

Latitudinal variation in *Dendroctonus ponderosae* (Coleoptera: Scolytidae) development time and adult size

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Abstract—*Dendroctonus ponderosae* (Hopkins) is widely distributed across western North America, feeding in at least 12 native species of *Pinus* L. (Pinaceae). We investigated the existence of heritable differences in two life-history parameters (adult size and development time) of *D. ponderosae* from a northern population (central Idaho, *Pinus contorta* Douglas ex Loudon) and a southern population (southern Utah, *Pinus ponderosa* Douglas ex P. and C. Lawson). We attempted to separate heritable from environmental effects by rearing individuals from both populations through two generations (F_1 and F_2) in a common standardized laboratory environment with a constant temperature. Two treatment effects were tested for in the F_2 generation: (1) geographic location (source host) for F_0 *D. ponderosae*; and (2) the F_2 brood host. We hypothesized that, if differences were observed and the F_0 source host and region had a greater effect on F_2 brood development time and adult size than did the host in which F_2 brood were reared, a heritable factor related to the F_0 parents was responsible. Time to emergence was significantly shorter for second-generation offspring of the northern population than for second-generation offspring of the southern population, regardless of the F_2 brood host. Although both the F_2 brood host and F_0 source parents were significant in explaining differences observed in the developmental-time distribution of F_2 brood, the F_0 source effect was found to be much greater. Also, F_2 males and females from southern source parents were significantly larger than F_2 brood from northern source parents when reared in both F_2 brood hosts. Geographic region and original host of F_0 source parents had a significant effect on F_2 offspring size, whereas the immediate food for F_2 brood was not significant in explaining differences. These results suggest genetically based regional differences in *D. ponderosae* populations.

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Résumé—*Dendroctonus ponderosae* (Hopkins) a une vaste répartition dans l'ouest de l'Amérique du Nord où il se nourrit d'au moins 12 espèces indigènes de *Pinus* (L.) (Pinaceae). Nous avons cherché les différences héritables de deux variables démographiques (taille des adultes et durée du développement) chez des *D. ponderosae* d'une population nordique (*Pinus contorta* Douglas ex Loudon du centre de l'Idaho) et d'une population australe (*Pinus ponderosa* Douglas ex P. et C. Lawson du sud du Utah). Nous avons essayé d'isoler les effets héritables des effets comportementaux en élevant des individus des deux populations pendant deux générations (F_1 et F_2) dans un environnement standardisé de laboratoire à température constante. Deux effets ont été testés chez la génération F_2 : (1) la position géographique (hôte d'origine) des coléoptères de F_0 et (2) l'hôte sur lequel la F_2 a été élevée. S'il y a des différences et que l'hôte d'origine et la région géographique de la F_0 ont un

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effet plus grand sur la durée du développement et la taille des adultes que les hôtes de la F_2 , nous posons en hypothèse qu'un facteur héritable relié aux parents de la F_0 est responsable. Le temps écoulé entre la ponte et l'émergence chez les rejetons de la F_2 de la population nordique était significativement plus court que celui enregistré chez les rejetons de la population australe, indépendamment de l'hôte d'élevage de la F_2 . Bien que les hôtes de F_2 et ceux de la génération parentale F_0 contribuent à expliquer de façon significative les différences observées dans le déroulement du développement de la F_2 , l'effet de l'hôte d'origine de la F_0 est beaucoup plus important. De plus, les mâles et femelles de F_2 issus des parents de la population australe étaient de taille significativement plus grande que ceux de la population nordique chez les deux hôtes sur lesquels la F_2 a été élevée. La région géographique et l'hôte d'origine de la génération F_0 ont un effet significatif sur la taille des rejetons de la F_2 , alors que la nourriture immédiate des individus de F_2 ne peut expliquer significativement les différences. Ces résultats reflètent probablement l'existence de différences régionales génétiques entre les populations de *D. ponderosae*.

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Introduction

Widely distributed insect species must adapt to varying environmental conditions along latitudinal and elevational gradients. Individuals within a species will often respond phenotypically to the local environment, and may display a variety of life-history traits (Nylin and Gotthard 1998). Many intraspecific physiological traits, such as development rate, diapause intensity, and body size, frequently exhibit geographic clines (Masaki 1967, 1978; Tauber *et al.* 1988; Ayres and Scriber 1994; Gomi and Takeda 1996). The observed differences among regions or populations may be heritable owing to long-term genetic differentiation or may merely be a direct physiological response to environmental factors such as temperature (Baldwin and Dingle 1986; Blanckenhorn 1997). Separating the differential effects due to heritable and environmental causes of phenotypic variation is vital to understanding population differentiation among geographic regions.

