when population size is small (Roff and Emerson 2006; Keller and Waller 2002). The genetic architecture of a trait, i.e., a description of allelic and genic interactions that influence trait variation, is therefore an important consideration when characterizing the genetic basis of trait differences among populations.

Phenotypic variation may also be influenced by environmental factors. Phenotypic plasticity, or the capacity of a given genotype to produce different phenotypes in different

environments, can itself be a heritable trait and therefore be important in evolutionary divergence among populations and adaptation to local environments (Via and Lande 1985; Gotthard and Nylin 1995; Lardies and Bozinovic 2008). Although phenotypic plasticity is an important mechanism for coping with novel or variable environments (Latta et al. 2007; Scoville and Pfrender 2010), there are limits to plastic responses (DeWitt et al. 1998). Adaptation to temperature increases associated with climate change (IPCC 2007) will be an important aspect of long-term population persistence. Knowledge of the direction and amount of plasticity in thermally-regulated traits, along with an understanding of the genetic architecture underlying trait variance, can provide insight into population-level adaptive potential in insect species with large geographic ranges that are experiencing climate changes. Latitudinal clines in thermally-regulated traits provide a natural framework within which to examine the genetic architecture and plasticity of traits in response to selection (Sgro and Blows 2003).

Dendroctonus ponderosae Hopkins (Coleoptera: Curculionidae, Scolytinae), the mountain pine beetle, is a phytophagous, eruptive insect species with an expansive range extending across western North America from southern California to central British Columbia. *Dendroctonus ponderosae* feed on the inner bark (i.e., the phloem) of all *Pinus* species within their range, and reproduction and offspring development typically results in death of the host tree. Over the past decade, *D. ponderosae* have caused tree mortality extending across millions of hectares throughout western North America. Suitable pine hosts extend to the north and south of the current *D. ponderosae* range, suggesting that climate is a constraint to population success. Outbreaks have become more widespread in recent years, and are currently found in areas where outbreak populations either were not recorded or were recorded only infrequently (Gibson et al. 2008; Safranyik et al. 2010).

Temperature is an important driver of physiological and reproductive rates in *D. ponderosae* and can have significant effects on survival and fitness (Bentz et al. 1991; Raffa et al. 2008). Annual thermal patterns can influence *D. ponderosae* survival by inducing appropriate verses inappropriate cold hardiness (Régnière and Bentz 2007), and by controlling developmental rates and ultimately adult emergence timing (Logan and Bentz 1999). Emergence timing is a major selection pressure in the field, as it is an important determinant of whether the number of adults attacking individual trees are sufficient to overcome host defences for successful reproduction (Powell and Bentz 2009). Body size is also strongly influenced by temperature (Atkinson 1994) and is a correlate of egg size and fecundity in *D. ponderosae* (Reid 1962; Elkin and Reid 2005). Given that the geographic range of this insect extends across pronounced latitudinal and elevational thermal gradients, it is not surprising that clinal phenotypic variability has been observed in important temperature-dependent traits such as developmental timing, cold hardiness, and body size (Sturgeon and Mitton 1986; Logan et al. 1998; Bentz and Mullins 1999; Bentz et al. 2001). However, the amount of plasticity and the underlying genetic architecture contributing to these clinal differences has not been investigated.

Our research focuses on *D. ponderosae* development time and adult size, traits that are targets of selection in seasonal environments. We investigate *D. ponderosae* trait plasticity by examining reaction norms of populations from multiple latitudes, including the southern most locale of the current distribution. Reaction norms describe the set of phenotypes expressed by a single genotype across a range of environmental conditions, and are representative of the amount of plasticity a genotype is able to express (Stearns 1992). We then describe the relative influences of additive and non-additive genetic variation on population differences in the two phenotypic traits at a single temperature, using line-cross experiments and joint-scaling tests (Mather and Jinks 1982). The joint-scaling test is a

goodness-of-fit test of observed generation-specific means (e.g., parents, F_1, F_2) to expected generation means derived from genetic models containing additive, dominance, digenic epistatic, and maternal effects. Combining information on genetic architecture and trait plasticity provides insight into the pattern and factors involved in historical divergence of thermally-regulated traits among *D. ponderosae* populations, and the complex relationships among genetic and environmental factors driving population response to temperature. This knowledge has important implications for understanding and predicting trends and geographic patterns in population success in a changing climate.

Methods

Thermal patterns at *D. ponderosae* collection sites

Dendroctonus ponderosae construct galleries under the bark of *Pinus* trees where they lay eggs and their offspring feed and develop. Hundreds of attacking adults can infest an entire tree which is subsequently killed by the feeding action of larval offspring. *Dendroctonus ponderosae* populations were collected by felling infested trees at four geographically-separated sites in 2004 (Table 1). The local thermal environment at each site was described using daily maximum and minimum temperature acquired from four National Climatic Data Center (NCDC) stations (www.ncdc.noaa.gov) (Table 2) for the 5 years prior to collection of *D. ponderosae*-infested trees. Biosim (Régnière and St-Amant 2007) was used to model daily temperatures at each collection location using NCDC weather station data. Heat units (number of degree days $\geq$10°C) and cold units (number of degree days $\leq$0°C) were calculated for each site and summed by month. Monthly values were then summed by season (Winter = December–February; Spring = March–May; Summer = June–August; and Fall = September–November).

