

EFFECT OF LIFE CYCLE DURATION ON FACTORS
LIMITING SURVIVAL OF THE MOUNTAIN PINE BEETLE

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Introduction

In the western United States, the mountain pine beetle (MPB), Dendroctonus ponderosae Hopkins (Coleoptera: Scolytidae), causes most severe tree killing of lodgepole pine, Pinus contorta var. latifolia Engelmann, growing in stands with significant numbers of trees 80 years or older that are greater than 20 cm in diameter at breast height (dbh). Trees with these characteristics produce the greatest number of beetles per unit area of bark. Equally important, the stands must be growing in locations where temperatures are optimum for beetle development so that development is synchronized with seasonal changes in weather patterns (Amman et al. 1977; Safranyik et al. 1974). In general, survival is best in locations where temperatures are such that the beetle completes development in 1 year (Amman 1973; Safranyik 1978). When the duration of the life cycle extends beyond a year, the prolonged exposure of developing broods to certain mortality factors further reduces survival from that recorded after the first season.

This paper reviews the relative importance of mortality factors known to affect survival of MPB populations at a site in northeastern Utah where the beetle completes development within a year. In addition, major mortality factors affecting populations with 2-year life cycles occurring along an elevational transect in northwestern Wyoming are identified and compared with those determined for populations completing development within a year.

Life Cycle Duration

The effect of weather and climate on the seasonal history and development of the beetle has been summarized for a number of locations in the western United States and Canada (Safranyik et al. 1974; Safranyik 1976; Amman 1973; Amman and Cole 1983; Amman, these proceedings). These findings show the usual 1-year life cycle occurs at elevations below 2,440 m. In infestations at these elevations, new adults emerge in mid-July or early August, with egg hatch following within a week of oviposition. The majority of the ensuing larvae reach the third and fourth stages prior to the onset of cold weather in

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October and November. The larvae remain dormant until warmer temperatures in April allow them to resume feeding until larval development is completed in June. The larvae pupate and transform to adults during late June to mid-July.

At higher elevations, the beetle often requires more than a year to complete a generation. For example, in northwestern Wyoming, measures of rate of development along with elevational transect revealed the beetle had a 1-year life cycle at 1920 and 2,130 m. At 2,450 m, part of the population completed development within a year, but the remainder required a second summer to complete a generation. At elevations between 2,580 and 2,750 m, most beetles required 2 years to complete a generation (Amman 1973). In Canada, Reid (1962) found the MPB usually had one generation per year in Invermere, British Columbia, while in 1956 in Banff National Park, Alberta, beetles required 2 years to complete a generation. Therefore, the duration of the beetle varies from 1 to 2 years because of elevation and latitude or variation in weather from year to year.

The key to life cycle duration appears to be the temperatures during the flight and oviposition periods in August and September. Cool temperatures or rainy weather delay flight, oviposition, and early larval development, so that a large percentage of the brood enters the winter as eggs and first and second stage larvae (Amman 1973; Safranyik 1978). Brood that survive the winter in these stages are usually unable to complete development within a year. Developmental rates of the four life stages, and thereby the duration of the life cycle, are governed by heat accumulation in terms of degree days above a stated temperature threshold (a degree day is 1 degree above the temperature threshold for 24 hours). Powell (1967) found development from egg to new adult required 348 degree days above 10°C, as measured in the bole of the tree. A second year is required to complete a generation when heat accumulations fail to reach this threshold during the first year of development.

Evaluation of Mortality Factors

To be an effective mortality factor, Amman and Cole (1983) suggested the factor should cause a departure from expected survival and emergence as predicted from phloem thickness. An effective mortality factor would then lessen the total number of trees killed or slow the expected rate of tree killing.

To evaluate the relative effectiveness of mortality factors common to MPB, life table samples were taken for 13 years from MPB populations in Montana, Idaho, Utah, and Wyoming (Cole 1974, 1975; Amman and Cole 1983; Amman 1984).