The mountain pine beetle *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), a cambial feeder, is widely distributed across western North America both latitudinally and elevationally. Adults are capable of successfully reproducing in at least 12 North American species of *Pinus* L. (Pinaceae), from southern British Columbia to Baja California (Wood 1982). Although strong geographical genetic differentiation, as determined from allele frequencies, was observed among *D. ponderosae* populations in Alberta (Langor and Spence 1991), others observed little allelic variation among geographically separated populations (Stock and Amman 1980; Stock *et al.* 1984; Sturgeon and Mitton 1986). It remains unclear if the species is composed of regionally adapted populations or if the *D. ponderosae* genotype is geographically robust with local phenotypic adaptations driven by the seasonal environment.

Regional and population differences in several *D. ponderosae* attributes that may be correlated with fitness have been reported. These include development time and brood production (Amman 1982; Langor 1989; Cerezke 1995), body size (Sturgeon and Mitton 1986; Logan *et al.* 1998), cold hardening (Bentz and Mullins 1999), and the timing of adult flight. Differences among regional and population traits have often been attributed to the host species within which larvae develop, or have been considered to be due simply to environmental differences among habitats. For example, brood production was found to be greater in ponderosa pine (*Pinus ponderosa* Douglas ex P. and C. Lawson) and limber pine (*Pinus flexilis* James) than in lodgepole pine (*Pinus contorta* Douglas ex Loudon) (Amman 1982; Langor 1989; Cerezke 1995). Logan *et al.* (1998) attributed differences in larval size to the host in which larvae were reared, although in

their study, collections from ponderosa pine came only from the southern portion of the *D. ponderosae* distribution, whereas collections from lodgepole pine came from the north. The effect of host and latitudinal distribution was, therefore, confounded. More recently, Logan and Bentz (1999) hypothesized that differences in developmental rates should vary as a function of latitude. They came to this conclusion through computer-simulation predictions of an adaptive seasonality that spanned a thermal range of approximately 2.5°C. They hypothesized that, to maintain an adaptive seasonality, populations from northern regions of the *D. ponderosae* distribution should require less time to develop at a given temperature than populations from southern regions. Increased time to complete a life stage concurrently implies increased size (Hilbert 1995; Roff 1980). The results of Logan and Bentz (1999), therefore, provide an alternative hypothesis for increased size and slower development that is based on latitudinal rather than host (nutritional) differences.

In this study, we attempted to test this hypothesis, and investigated whether heritable differences in development time and adult size exist between two populations of *D. ponderosae*, one from lodgepole pine in central Idaho (northern population) and one from ponderosa pine in southern Utah (southern population). We attempted to separate heritable from environmental effects by rearing individuals from the two populations in a common standardized laboratory environment with a constant temperature. If the differences that were observed between northern and southern populations in their respective geographic locations are minimized, then we can conclude that the life-history variation reflects phenotypic responses to local conditions. The alternative hypothesis, that differences between the populations are due to heritable effects, would be supported if differences in development time and adult size were maintained in the common laboratory environment. The extent of such variation among geographically distinct populations is an important factor to consider, especially when attempting to manage insect-related impacts. If there are true differences among *D. ponderosae* populations that are based on either host type or geographic region, it may be necessary to develop individual management strategies and population-prediction and risk models for each region and (or) host type. Our overall objective is to more fully understand the nature of intraspecific variability among *D. ponderosae* populations in different regions.

Methods

Laboratory rearing

Live pines and pines infested with *D. ponderosae* were felled and cut into bolts 38–46 cm long. Bolt ends were sealed with paraffin wax to reduce desiccation, and bolts were stored at 0°C until needed. One live and one infested lodgepole pine were collected from at the Sawtooth National Recreation Area near Stanley, Idaho (44°07'N, 114°51'W) (hereinafter northern-1 population), during May 1998, in an area considered to have a building *D. ponderosae* population. One live and one infested ponderosa pine were collected from the Dixie National Forest near Panguich Lake, Utah (37°30'30"N, 112°37'30"W) (hereinafter southern population), during March 1998, from an area with a declining *D. ponderosae* population. One live and one infested western white pine (*Pinus monticola* Douglas ex D. Don) were collected from the Spotted Bear Ranger District, Flathead National Forest, Montana (48°10'N, 113°50'W) (hereinafter northern-2 population), in September 1997. One live lodgepole pine was collected from the Logan Ranger District, Wasatch Cache National Forest, Utah, in April 1998, and used as the F₁ brood host.