Investigation of trait plasticity using reaction norms

Dendroctonus ponderosae from field-cut infested trees collected from each site (Table 1) were reared in the laboratory at room temperature ($\sim$22°C). Adult beetles from each population were collected as they emerged from under the bark of infested tree bolts. Adult beetles were randomly selected during the entire emergence period to maximize sampling of genotypes. Sex was determined for each adult using characteristics of the 7th tergite (Lyon 1958). Male/female pairs were manually inserted into fresh bolts (38 cm) cut from a live

Table 1 Collection information for sampled *D. ponderosae* populations

Closest city	Elevation (m)	Location	Host tree	Abbreviation
Stanley, ID	2,088	N 44.14157 W −114.89354	*Pinus contorta*	ID
Deadwood, SD	1,961	N 43.81669 W −103.7666	*P. ponderosa*	SD
Big Bear Lake, CA	2,127	N 34.26277 W −116.91289	*P. monophylla*	CA1
Idyllwild, CA	1,720	N 33.7692 W −116.74491	*P. lambertiana*	CA2

Table 2 National climatic data center stations used for predicting temperatures at each *D. ponderosae* collection location listed in Table 1

Station name	State	Location	Elevation (m)
Stanley	ID	N 44.22 W −114.93	1,911
Custer	SD	N 43.77 W −103.62	1,670
Big Bear Lake	CA	N 34.25 W −116.90	2,060
Idyllwild Fire Dept.	CA	N 33.75 W −116.70	1,639

lodgepole pine (*Pinus contorta* Dougl.) on the Wasatch-Cache National Forest, UT. For each mating pair, a small hole was drilled into the phloem layer on the cut-side of the bolt, and the female and male manually inserted into the hole. A small piece of mesh fabric was fixed over the hole to prevent adult escape and the bolt was turned vertically upright to allow upward movement of adults through the phloem. In *D. ponderosae* mating occurs within the phloem, followed by egg gallery construction and oviposition. Ten to 15 adult pairs were introduced into each bolt, depending on bolt circumference, with equal distance among all male/female insertions. Each population was allowed to develop at room temperature ($\sim$22°C) in the common host (*P. contorta*) to minimize potential maternal effects due to food source. All subsequent laboratory generations were also reared in this host tree species.

We used a common garden environment to describe reaction norms for the four *D. ponderosae* populations. Adult emergence from laboratory populations (2nd generation in the laboratory) was monitored daily, and to maximize sampling of genotypes, a random sample from across the emergence distribution of each population was chosen to begin the next generation. Two live, uninfested *P. contorta* were felled on the Wasatch-Cache National Forest, UT and cut into bolts (38 cm) for rearing the next generation of beetles. Adults from each population were manually inserted as described previously into four bolts randomly chosen from each live tree (eight bolts total per population) and placed at room temperature for 7 days to allow initial ovipositional gallery development. Two bolts (one bolt from each tree) infested with adults from each population were then placed in one of four constant temperatures: 12.5°C, 17.5°C, 22.5°C, 27.5°C until development was complete. Caging material was placed around each bolt to allow collection of emerging adult beetles. Emerged adults at all temperatures were collected daily and sorted by population. Total development time was estimated for each individual as the difference between emergence date and the date when each bolt was initiated with male/female matings. Total development time includes the time required for oviposition, larval, pupal and teneral adult development, and includes time required for maturation feeding of the adult prior to emergence through the outer bark. Pronotal width was measured and gender determined for each beetle before storing at 2°C in petri dishes with distilled water-moistened filter paper for use in further laboratory generations. Pronotal width has been found to be a good proxy for adult size in beetles because it is highly correlated with weight (Kozol et al. 1988).

In *D. ponderosae*, lifestage-specific temperature thresholds influence the timing of phenological events (Bentz et al. 1991; Powell et al. 2000). Variability in traits that control each event will ultimately produce variability in total development time and adult emergence timing among individuals. Therefore, variability among individuals in total development time, in addition to the median, can be important in describing differences among populations

and rearing temperatures. The interquartile range (IQR) is a measure of dispersion that is equal to the difference between the third and first percentiles in a time series of data, is considered a robust estimate of the middle spread, and can be used for comparisons among data sets (Ott 1977). IQR was calculated for each population by temperature combination. Mixed model analyses were used to test for differences in adult size, total development time, and IQR of development time among all populations at each rearing temperature. Random effects included rearing tree (i.e., tree-1 or tree-2), temperature × population × rearing tree, and temperature × population × rearing tree × sex. Differences among populations and within temperature treatment were tested with Tukey's Honestly Significant Difference multiple comparison procedure, and were based on Tukey-adjusted p-values with a 0.05 threshold (SAS Institute, Cary, North Carolina, USA, version 9.1.3).

Investigation of genetic architecture using line-cross analysis

The contribution of additive and non-additive genetic effects to observed differences in adult size and total development time between populations was estimated from parent and hybrid phenotypic means and variances (Bradshaw and Holzapfel 2000). Adults from three *D. ponderosae* populations (CA1, SD, and ID) reared in a common host at 22°C (see above) were included in the line-cross analysis. The CA1 population is from the southernmost edge of the current *D. ponderosae* distribution, the SD population is from the eastern edge of the range, and ID was collected from a latitude similar to SD, although situated in a central position within the species' range (Table 1). These populations characterize a substantial portion of the range of thermal conditions experienced by *D. ponderosae*. Adults from each population were randomly selected from across the emergence distribution and mated within populations as described above. Adults from each population were also crossed to produce F_1 and F_2 generations and two backcross generations (B_1, B_2) following the same procedure. Reciprocal crosses to test the influence of parental sex on trait inheritance patterns were established for the F_1 crosses only. Two fresh lodgepole pine bolts with 10 to 15 male/female mating introductions per bolt, spaced equidistantly around the circumference of the bolt to maintain a consistent density, were used for each cross. All bolts were kept in the laboratory at room temperature ($\sim$22°C) and adult emergence monitored daily. Total development time and pronotal width, by sex, were determined for each emerged adult as described previously.