Effectiveness of the mortality factors were measured on two 230 cm² samples removed within 30.5 cm of the 1.4, 3.7, and 6.1 m levels from the same trees at four times - October, May, later June, and late July to early August (Carlson and Cole 1965). Trees were stratified by diameter classes: 23 cm dbh and less (trees 30.2 cm dbh); 30.5 cm dbh (trees 30.5 to 37.9 cm dbh); and 38.1 cm dbh and greater. The number of attacks, total length of egg gallery, all stages of the MPB, and associated insects were counted.

Initial MPB densities were established by determining the number of live MPB stages and dead adults in the first (October) sample. Dead stages were assigned to 11 sources of mortality, as follows:

1. Within competition: Mortality was attributed to this factor when two larval mines from the same egg gallery coalesced and only one larva was present, or one of the two larvae was partially consumed.
2. Between competition: Mortality attributed to this factor had the same appearance as the within competition, except the larvae involved were from mines from adjacent egg galleries.
3. Clerids: Larvae of two species, Thanasimus undatulus Say and Enoclerus spegeus F. (Coleoptera: Cleridae), were the most common; additionally, tunnels were present, filled with characteristic bits of phloem left by the larvae as they chew to enlarge MPB larval mines in search of the larva or pupae at the end of the mine.
4. Coeloides: Parasitism by Coeloides rufovariegatus (Provancher) (Hymenoptera: Braconidae) was identified by its characteristic larval form or cocoon at the end of a larval mine.
5. Medetera: The area surrounding larvae killed by the predacious fly Medetera aldrichii Wheeler (Diptera: Dolichopodidae) was surrounded by a characteristic staining likely caused by fungi developing on the MPB remains.
6. Pathogens: Larvae killed by pathogens had normal colour but were

flaccid or less active. In the latter stages of infection, the larvae were often covered with the fungi.

7. Woodpeckers: Predation by woodpeckers, Picoides tridactylus (L.) and P. villosus (L.), was identified by the holes pecked through the bark above larval mines. When bark was chipped off the tree, the number of MPB brood destroyed was estimated by determining the larval densities nearby and noting the area of bark removed.
8. Temperature: Larvae killed by sub-freezing temperatures can be identified by their black colour. The approximate time of death was determined by the degree to which the body had dried and shriveled. If larvae were soft and only partially black, death likely occurred within weeks.
9. Drying of the Phloem: Larvae thought to be dead from drying of the bark were often shriveled and cream-coloured rather than black like those killed by cold temperatures.
10. Pitch: Larvae killed by pitch were found in areas of the bark characterized by particularly tacky accumulations of pitch.
11. Unknown: Dead larvae for which there was no apparent cause of mortality were listed as unknowns.

Major Factors - 1-Year Cycle

Figure 1 shows the relative importance of the mortality factors studied, based on their probability of causing the death of mountain pine beetle brood that complete development within 1 year. The data used to develop these relationships were recorded in an infestation in the Wasatch National Forest in northwestern Utah (Amman and Cole 1983). The infestation level was classified as "high endemic," based on annual tree mortality and beetle survival rates during the 9 years of the study. Analysis of the data revealed that cold winter temperatures and drying of the phloem were the two major causes of mountain pine beetle brood mortality. The results were typical of those observed elsewhere (Cole 1981). The greatest effect of these two agents was on beetles infesting small diameter trees; the least was in large diameter trees. The effect cooler temperatures at the higher elevations have on MPB emergence, and ultimately survival, is shown in Figures 2 and 3. The cooler temperatures delay peak emergence as much as 21 days over that observed

