11. Variation in Two Life History Traits of *Dendroctonus ponderosae* from Lodgepole and Ponderosa Pines in Idaho and Utah

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The polyphagous nature of the mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae), is well documented. Adult mountain pine beetle can successfully reproduce in at least 13 species in the genus *Pinus* (Cerezke 1995, Furniss and Schenk 1969, Wood 1963), although populations are most often found in lodgepole pine, ponderosa pine, limber pine, whitebark pine, and western white pine. In mixed species stands, mountain pine beetle brood may infest a different host species than the one they were reared on, suggesting a preference in host selection (Baker and others 1971, Wood 1963). In a laboratory study in which adult beetles from lodgepole pine were allowed to infest ponderosa, whitebark, western white and lodgepole pine, Amman (1982) observed that brood did best, overall, in ponderosa pine, and poorest in lodgepole pine, despite the fact that parent beetles came from lodgepole pine. Additionally, mountain pine beetle development, survival, and reproduction was greater in limber than in lodgepole pine in an area where both hosts occurred (Langor 1989). Differences in fitness parameters such as larvae size (Logan and others 1998), emergence time (Bentz, unpublished data), and cold-hardiness (Bentz and Mullins, in press) in mountain pine beetles from lodgepole and ponderosa pine in Idaho and Utah have also been documented.

Differential host use has been associated with genetic differentiation in several phytophagous insect species, including the mountain pine beetle (Anderson and others 1979, Edmunds and Alstad 1978, Mitter and Futuyma 1979, Stock and Amman 1980, Sturgeon and Mitton 1986). Stock and Amman (1980) and Sturgeon and Mitton (1986) attributed observed differences in allele frequencies in mountain pine beetles from lodgepole and ponderosa pine to be more associated with host tree species than with geographic distances among the sites. Langor and Spence (1991), however, made the argument that genetic differentiation found among beetles from the two hosts may be due to differential survival of beetle genotypes in response to selection pressures within each host. In this same study they also observed relatively high levels of genetic differentiation among beetles from different sites in Alberta and British Columbia (Langor and Spence 1991). Although past research has shed light on the matter, the question still remains whether the differences in mountain pine beetle fitness and behavioral parameters are due to host factors, environmental factors (for example, temperature), or whether they are based on genetic differences among beetles from the different host species or geographic locations.

We chose to explore this puzzle by rearing mountain pine beetles from different hosts in the laboratory, maintaining a constant environment (temperature and humidity) so that the host the brood was reared in was the only factor varied. Our assumption was that if environment was held constant, any differences observed in fitness parameters between beetles reared in the host they came from or an alternative host could be due to some host-related inherited influence.

Adult beetles from naturally infested lodgepole pine were manually infested into half of a lodgepole pine bolt and half of a ponderosa pine bolt. Likewise, beetles from a naturally infested ponderosa pine bolt were manually infested into the other half of both the lodgepole and ponderosa pine bolts. This resulted in replicates consisting of a brood reared in the host its parents came from and in the alternate host: 1) parents reared in lodgepole pine and brood reared in ponderosa pine {LP®PP}, 2) parents reared in lodgepole pine and brood reared in lodgepole pine {LP®LP}, 3) parents reared in ponderosa pine and brood reared in lodgepole pine {PP®LP}, and 4) parents reared in ponderosa pine and brood reared in ponderosa pine {PP®PP}. Because of the available distribution of naturally infested hosts in the field, beetles came from two geographic regions. Infested lodgepole pine billets were collected from central Idaho, and infested ponderosa pine billets were collected from southern Utah. A male and female pair was initiated into pre-drilled holes in the phloem of each bolt. A consistent spacing between parent galleries was maintained among bolts. Equal replicates of the bolts

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were kept at 17°C and 21°C until brood emergence. Total time for development and pronotum width of emerged adults were measured.

An interaction between temperature and development time was observed, although not consistently across the hosts. The PP®PP brood remained relatively the same size and required, on average, a similar amount of time to develop at both 17°C and 21°C. In contrast, the LP®LP brood required significantly less time to develop at 21°C than at 17°C, and individuals were slightly smaller at 17°C. At 17°C the LP®LP brood individuals were smaller and took longer to develop than the PP®PP brood at the same temperature. At 21°C the LP®LP brood was still smaller than the PP®PP brood, although they developed significantly faster. At both 17°C and 21°C, the LP®PP brood developed faster than did the PP®LP brood. At 21°C, broods from LP®PP and PP®LP were similar in size, although at 17°C the LP®PP brood was smaller than the PP®LP brood.

In summary, individuals with parents from lodgepole pine were always smaller than individuals with ponderosa pine parents, no matter the host they were reared in. Individuals with lodgepole pine parents developed faster when reared in ponderosa pine at 17°C, and were slightly larger when reared at 21°C (as compared to being reared in lodgepole pine at both temperatures). In contrast, individuals with ponderosa pine parents developed slower and were smaller when reared in lodgepole pine at both 17°C and 21°C (as compared to being reared in ponderosa pine). These results indicate that ponderosa pine is a better host for mountain pine beetle in terms of faster development time and larger size. At 21°C, individuals reared in ponderosa pine that came from parents reared in lodgepole pine developed almost 20 days faster than individuals that were reared in ponderosa pine that had parents also from ponderosa pine. Those individuals with ponderosa pine parents were always larger however.

The minimum development time required to complete a generation was approximately 60 days, accomplished by beetles with lodgepole pine parents, reared at 21°C in either lodgepole or ponderosa pine. Beetles with parents from lodgepole pine made more fitness-tradeoffs, reducing adult size for a faster development time when given warmer temperatures or the better food source of ponderosa pine. A trade-off between development time and size at maturity is a common component of life-history models, with current theory involving a trade-off in fitness advantages between obtaining a large size and taking less time to develop through a single generation (Nylin and Gotthard 1998). Although in many situations a faster development time is advantageous, the importance of such fast development time varies, such as in cold vs. warm climates.

Because parent beetles came from different geographic regions, as well as different hosts, it is difficult to separate host differences from regional population differences. Parent beetles collected from lodgepole pine in central Idaho had experienced significantly colder winter temperatures than had those beetles collected from ponderosa pine in southern Utah (Bentz and Mullins, in press). The capacity of a brood from lodgepole pine parents to compromise size for development time could be due to a selection pressure in the colder environment for putting all resources into making sure development occurs in a single generation. In the warmer climate, where parents from ponderosa pine were collected, the developmental season is longer and selection pressure may be greater on the size fitness component. Inheritance of body size has been shown with several insect genera (see Roff 1980), while it is unclear if development time is also an inheritable trait. Although host and regional effects are confounded in this preliminary data, under constant environmental conditions, the source of parent beetles had a significant effect on size and developmental fitness characteristics of first-generation brood adults regardless of the brood host. This suggests a genetic basis to observed differences. These observed differences and tradeoffs in mountain pine beetle fitness components most likely help to maintain the polyphagous nature and widespread distribution of this important bark beetle species.