The joint-scaling test is a goodness-of-fit test of observed generational means to the generational means expected if the parents differ in additive, dominance, or other genetic effects. Means and variances of total development time and adult size of progeny resulting from crosses between any two parental populations were used in the test. A weighted least-squares model was used to fit observed generational means and variances of total development time and adult size to the expected means and variances by assuming only additive effects or additive and dominance effects. If observed additive and dominance effects are significantly different from expected values, epistasis is inferred. Model parameters were estimated (Mather and Jinks 1982, Lair et al. 1997) as follows:

$$\hat{x} = (C'E^{-1}C)^{-1}C'E^{-1}y$$

$$Var(\hat{x}) = (C'E^{-1}C)^{-1}$$

$$\hat{y} = C\hat{x}$$

where $\hat{x}$ is the vector of mean (m), additive (d), dominance (h), additive × additive epistasis (i) and additive maternal (d_m) parameters, C is the matrix of coefficients for the parameters from equations for predicted line means (Table 3), C' is the transpose, E^{-1} is a diagonal matrix of error variances of the line means (squared phenotypic standard error), and $\hat{y}$ is the vector of predicted line means representing the parents (P_1 and P_2), the F_1 and its reciprocal (F_1R), F_2, and the first and second backcross (B_1, B_2) (Table 3). Matlab (The MathWorks, Inc.) was used for matrix analyses.

The observed generational means were first used to estimate parameters of a model that contained only a generational mean and additive effects. These parameters were then used to calculate expected generation means. Chi-square analysis was used to test the goodness of fit between observed and expected generation means as:

$$\chi^2 = y'E^{-1}y - y'E^{-1}\hat{y}$$

A significant χ^2 indicated a significant difference between observed and expected means, implying that an additive only model was not sufficient to explain the data. If the additive model was not sufficient to explain differences in observed and expected means, additional parameters were added, beginning with dominance, then additive maternal effects, and additive × additive epistasis. The significance of each additional parameter was tested using a χ^2. Degrees of freedom were calculated as the number of generation means minus the number of parameters. A 7-parameter model (i.e., P_1, P_2, F_1, F_1R, F_2, B_1, B_2) was possible in our study. Acceptance of the full model would indicate that additive, dominance, maternal and epistatic effects were adequate to account for genetic divergence in total development time and/or adult size. Rejection of this model would indicate that genetic divergence between the two parental populations crossed also involved effects that were not measured, including higher order epistatic interactions.

Results

Thermal patterns at *D. ponderosae* collection sites

Modeled ambient air temperature at the four collection locations was used to calculate heat units (≥10°C) and cold units (≤0°C) by season over a 5 year period. In all seasons, ID was

Table 3 Parameter coefficients used in model for expected generation means between two populations (i.e., P1, P2), based on notation in Mather and Jinks (1982)

		m	d	h	d_m	i
P_1	ID, SD, or CA1	1	1	0	1	1
P_2	ID, SD, or CA1	1	−1	0	−1	1
F_1	$P_1 \times P_2$	1	0	1	1	0
F_1R	$P_2 \times P_1$	1	0	1	−1	0
F_2	$(P_1 \times P_2) \times (P_1 \times P_2)$	1	0	0.5	0	0
B_1	$P_1 \times (P_1 \times P_2)$	1	0.5	0.5	1	0.25
B_2	$P_2 \times (P_1 \times P_2)$	1	−0.5	0.5	−1	0.25

Observed generation mean (m), additive (d), dominance (h), additive maternal (dm), additive × additive epistasis (i)

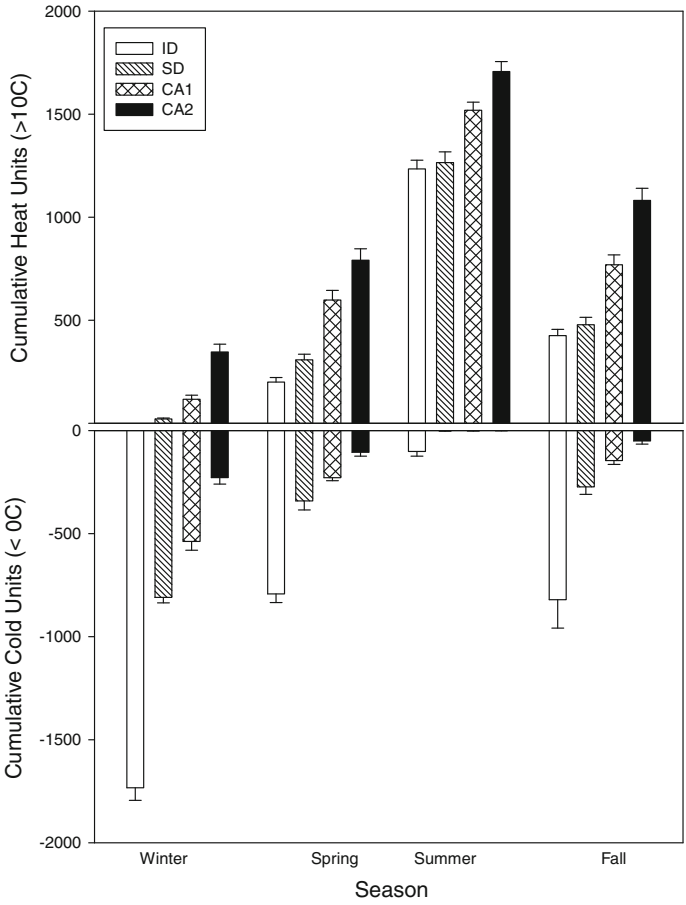

Fig. 1 Modeled cumulative heat units (≥10°C) and cold units (≤0°C) (±SE) by season (1999–2004) at four *D. ponderosae* collection sites (Table 1)

the coolest and CA2 was the warmest (Fig. 1). The two southern sites (CA1 and CA2) were warmer than both northern sites (SD and ID) in all seasons (Fig. 1).