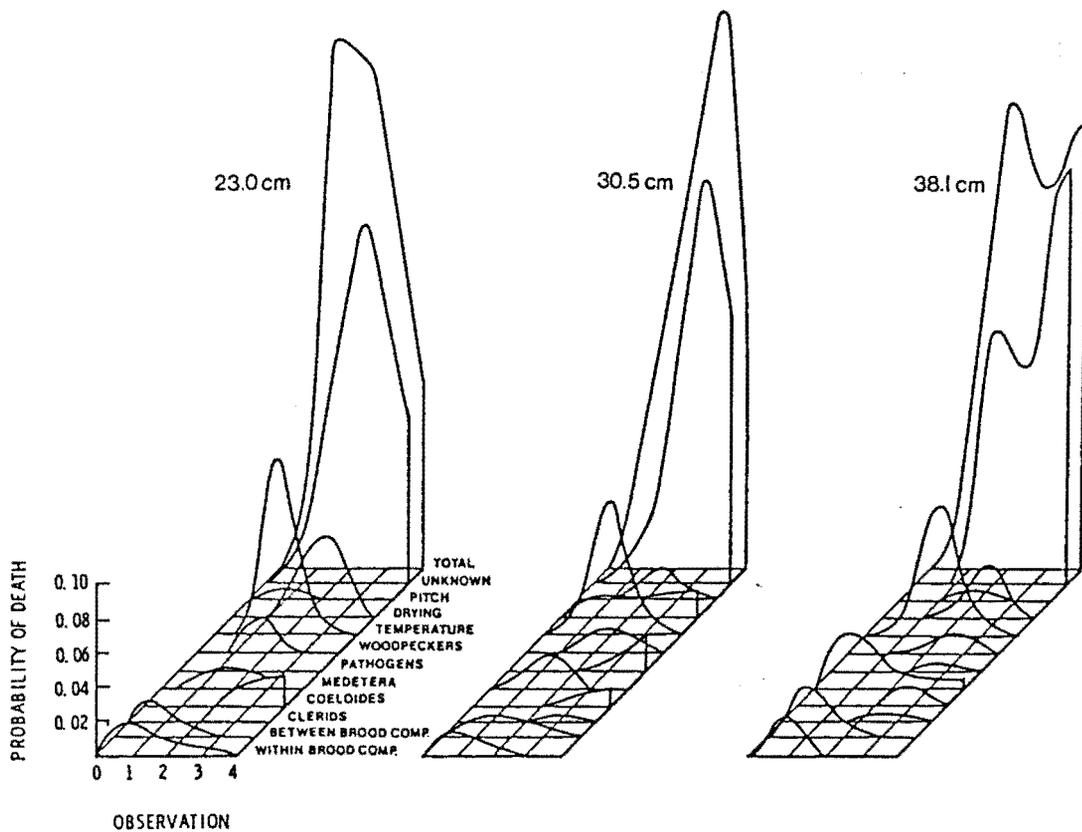


Figure 1. Probability of mountain pine beetle death from specific factors in three diameter classes, Logan Canyon, Wasatch National Forest, Utah, 1971 - 1980.

at 2,440 m. Additionally, the slower rate of development at the higher elevations results in a high percentage of eggs comprising the pre-winter population (Figure 3). The greater the percentage of eggs in the pre-winter population, the more likely the brood will suffer a proportionally high mortality from winter temperatures.