The experimental design included a combination of F_0 source *D. ponderosae* and F_2 brood hosts with a common F_1 brood host, to minimize potential maternal effects (Mousseau and Dingle 1991) (Fig. 1). For each generation–treatment, emergence was monitored every other day and adult *D. ponderosae* were sorted by sex. The pronotal width of each adult was measured using an ocular microscope scale (± 0.025 mm). Adults were randomly paired into male–female combinations. Holes (5 mm) were drilled in the phloem cross-section of live pine bolts, maintaining an equal spacing of 6 cm. Using forceps, a female and male *D. ponderosae* were manually inserted into each predrilled hole, and a mesh screen was stapled over the hole to prevent their escape. A common spacing was used between parent introductions for all bolts, to minimize and standardize the level of competition among brood. All bolts were maintained at room temperature (approximately 21°C) in enclosed containers during brood development. Owing to fungal growth in the green western white pine bolts, we were unable to include this treatment in the F_2 generation; however, F_1 adults from the naturally infested western white pine were introduced into bolts of the two other hosts (Fig. 1).

Data analysis

Rather than statistically compare the number of days to 50% emergence among the treatments, which would mean a loss of the information contained in the shape of the developmental distribution, we used survival analysis (SPSS 1997) to compare the emergence distributions of F_2 adults, testing the effects due to F_0 source parent and F_2 brood host. In this sense, time of emergence is equivalent to survival time. Wald's statistic (W) (Nelson 1982) was used to compare treatment effects. A t test was used to analyze differences in pronotal widths of F_0 adults from the northern-1 and southern source parents ($\alpha = 0.05$). Analysis of variance (ANOVA; S-PLUS 1997) was used to test for significant differences among pronotal widths of adult F_2 *D. ponderosae*. Logistic regression (S-PLUS 1997) was used to compare the proportion of females among treatments. Because there was no complete replicate of the northern-2 population (western white pine) treatment, individuals from this source were not included in the statistical analysis, although they were included in figure graphs for a relative comparison.

Two treatment effects were tested for in the F_2 generation: (1) F_0 source parent geographic location and host; and (2) the F_2 brood host. We hypothesized that, if differences were observed and the F_0 source host and region had a greater effect on F_2 brood development time and adult size than the host in which F_2 brood were reared, a heritable factor related to the F_0 parents was responsible.

Results

Median emergence time was shorter for the F_1 generation from northern-1 source parents (64 d) than for the F_1 generation from southern source parents (82 d) (Table 1). Because all F_0 adults came from naturally infested field populations, these differences in F_1 development time, and differences in development time between F_1 and F_2 adults from the same F_0 source, could reflect either maternal influences, the previous host, or fungal and yeast associates. Parents of all F_2 brood experienced a common environment (lodgepole pine host; 21°C), whereas parents of the F_1 generation came from their respective field environments and hosts.

F_2 brood from the northern populations developed faster than F_2 brood from the southern population, regardless of the brood host (Fig. 2). Results of the survival analysis showed that, although both the brood host and F_0 source parent were significant in explaining differences observed in the developmental-time distribution of F_2 brood, the

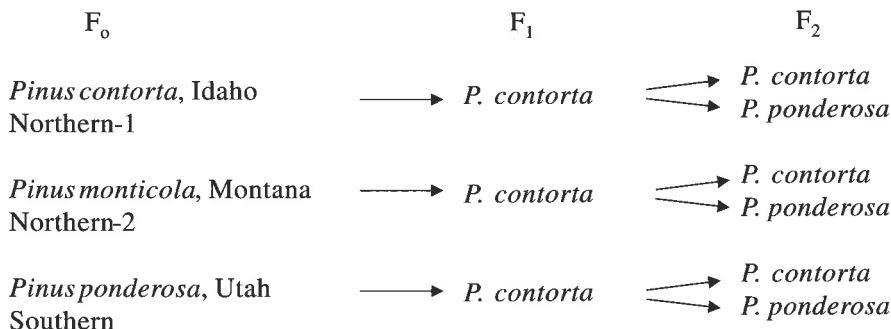


FIGURE 1. Experimental design of *Dendroctonus ponderosae* laboratory rearings using F_0 source parents that were collected from naturally infested trees in the respective geographic locations and reared in *Pinus contorta* in the F_1 generation and either *P. contorta* or *P. ponderosa* in the F_2 generation.

TABLE 1. Median emergence time of F_1 and F_2 *Dendroctonus ponderosae* brood reared at 21°C in two brood hosts; F_0 source parents were from Idaho (northern-1) *Pinus contorta* and Utah (southern) *P. ponderosa*.

F_0 source	Brood host		<i>n</i>	Days to 50% emergence
	F_1	F_2		
Northern-1	<i>P. contorta</i>	—	815	64
	<i>P. contorta</i>	<i>P. contorta</i>	392	57
	<i>P. contorta</i>	<i>P. ponderosa</i>	548	64
Southern	<i>P. contorta</i>	—	421	82
	<i>P. contorta</i>	<i>P. contorta</i>	499	99
	<i>P. contorta</i>	<i>P. ponderosa</i>	415	108

F_0 source effect was much greater ($W = 1489$, $P < 0.0001$ for F_0 source effects compared with $W = 136$, $P < 0.0001$ for F_2 brood host effect). The development time of F_2 offspring of the northern-2 population source parents, reared in both lodgepole and ponderosa pine, was more similar to that of brood from northern-1 population source parents than to that of brood from southern population source parents (Fig. 2).