Investigation of trait plasticity using reaction norms

Reaction norms show that effects due to the environment (temperature), genetics (population), and their interaction affect *D. ponderosae* adult size (Fig. 2). Temperature, sex, population, the temperature × population interaction, and the sex × population interaction were all significant in explaining adult size (Table 4). A significant effect due to population source suggests that part of the variation in size is genetic, in addition to some amount of genetic variation in size plasticity, as evidenced by a significant temperature × population interaction. Females were significantly larger than males in all populations at 17.5°C and 22.5°C (Table 4). Due to low male emergence, this relationship was not tested at 27.5°C. Male verses female sizes were not significantly affected by temperature. Adult size at 17.5°C was significantly larger than adult size at 22.5°C in all populations except CA1

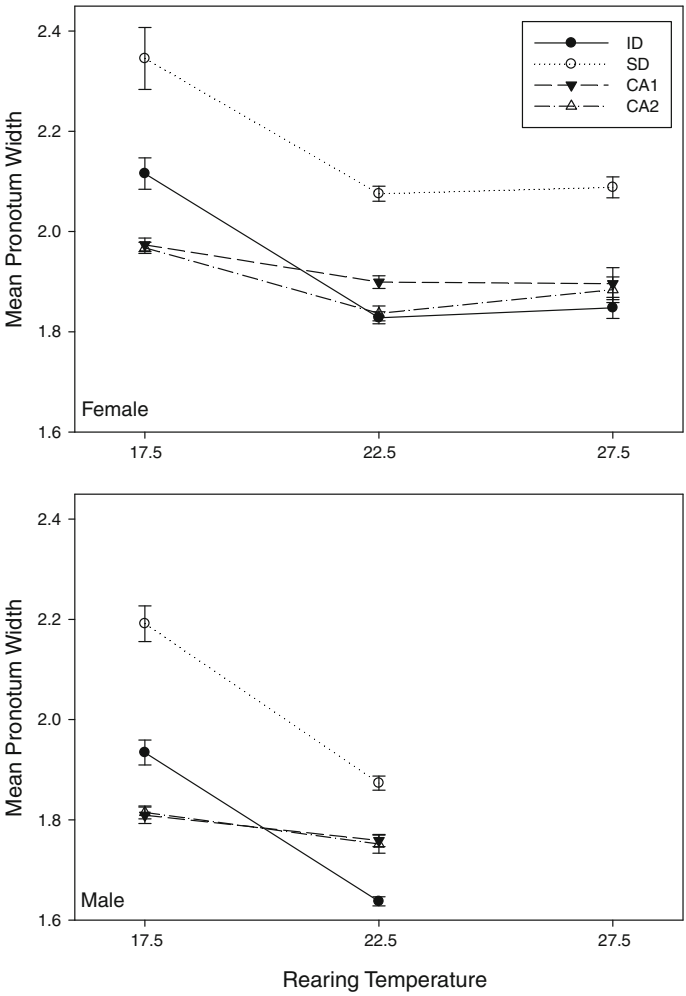

Fig. 2 Mean (±SE) pronotum width of female and male *D. ponderosae* from four locations (Table 1) reared at three constant temperatures (°C) in a common garden environment. Male size at 27.5°C is not shown due to low emergence at this temperature (see Table 5)

(ID: $t_9 = 10.93$, $P < 0.0001$; CA2: $t_9 = 4.28$, $P = 0.0420$; SD: $t_9 = 8.37$, $P = 0.0004$) (Fig. 2). Adult size at 22.5°C was not significantly different than size at 27.5°C in any population. The two southern populations were significantly smaller than both northern populations at 17.5°C, and at all temperatures SD adults were significantly larger than adults from all other populations (Table 5).

No emergence was observed within 160 days for any *D. ponderosae* population maintained at a constant 12.5°C. Less than five individuals from each population emerged after that time, and these individuals were not considered in this analysis. Required temperature thresholds for pupation that are greater than 12°C (Safranyik and Whitney 1985; Bentz et al. 1991) most likely resulted in the reduced emergence. Examination of galleries in these bolts after 160 days showed that the majority of individuals were in the pre-pupal stage (data not shown). Although our study was not designed to evaluate offspring

Table 4 Mixed model results testing for differences in *D. ponderosae* adult size, total development time and IQR of development time among four populations reared at 17.5°C, 22.5°C and 27.5°C

Effect	$DF_{num,\ den}$	F	$P > F$
Adult size (pronotum width)			
Temperature	2, 9	94.11	<0.0001
Sex	1, 9	86.86	<0.0001
Population	3, 9	72.27	<0.0001
Temperature × population	6, 9	10.52	0.0012
Total development time			
Temperature	2, 10	78.04	<0.0001
Population	3, 10	17.70	0.0003
Temperature × population	6, 10	10.69	0.0007
IQR of development time			
Temperature	2, 10.06	10.13	0.0039
Population	3, 10.05	3.32	0.0647
Temperature × population	6, 10.04	6.95	0.0040

Due to low male emergence at 27.5°C, only data from 17.5°C and 22.5°C are included in size analyses

Table 5 Female and male adult pronotum size (mm) from four *D. ponderosae* populations (Table 1) reared at three constant temperatures

Rearing temperature/ population	Female mean size (SD), N*	Male mean size (SD), N*	Number emerged (male: female ratio)
17.5°C			
ID	2.12 (0.17), $28^{a,b}$	1.93(0.12), $25^{a,b}$	53 (1:1.12)
SD	2.35 (0.27), $19^{a,b}$	2.19(0.13), $14^{a,b}$	33 (1:1.36)
CA1	1.97 (0.13), 89^{a}	1.81(0.14), 70^{a}	159 (1:1.27)
CA2	1.97 (0.11),105^{b}	1.81(0.12), 84^{b}	189 (1:1.25)
22.5°C			
ID	1.83 (0.12), 100^{a}	1.64(0.09), $91^{a,b}$	191 (1:1.10)
SD	2.08 (0.14), $89^{a,b}$	1.87(0.10), $54^{a,b}$	143 (1:1.65)
CA1	1.90 (0.13), 113^{a}	1.76(0.11), 88^{a}	201 (1:1.28)
CA2	1.84 (0.12), 70^{b}	1.75(0.14), 57^{b}	127 (1:1.29)
27.5°C			
ID	1.85 (0.12), 31^{a}	1.65(0.06), 4	35 (1:7.75)
SD	2.09 (0.10), $24^{a,b,c}$	0.0(0.00), 0	24 (0)
CA1	1.91 (0.12), 16^{b}	1.74(0.12), 5	21 (1:3.20)
CA2	1.89 (0.08), 10^{c}	1.88(0.17), 2	12 (1:5.00)