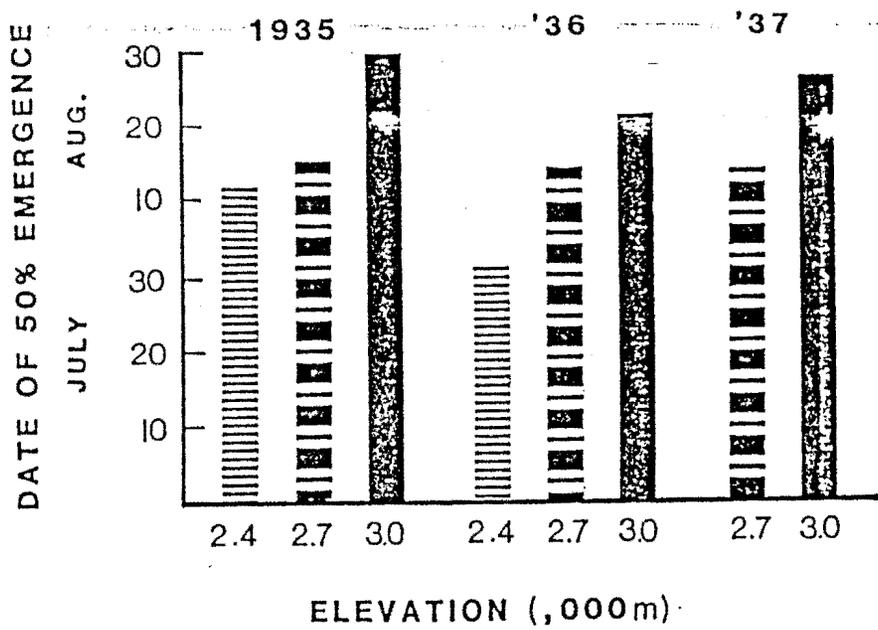


Figure 2. Effect of elevation on the rate of MPB emergence, Medicine Bow National Forests, Wyoming, 1935 - 37. After DeLeon (1940).

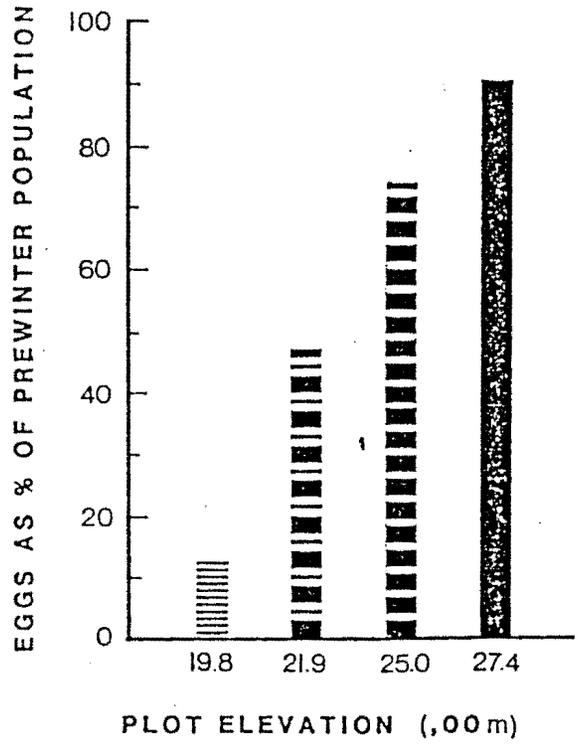


Figure 3. Effect of elevation on the percentage of eggs in the prewinter MPB population.

With the exception of the predacious fly, Medetera, the probabilities of death resulting from parasites, predators, pathogens, and pitch was notably less than those recorded for temperature or drying, regardless of tree size. Data from the 38.1 cm diameter class showed that the probability of death from Medetera was slightly greater than that from drying but less than that from cold temperature.

Comparison of the mortality caused by predators and parasites revealed the probability of death from clerid larvae was least, from Medetera was the greatest, and from Coeloides, intermediate to the two. Parasitism by Coeloides was greatest in the smallest diameter class and least in the largest, while predation by Medetera larvae was greatest in the largest diameter class and least in the smallest diameter class.

The probability of death caused by woodpeckers was greatest in the 23 cm and 30.5 cm classes, as were losses to pathogens and pitch. Increased resinosis in these two classes is likely due to the low attack densities sustained by trees in these diameter classes.

Results obtained from study of mountain pine beetle populations with a 1-year life cycle at the Logan Canyon site substantiate findings of earlier life table analyses conducted elsewhere (Cole 1981). Overall, the findings suggest that none of the natural control factors acting in the presence of others are effective in suppressing MPB populations below acceptable levels. The Logan Canyon population maintained a high endemic level for 9 years, with little changes in the abundance or effectiveness of natural controls. The population has only recently begun to decline because the large diameter trees that provide for optimum brood survival have been killed.

Major Factors - 2-Year Cycle

Comparison of the number of MPB killed per sample by selected mortality agents along an elevation transect in northwestern Wyoming revealed that cold temperatures, predators and parasites, and woodpeckers were the most effective agents (Table 1). In general, the effect of cold temperature tended to increase with increasing elevation with the exception of the site at 2,130 m. The severe losses to cold temperature at this elevation are attributable to lower than usual maximum temperatures during August and September 1968. This delayed adult emergence so that much of the brood entered winter as eggs and first stage larvae, which are especially susceptible to cold winter temperatures.