F_0 adults reared from the southern population were significantly larger than those from the northern-1 population (female: $t_{1070} = -8.7$, $P < 0.0001$; male: $t_{707} = -24.5$, $P < 0.001$) (Fig. 3). Differences in adult size due to F_0 source parent were maintained through two generations in a common laboratory environment. F_2 adults from southern source parents were significantly larger than F_2 adults from northern-1 source parents, when reared in both F_2 brood hosts, as indicated by the significant F_0 source parent term in the ANOVA (Table 2; Fig. 4). Overall, F_2 males were significantly smaller than females from the same F_0 source parent (Table 2; Fig. 4). F_0 source parent (from different latitudes and hosts) had a highly significant effect on F_2 offspring size, whereas the immediate food for F_2 brood was not significant in explaining differences (Table 2). Emergence day and the interaction emergence day $\times$ sex were also highly significant in explaining differences in size among all F_2 brood (Table 2). As emergence time increased, male and female adult size decreased (Fig. 5).

Emergence day, F_0 source parent, and the interaction emergence day $\times$ F_0 source parent were also significant in explaining differences in the proportion of females in F_2

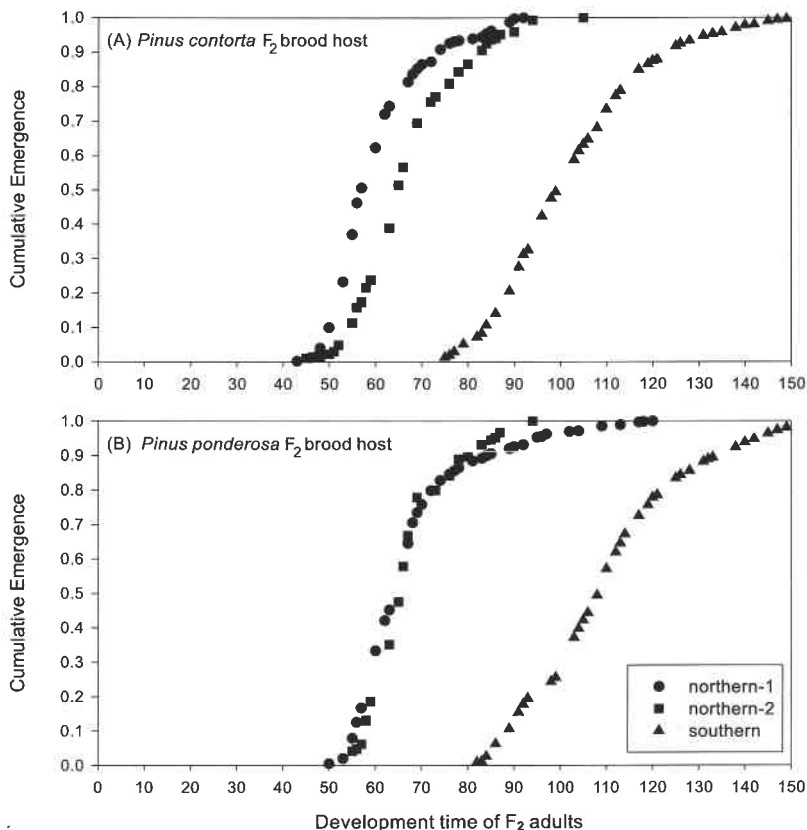


FIGURE 2. Cumulative emergence of *Dendroctonus ponderosae* F₂ offspring from the northern-1, northern-2, and southern source parents raised in *Pinus contorta* (A) and *P. ponderosa* (B).

offspring, whereas F₂ brood host was not (Table 3). The median time to emergence was shorter for females than males among F₂ adults from southern source parents raised in both ponderosa and lodgepole pine (Fig. 6). This trend was not apparent in F₂ offspring from northern-1 source parents.

F₂ offspring from both northern-1 and southern source parents developed significantly faster when reared in lodgepole pine than when reared in ponderosa pine ($W = 75.6$, $P < 0.0001$ for northern-1, and $W = 34.5$, $P < 0.0001$ for southern). When F₂ brood were reared in a host other than the one from which their F₀ parents originally came, adult size was reduced.