Also shown are the total number of individuals that successfully emerged at each temperature and the male: female sex ratio. Ten to 15 adult pairs were introduced into each bolt, depending on bolt circumference, with equal distance among all male/female insertions (2 bolts per population per temperature). Statistical tests were not performed on male size at 27.5°C due to the low number of male adults that emerged at this temperature

* Means with same letter (i.e., a, b or c) within a temperature are different at $P < 0.05$

production, at 17.5°C the total number of emerged adults from the two southern populations (CA1, CA2) was approximately 75% greater than emergence from the two northern populations (ID, SD) (Table 5). These results also suggest a role for latitudinally-varying thermal thresholds in the completion of a lifecycle and successful adult emergence. The number of emerged adults at the warmest rearing temperature (27.5°C) was low for all populations, suggesting a heat tolerance threshold, and sex ratios were highly skewed toward females (Table 5). Although sex ratios of *D. ponderosae* are known to be female-skewed (Amman and Cole 1983), reduced survival of male *D. ponderosae* at 27.5°C may be due to stressful conditions. Males have previously been shown to have an increased susceptibility to stress relative to females (Amman and Pace 1976).

The reaction norms show that *D. ponderosae* total development time and within-population temporal distribution of development time (i.e., IQR) are affected by environmental (temperature) and genetic (population) factors (Figs. 3, 4). Temperature, population,

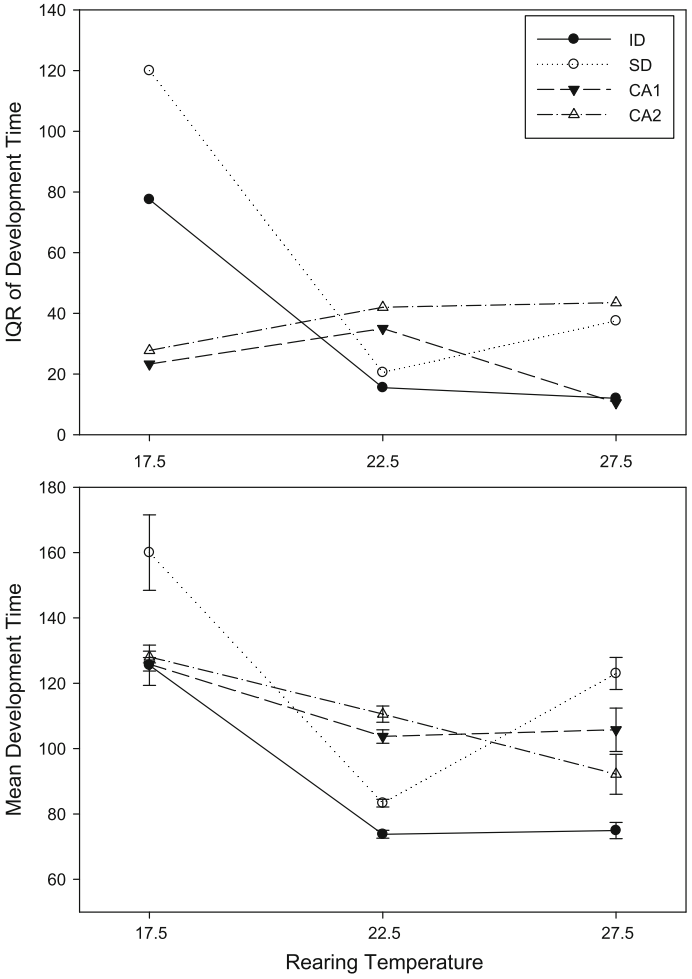

Fig. 3 Reaction norms of IQR of development time (*top*) and mean development time (±SE) (*bottom*) of *D. ponderosae* collected from four locations (Table 1) and reared at three constant temperatures (°C) in a common garden environment

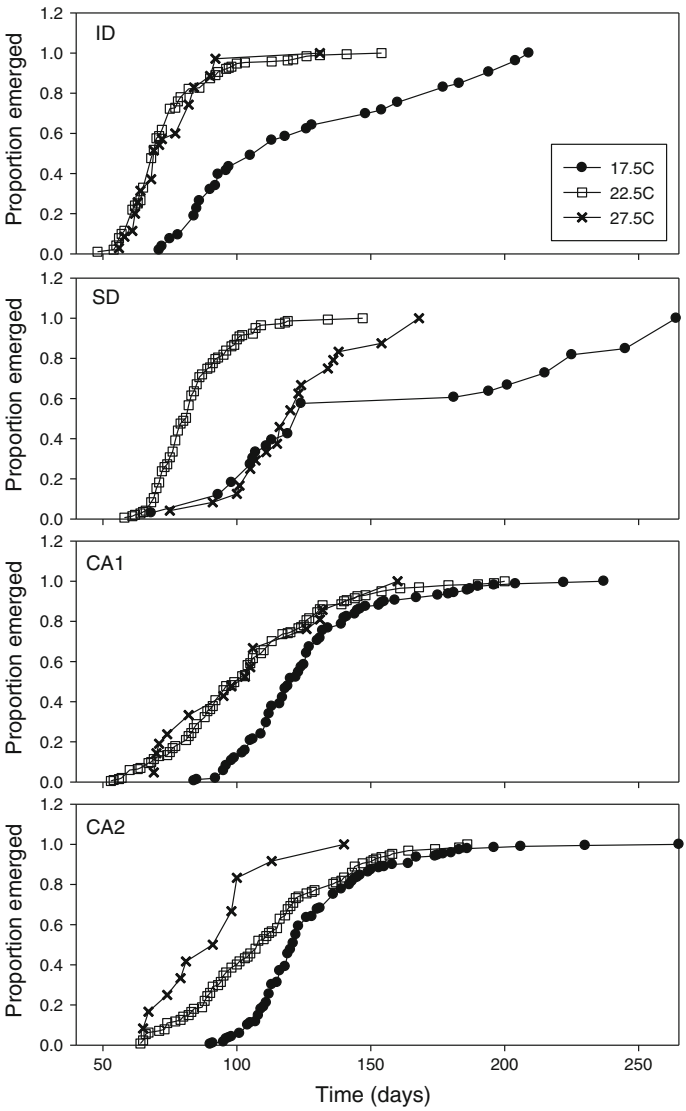

Fig. 4 Cumulative emergence distribution of four *D. ponderosae* populations (Table 1) reared at three constant temperatures (°C). Time in days is the total time required to develop from oviposition to adult emergence