Table 1. - Effect of elevation on life cycle duration and mortality by selected agents, northwest Wyoming, 1967 to 1969

Mortality	Agent	Number of MPB killed per m ²			
		1 Year		Transition	2 Year
		1920 m	2130 m	2450 m	2750 m
Predators and parasitoids		30.1	36.6	10.8	34.4
Temperature		7.5		15.1	74.3
Woodpeckers		2.2	8.6	8.6	8.6
Within competition		2.2	<0.1	<0.1	<0.1
Between competition		2.2	<0.1	<0.1	<0.1
Pathogens		0.2	<0.1	<0.1	<0.1
Drying of phloem		<0.1	<0.1	<0.1	4.3

Mortality resulting from predator and parasites was rather constant for the three life cycle durations, except that in the "transition" where both 1-year and 2-year MPB life cycles are evident. Under these conditions, many MPB larvae may be smaller than those normally preferred by the parasite Coeloides rufovariegatus, thereby reducing its effectiveness.

Woodpeckers took 54 percent of the parent adults at 2,580 to 2750 m, 37 percent at 2,450 m, and 27 percent at 2,130 m. Woodpecker predation was not determined at the 1,920 m site, but 67 percent parent adults survived, and woodpeckers likely took only a small number of parents at this site. Additionally, they may have taken fewer parents at the lower elevation because larvae at this elevation were more numerous and larger (Amman 1973). Conversely, at the higher elevations MPB larvae were

generally smaller, accounting for the preference for parent adults (Koplin and Baldwin 1970). Despite this preference for parent beetles, other brood stages are dislodged as woodpeckers search for suitable prey. Removal of patches of outer bark speeds drying of the phloem, often causing dessication of adjacent brood, and further reducing survival. Such mortality is often difficult to assess (Moeck and Safranyik 1984; Otvos 1979).

Competition for phloem was greatest at the lowest elevation because larvae were more numerous in contrast to the higher elevations, where most of the mortality to early stage larvae occurred during the winter. Consequently, larval competition did not occur.

Overall MPB survival declines sharply when the duration of the life cycle exceeds 1 year (Table 2). There was much less difference in survival between broods requiring 2 years to complete a generation and those at the "transition site" where the beetle undergoes both 1-year and 2-year cycles, depending on micro-environmental factors such as the aspect of the tree infested. The difference in survival rates between 1-year and 2-year cycles was due almost entirely to the effects of cool temperatures that delay development so that a large percentage of the developing larvae fail to reach the third and four stages, and hence, are especially susceptible to winter temperature.

Table 2 - Survival of the MPB in relation to duration of life cycle, northwest Wyoming, 1967 to 1969

	1 Year		Transition	2 Year
	1920 m	2130 m	2450 m	2750 m
Generation survival (%)	17.6	2.6	7.4	4.0
Emerging adults	36.0	5.0	6.0	6.0
Percent change	+172	-411	-326	-372

Conclusions

Data amassed to date suggest that cool temperatures that retard MPB emergence and oviposition result in poor synchrony of the beetle life cycle with subsequent weather conditions. This results in life cycle durations that exceed 1 year and reduced survival, particularly at high elevations. In general, the mortality factors that are most important during the 1-year life cycle cause similar levels of mortality when more than 1 year is required to complete a generation.

Because survival and emergence are reduced at the higher elevations, fewer trees are killed at these elevations than at low elevations. For example, Amman and Baker (1972) found that 75 percent of the trees 23 cm dbh and larger survived MPB infestation at 2,670 m elevation on the northwestern Wyoming transect. Only 37 percent survived at 2,060 m near the base of the transect. Therefore, phloem thickness that regulates MPB populations at lower elevations is not a limiting factor at higher elevations. At the higher sites and northern latitudes, cool temperatures that delay brood development and increase losses to winter temperatures replace food as the factor limiting population survival.

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