Discussion

Temperature is a commonly accepted source of environmentally induced variation in life-history traits that are important components of fitness. By removing temperature as an influencing variable, we have shown that there are genetically based life-history differences among two latitudinally separated *D. ponderosae* populations. In a common environment, differences in adult size and development time were much less affected by the F₂ brood host than they were by the geographic origin and host of the F₀ source parents. Allozyme differences have been found among *D. ponderosae* infesting different

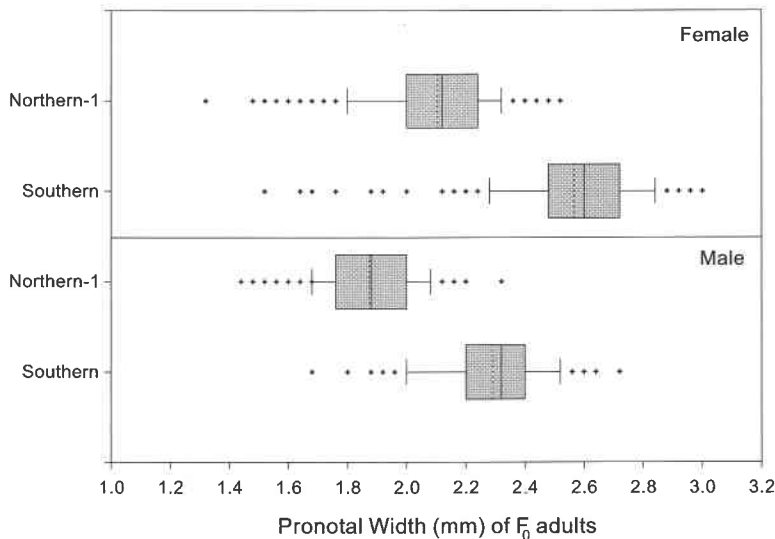


FIGURE 3. Pronotal width of *Dendroctonus ponderosae* F₀ offspring from the northern-1 and southern populations. Boxes represent the 25th (left edge) and 75th (right edge) percentiles. Within the box, the dotted vertical line is the median and the solid vertical line is the mean. Vertical lines outside the box are the 10th (left) and 90th (right) percentiles, and + are outliers.

TABLE 2. Results of ANOVA testing the effect of emergence day, sex, F₀ source parent, and F₂ brood host on F₂ pronotal width of adult *Dendroctonus ponderosae*.

Effect	Coefficient	<i>t</i>	<i>P</i>
Intercept	2.500	121.10	0.0000
Emergence day	−0.005	20.30	0.0000
Sex	−0.230	11.10	0.0000
F ₂ brood host	0.030	1.20	0.2302
F ₀ source parent	0.280	13.56	0.0000
Emergence day × sex	0.001	4.54	0.0000
Emergence day × F ₂ brood host	0.000	0.68	0.4993
Sex × F ₂ brood host	0.005	0.02	0.8200
Emergence day × F ₀ source parent	0.000	0.24	0.8087
Sex × F ₀ source parent	−0.070	3.44	0.0006
F ₂ brood host × F ₀ source parent	0.073	3.60	0.0003
Emergence day × sex × F ₀ source parent	0.000	2.01	0.0446
Emergence day × F ₂ brood host × F ₀ source parent	−0.001	2.78	0.0055
Sex × F ₂ brood host × F ₂ source parent	0.019	0.95	0.3427

hosts (Stock and Amman 1980; Sturgeon and Mitton 1986), although Langor and Spence (1991) observed that the effect due to sex and geographic site on overall *D. ponderosae* shape and size was greater than that due to brood host species. Our results suggest that, although nutritional effects due to the immediate brood host are important at the local level, *D. ponderosae* adult size and development time is more a product of latitudinal region and local selection pressures, such as seasonal temperature, than of the host in which brood are reared. In southern Utah, temperatures are much warmer throughout the growing season than in central Idaho (Bentz and Mullins 1999).