and the population × temperature interaction were all significant in explaining differences in development time, although sex was not (Table 4). Population source was a significant effect, indicating a genetic component to variation in development time, as well as genetic variation for plasticity as evidenced by a significant temperature × population effect. Variability among populations due to temperature ($F_{2,10} = 78.04$) was much greater than that due to source population alone ($F_{3,10} = 17.70$). Differences in IQR among temperatures and the population × temperature interaction were also significant, suggesting that the variability is due to plasticity and genetic variation for that plasticity (Table 4). Total

development time of all populations was longest at the coolest temperature (17.5°C), and the development time for SD beetles at this temperature was significantly longer than all other populations (ID: $t_{12.65} = -4.29$, $P = 0.0278$; CA1: $t_{10.02} = -4.51$, $P = 0.0193$; CA2: $t_{9.87} = 4.33$, $P = 0.0258$). The temporal distribution of development time (i.e., IQR) for SD beetles was also significantly higher than for CA1 ($t_{10.26} = -5.12$, $P = 0.0125$) and CA2 ($t_{10.26} = -4.89$, $P = 0.0171$) beetles at this temperature (Figs. 3, 4). At 22.5°C, both northern populations (ID, SD) developed significantly faster than the two southern populations (CA1, CA2) (ID × CA1: $t_{6.28} = -5.80$, $P = 0.0024$; ID × CA2: $t_{6.79} = -6.00$, $P = 0.0018$; SD × CA1: $t_{6.80} = 4.02$, $P = 0.0434$; SD × CA2: $t_{7.38} = -4.23$, $P = 0.0304$). In both northern populations, IQR was significantly greater at 17.5°C than 22.5°C (ID: $t_{10} = 4.06$ $P = 0.0531$; SD: $t_{10.26} = 5.26$, $P = 0.0103$) and 27.5°C (ID: $t_{10} = 4.29$; $P = 0.0393$; SD: $t_{10.26} = 4.39$, $P = 0.0344$). Although the IQR was smaller in both northern populations than in the southern populations at 22.5°C, differences were not significant. The steep reaction norms in both ID and SD suggest a greater phenotypic plasticity relative to southern (CA1, CA2) populations.

Investigation of genetic architecture using line-cross analysis

All crosses between the two northern populations, ID and SD, and a southern population, CA1, produced fewer than 11 F_2 hybrids, suggesting severe hybrid breakdown (Table 6). These crosses were replicated and hybrid breakdown was again observed with few individuals produced.

In none of the hybrid crosses were differences in development time and adult size adequately explained by a simple additive model, and additional parameters were needed to improve model fit (Table 7) (Fig. 5). In all crosses, models including dominance (*h*) and additive maternal effects (*dm*) remained highly significant for both development time and adult size. When epistatic effects were included, development time in the ID × SD and SD × CA1 crosses, and adult size of the SD × CA1 cross, were adequately described (i.e., a non significant χ^2). All other crosses remained significantly different for development

Table 6 Generation sample size (number of adults emerged) for line-cross analyses of three *D. ponderosae* populations (see Table 1 for population identification). Ten to 15 adult pairs were introduced into each bolt, depending on bolt circumference, with equal distance among all male/female insertions (2 bolts per cross)

Generation—cross	Sample size
F_1—ID × SD	485
F_1—ID × CA1	468
F_1—SD × CA1	383
B_1—(ID × SD) × ID	211
B_2—(ID × SD) × SD	158
B_1—(ID × CA1) × ID	315
B_2—(ID × CA1) × CA1	141
B_1—(SD × CA1) × SD	312
B_2—(SD × CA1) × CA1	280
F_2—ID × SD	303
F_2—ID × CA1	5
F_2—SD × CA1	10
Parent—ID	875
Parent—SD	331
Parent—CA1	340

Table 7 Estimates of composite genetic effects contributing to differences in total development time (at 22.5°C) and adult size between *D. ponderosae* populations from Idaho (ID), South Dakota (SD) and southern California (CA1) (see Table 1)

Phenotype	Parameter estimate	Cross		
		ID × SD	ID × CA1	SD × CA1
Development time	m	104.02***	108.28***	110.38***
	d	−2.33***	−5.66***	−5.91***
	h	−22.59***	−20.39***	−26.27***
	dm	−2.54***	−4.36***	1.30***
	i	−29.34	−28.80***	−26.36
	χ^2	0.0001 NS	47.01***	1.31 NS
Adult size	m	2.180***	2.3217***	2.274***
	d	−0.107***	−0.0042***	0.0868***
	h	−0.0881***	−0.4117***	−0.1361***
	dm	−0.0203***	−0.0054***	0.0263***
	i	−0.1457***	−0.4333*	−0.1989
	χ^2	82.16***	5.89*	0.04 NS

χ^2 values were calculated using models that included parameter values shown for each cross

Observed generation mean (m), additive (d), dominance (h), additive maternal (dm), additive × additive epistasis (i)

NS not significant

*** Significant at $P < 0.001$, * $P < 0.05$

time and adult size with the inclusion of epistatic effects (Table 7) suggesting higher order interactions are required to explain the observed generational means.

F_2 hybrids produced from the SD × ID cross had development times that were much longer than values observed for all other generations in this cross (Fig. 5). Although only 10 F_2 were produced from the SD × CA1 cross, these individuals also showed prolonged development time relative to parental means (data not shown), and backcross hybrids produced in the other crosses also displayed longer development times than either parent. Extreme phenotypes in body size of both backcross hybrids was only observed in the ID × CA1 cross (Fig. 5).

Discussion

Our results show significant genetic and phenotypic variation among *D. ponderosae* populations in development time and body size, and suggest that dominance and epistasis have contributed to genetic divergence of these important thermally-regulated traits. Observed hybrid breakdown in F_2 hybrid crosses between northern and southern populations is also an indication of epistatic interactions among loci. Reaction norms show that the degree of plasticity in both traits is greatest in the two northern populations. Additionally, genetic variation in the plastic responses of both development time and adult size were observed, indicating that plasticity in these traits could be the target of selection and contribute to increased fitness under varying thermal environments (Via and Lande 1985).

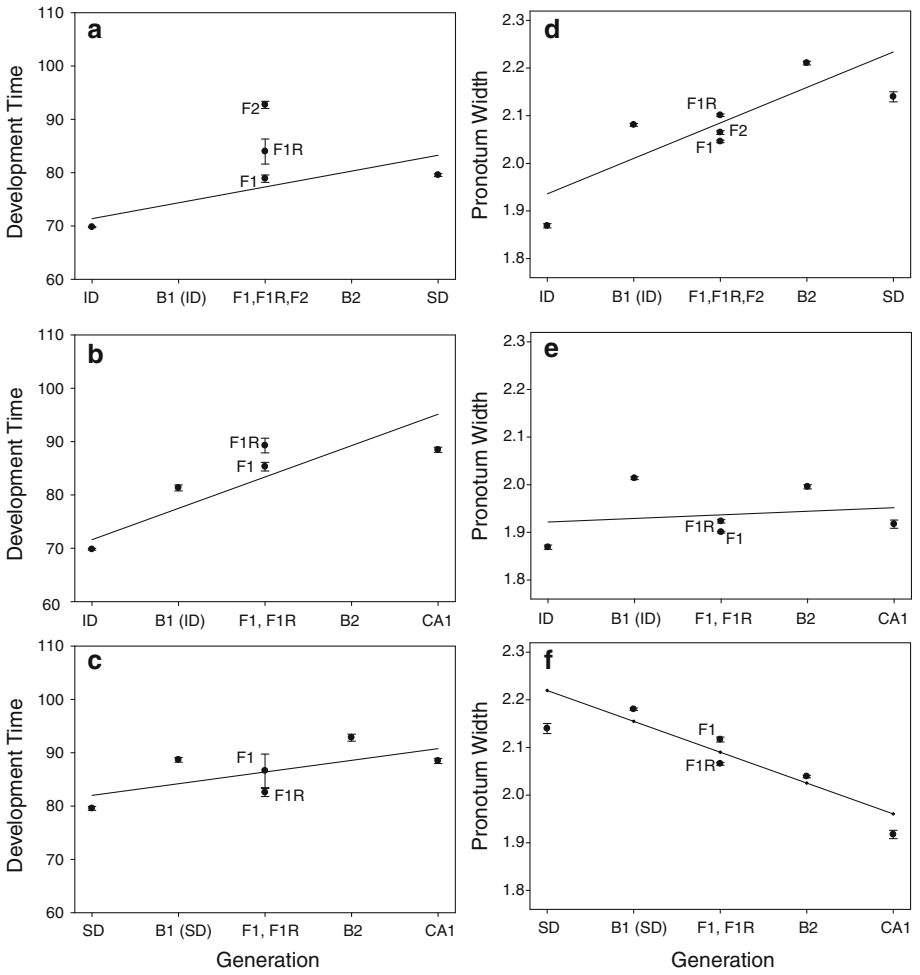

Fig. 5 Observed parent and hybrid development time (mean ± 2 SE) (**a–c**) and adult size (pronotum width, mm) (mean ± 2 SE) (**d–f**) for three *D. ponderosae* population crosses: **a, d** ID × SD; **b, e** ID × CA1; and **c, f** SD × CA1 (Table 1). Generations shown are parents (SD, ID, CA1), F_1, F_1 reciprocals (F1R), F_2, and backcrosses to both parents [B1 (backcross parent) and B2]. The *regression line* shown on each graph is the weighted least-squares estimate of a simple genetic model with only the overall mean and additive effects, incorporating all of the generation means. Less than 10 individuals were produced in F_2 hybrid crosses between both northern populations (ID, SD) and CA1; these data are not shown

Our results support previous studies that show phenotypic plasticity is a genetic and heritable trait in insects (Ellers and Driessen 2010).

Body size and development time are phenotypically correlated traits, often considered positively correlated for the simple reason that longer development time should produce larger adult size (Stearns 1992; Roff 1992). Within a population, individuals reared at the lowest temperature in the common garden were larger than those reared at the two warmer temperatures, which is consistent with the temperature-size rule that higher temperatures result in smaller individuals (Atkinson 1994). However, progeny of beetles collected from both the coolest (ID) and warmest (CA2) geographic sites were often the smallest in

laboratory rearings, and progeny of populations collected from similar latitudes (ID and SD) were dramatically different in size at all common garden temperatures. Each source population was field-collected from a different host tree (Table 1) and varying climatic regime (Fig. 1). Potential local adaptation to host tree and climate is therefore confounded, although in the laboratory we reared all population progeny in a common host and common temperature. Our results highlight the complexity of tradeoffs in life-history traits (Kingsolver and Huey 2008). Because both size and development time are controlled in part by temperature, selection on one trait will produce a response in the other, but the joint response to selection will depend on the environment to which each population has become adapted. Due to this adaptation, processes that decrease development time may not necessarily also decrease body size due to multiple and interactive constraints (Nijhout et al. 2010). Our results suggest complex phenotypic tradeoffs in *D. ponderosae* traits that are not linear across the large thermal range that this species occupies.