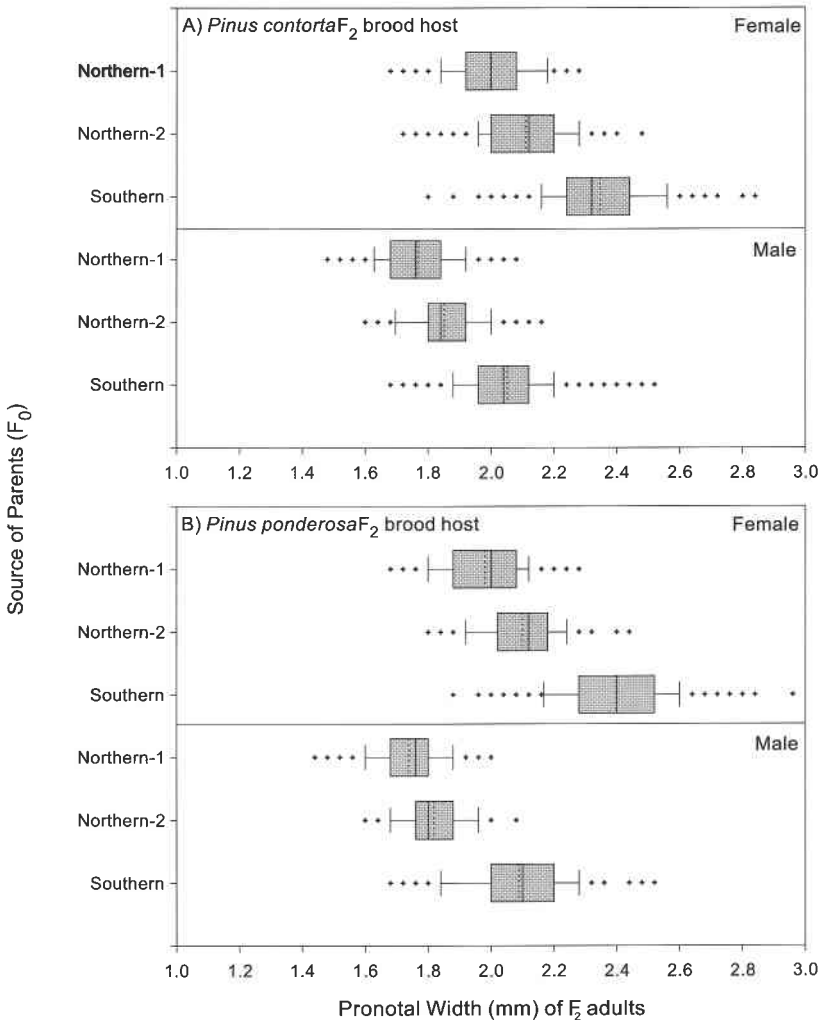


FIGURE 4. Pronotal width of *Dendroctonus ponderosae* F₂ offspring from the northern-1, northern-2, and southern source parents raised in *Pinus contorta* (A) and *P. ponderosa* (B). Boxes represent the 25th (left edge) and 75th (right edge) percentiles. Within the box, the dotted vertical line is the median and the solid vertical line is the mean. Vertical lines outside the box are the 10th (left) and 90th (right) percentiles, and + are outliers.

Selection pressure in the colder environment, where time available for growth is less, would maintain a faster development time. Conversely, in the warmer climate, where the season for development is longer, selection for large size would be stronger.

Our results are consistent with the expectation that adult size and development time decrease with increasing latitude (Masaki 1967, 1972, 1978; Roff 1980; Blanckenhorn 1997). Also, a direct trade-off between the fitness advantages of large size, most notably larger and more eggs (Reid 1962; Amman 1972), and the disadvantage of long development time is common (Nylin and Gotthard 1998). A life-history strategy must be, to some extent, a compromise. Size and development time are inversely related—an organism cannot grow to a large size in a short time. Typically, growth becomes faster and size becomes smaller as the amount of time available for