Tradeoffs in size and development time were also found to be sexually dimorphic. Males from each population were significantly smaller than their female counterparts at all rearing temperatures, although there were no significant differences in mean development time between the sexes at any rearing temperature. Females attained a larger size than males within a similar amount of development time, suggesting an increased growth rate for females. Differential allocation of energy to fitness characters between the sexes has also been found in other insect systems (Holloway et al. 1993). Because increased growth rate can translate into enhanced net reproductive rate via greater fecundity and egg size, increased female size, relative to male counterparts, is thought to evolve via fecundity selection on females (Honek 1993). Indeed, previous research has shown that larger female *D. ponderosae* oviposit larger eggs than smaller females (Elkin and Reid 2005). Males attained a smaller body size by the final adult stage, suggesting that temperature may have a stronger effect on development time than on growth rate in this sex (Kingsolver and Huey 2008). Sexual size dimorphism is widespread among plants and animals (Fairbairn 1997), although the evolution of this trait in *Dendroctonus* has not been adequately described (Reid and Baruch 2010). The consistent differences we observed among populations and temperatures do suggest that selection, at least on thermally-regulated traits, may differ between the sexes.

Temperature contributed to substantial variation among populations in development time although source population was also significant, suggesting roles for both phenotypic plasticity and genetic variation in latitudinal clines of *D. ponderosae* development traits. At 22.5°C both northern populations developed significantly faster and with less temporal spread among individuals than the two southern populations, similar to results found by Bentz et al. (2001). However, at warmer and cooler temperatures than 22.5°C the relationships among latitudinally-separated populations differed. In addition to a significant population × temperature interaction, these results suggest substantial genetic variation for plasticity in development traits among populations. Because synchrony in emergence is important to the mass attack process that facilitates successful host tree entry in this species (Logan and Bentz 1999), emergence timing can be a strong selection factor in the field and similarity among individuals within a population in developmental-timing traits can be advantageous. It has been suggested that faster development equates to higher fitness and that selection will act strongly to increase that rate (Taylor 1981). If localized adaptation to annual temperature regimes is also considered, however, optimal developmental timing may not necessarily be the fastest. Thermal windows for important fitness traits likely evolve to be as narrow as possible at a given locale to minimize physiological costs (Pörtner and Farrell 2008). If we assume that the optimum is a lifecycle duration of single

year (Logan and Bentz 1999), our results suggest that time constraints in growth season have selected for fast development rates of one or more lifestages in more northern latitudes and slow rates or different developmental thresholds in southern latitudes, thereby ensuring a generation is completed annually in both climates.

In replicated experiments, F_2 crosses between the two northern populations (ID and SD) and a southern population (CA1) produced fewer than 11 individuals. Evidence of such severe hybrid breakdown suggests that there are substantial genetic differences between populations, and that some populations could be in the early stages of differentiation and species formation. Indeed, subsequent mating of several *D. ponderosae* populations from along a latitudinal gradient found reproductive isolation in the form of hybrid male sterility (Bracewell et al. 2010). Genetic differences among the populations, as evidenced by divergent reaction norms, could not be explained by simple additive genetic models. Non-additive effects resulting from allelic and genic interactions underlie the variation observed in thermally-regulated traits between all *D. ponderosae* populations in this study, including the two populations that produced offspring with severe hybrid breakdown. High levels of dominance and epistatic genetic variation were also found in comparable studies between *Wyeomyia smithii* populations collected from across a latitudinal gradient (Lair et al. 1997) and between *Drosophila melanogaster* populations exposed to environmental stress (Blows and Sokolowski 1995). The evolution of epistatic interactions is more likely when populations have been isolated for some time, thereby limiting gene flow (Whitlock et al. 1995), although increased geographic distance between populations is not always a direct correlate with epistasis (Schiffer et al. 2006). Our finding that trait variance between *D. ponderosae* populations has a significant epistatic component is consistent with the clinal variation in gene flow described by Mock et al. (2007). Moreover, Pleistocene glacial refugia of several *D. ponderosae* host tree species have been found, revealing genetically differentiated host tree populations that are currently separated by relatively small geographic distance (Richardson et al. 2002; Godbout et al. 2008). Our populations were collected from habitats that varied climatically, and epistatic variance in thermally-regulated traits may also result from these differences, irrespective of geographic distance. The fact that we find differences in mean phenotype and genetic architecture between *D. ponderosae* populations suggests that population divergence has involved a complex set of genetic interactions and potentially different genes, with variable contributions to the ultimate phenotype (Gilchrist and Partridge 1999).

Even under conservative estimates, mean temperature is projected to increase 2–4°C during this century (IPCC 2007), leading to warmer winters, longer growing seasons, and new challenges and opportunities for species that rely on thermally-regulated traits for population success (Bradshaw and Holzapfel 2008; Bentz et al. 2010). Phenotypic plasticity can allow close tracking of changing environmental conditions, and thereby enhance the potential for rapid numerical increase, a hallmark of outbreak species such as *D. ponderosae* (Barbosa and Baltensweiler 1987). Populations may be increasingly exposed to conditions, however, that exceed the capacity of existing phenotypic plasticity to maintain developmental synchrony with environmental conditions. Although it is clear that changes in temperature result in phenotypic changes in *D. ponderosae* population trait values, the potential for corresponding changes at the genetic level are currently unknown. Studies that use a combination of classic quantitative genetics and high-throughput genomic approaches to detect adaptive changes will provide substantial insight into climate change-induced evolutionary responses of eruptive species like *D. ponderosae*, and enhance our ability to predict future population persistence.

Acknowledgments Jim Vandygriff and Matt Hansen provided invaluable assistance with collection of *D. ponderosae*-infested trees and laboratory rearing of beetles. We thank Alan Dymerski for collection of the South Dakota population, and Laura Merrill for help locating the California populations. The USDA Forest Service, Rocky Mountain Research Station and Forest Health Monitoring contributed funding for this research.

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