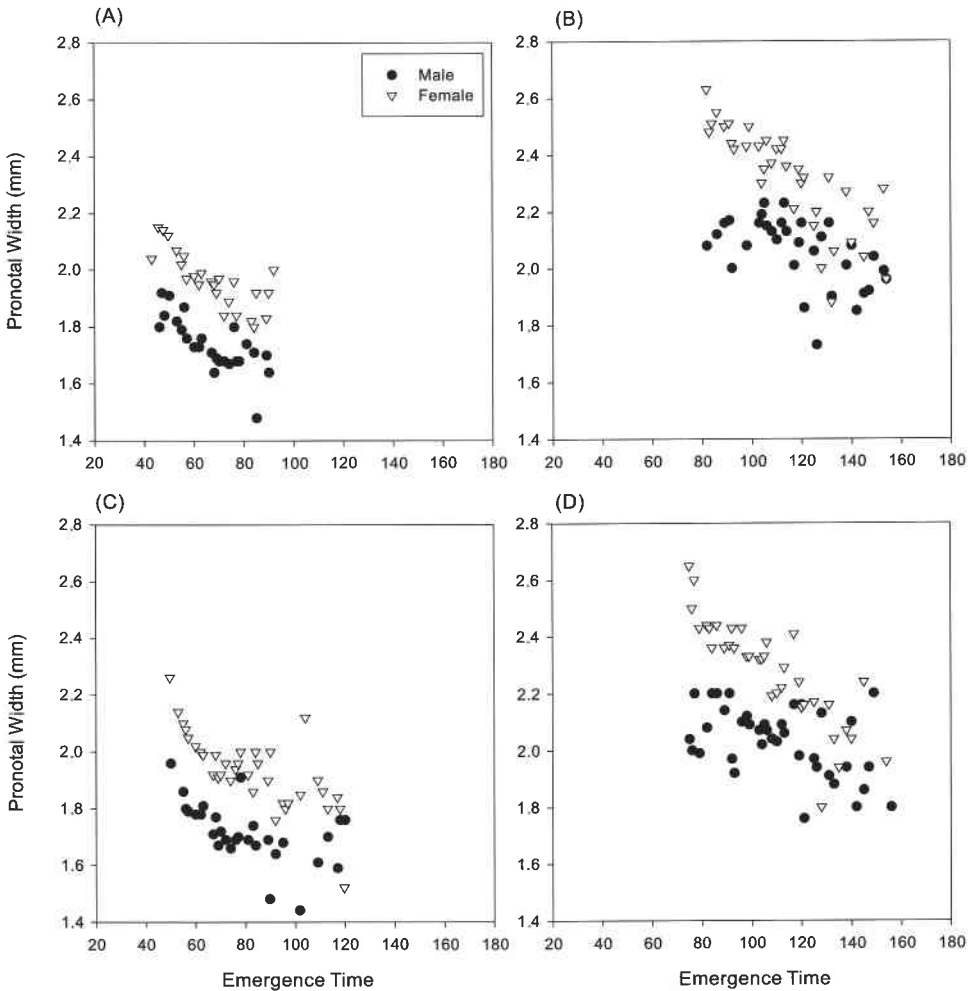


FIGURE 5. The relationship between pronotal width and number of days to emergence for F_2 male and female brood from northern-1 source parents raised in *Pinus contorta* (A), southern source parents raised in *P. ponderosa* (B), northern-1 parents raised in *P. ponderosa* (C), and southern parents raised in *P. contorta* (D).

development decreases (Roff 1980; Atkinson 1994). Results from a phenology model developed for *D. ponderosae* indicate that direct temperature control, resulting in a strong adaptive phenology, may provide a barrier to selection for decreasing generation time in more southern populations, resulting in a trade-off for large size (Logan and Bentz 1999). These results are corroborated in this study. Such trade-offs in fitness-related traits are often more apparent in species such as *D. ponderosae* that have no diapause and rely on direct temperature control for seasonality (Nylin and Gotthard 1998; Logan and Bentz 1999).

Male adults reared in both brood hosts were smaller than females that had come from the same F_0 source parents. Sex-linked size differences are common, and have previously been observed for *D. ponderosae* (Hay 1956; Amman and Cole 1983). Adult offspring from the southern population were always larger than offspring from the

TABLE 3. Results of logistic regression testing the effect of emergence day, F_0 source parent, and F_2 brood host on the proportion of female *Dendroctonus ponderosae* in each treatment.

Effect	Coefficient	<i>t</i>	<i>P</i>
Intercept	3.25	10.10	0.0000
Emergence day	-0.03	7.83	0.0001
F_2 brood host	0.01	0.23	0.8181
F_0 source parent	2.02	6.27	0.0001
Emergence day $\times$ F_0 source parent	-0.02	4.47	0.0001
F_2 brood host $\times$ F_0 source parent	0.11	2.21	0.0272

northern population, whereas adults reared from ponderosa pine were not always larger than those reared from lodgepole pine. Our results are inconsistent with those of Amman (1982), which showed that F_1 offspring of *D. ponderosae* originally from lodgepole pine were larger when reared in ponderosa pine than when reared in lodgepole pine. Amman's study involved only one generation, however, and maternal effects could have influenced the size of F_1 offspring. The larger size of field-collected *D. ponderosae* from ponderosa pine has been noted previously (Logan *et al.* 1998), although direct comparisons with *D. ponderosae* from other hosts in the same geographic region have typically not been made. In a study that did make a direct comparison, Hay (1956) found that the mean length of adults from lodgepole pine in the Sawtooth National Forest in Idaho were shorter (5.09 mm, $n = 200$) than that of adults from ponderosa pine in the Roosevelt National Forest in Colorado (5.64 mm, $n = 141$). Hay also compared mean adult *D. ponderosae* length from both lodgepole (5.39 mm, $n = 142$) and ponderosa (5.52 mm, $n = 128$) pine collected from a site between Idaho and Colorado on the Ashley National Forest in Utah. These adult lengths were intermediate between those from Idaho and Colorado. The gradient in decreasing adult *D. ponderosae* size from south to north observed in our study is consistent with the results of Hay (1956).

For all treatments, size of male and female adults significantly declined over the emergence period (Fig. 5). This was also observed for a wild population of *D. ponderosae* in lodgepole pine in southeastern British Columbia (Safranyik and Jahren 1970) and for a laboratory population reared in limber pine and jack pine (*Pinus banksiana* Lamb.) (Cerezke 1995). One possible explanation is that late emerging individuals develop in a more competitive larval environment than individuals that come from eggs laid early during the 2- to 3-week oviposition phase. Alternatively, when individuals are under a time stress to emerge (*e.g.*, those that emerge late), they may sacrifice final mass to maintain development time within an adaptive time frame (Nylin and Gotthard 1998). Synchronous emergence is important for adults of this species, to insure that tree-host defenses are successfully overcome by a mass attack.

We observed a reduction in adult size and egg-to-adult development time between the southern and northern *D. ponderosae* populations sampled, although both populations were univoltine. Others have found that, as a population moves into habitats that are farther south (*e.g.*, warmer), transition areas where populations shift from a univoltine to a bivoltine life cycle exist. Development time and body size typically decrease in these transition areas and then increase again in more favorable areas (Masaki 1972; Roff 1980). Although no bivoltine populations of *D. ponderosae* have been reported in the literature, by measuring the development time and body size of more southern populations and comparing them with observed development time and body size of southern Utah populations, we may be able to predict those transition areas in which bivoltine populations are possible, especially given predicted climate warming.

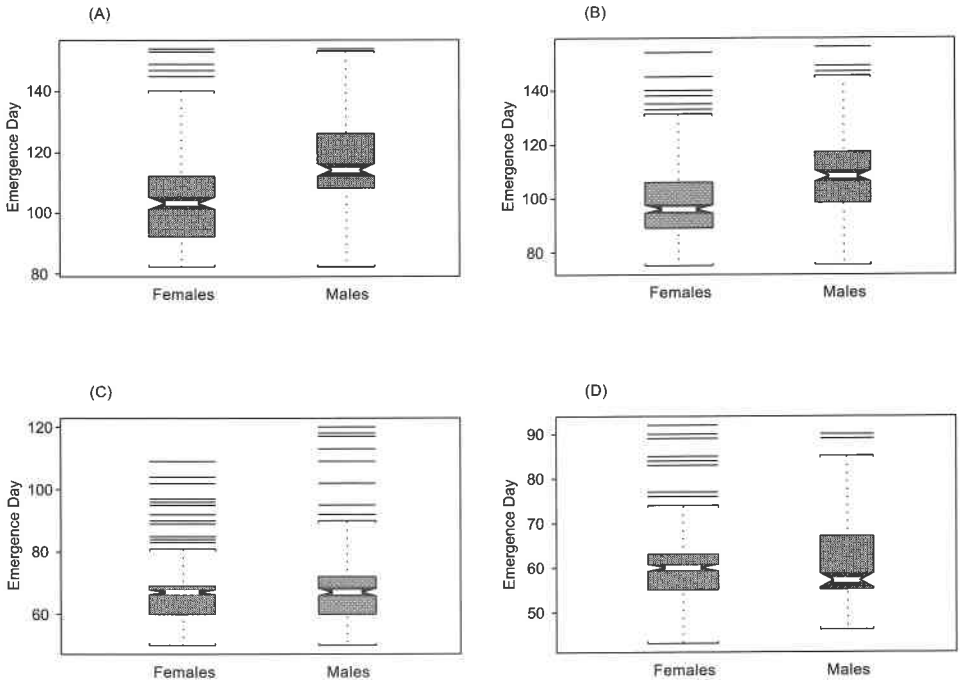


FIGURE 6. Median number (notch) of female and male F₂ adult *Dendroctonus ponderosae* as a function of emergence day. (A) Southern F₀ source parents and *Pinus ponderosa* F₂ brood host. (B) Southern F₀ source parents and *P. contorta* F₂ brood host. (C) Northern-1 F₀ source parents and *P. ponderosa* F₂ brood host. (D) Northern-1 F₀ source parents and *P. contorta* F₂ brood host. Boxes represent the 25th (lower edge) and 75th (upper edge) percentiles, dotted lines include the 10th (below) and 90th (above) percentiles, and horizontal lines represent outliers. Note the difference in scales.

Our data suggest that the *D. ponderosae* species is a composite of regionally adapted populations. Both development time and adult size are heritable traits. It appears that genotypes may be adapting to local thermal regimes along a latitudinal gradient. There may also be temperature-influenced differences among the populations that result in differential response in life-history traits (Baldwin and Dingle 1986). The fact that development rate is heritable, rather than a short-term phenotypic response to temperature, will have important implications for population response to climate warming. Although individuals could respond instantaneously to warmer temperatures, gene-frequency alterations may require longer times, resulting in a delay in population response to global warming. Given the high heritability in development time we observed however, population response to a change in climatic regime could occur in a relatively short evolutionary time scale, even decades.

Certainly, the host species from which brood are reared will have an important nutritional effect on offspring. Five-needle high-elevation pines, including limber, western white, and whitebark (*Pinus albicaulis* Engelm.), have been found to be more favorable than the two- and three-needle pines, lodgepole, jack, and ponderosa, for reproduction, development, and survival of *D. ponderosae* (Amman 1982; Langor 1989; Langor *et al.* 1990; Cerezke 1995). In our study, brood host was found to be significant in explaining differences observed in emergence time, although not in adult size. The effects due to F₀ source host and geographic region were much more significant, suggesting

genetically based regional differences in *D. ponderosae* populations. Our results add to the growing literature base reporting latitudinal differences in insect populations.

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