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Mountain Pine Beetle Dynamics in Lodgepole Pine Forests
Part II: Population Dynamics

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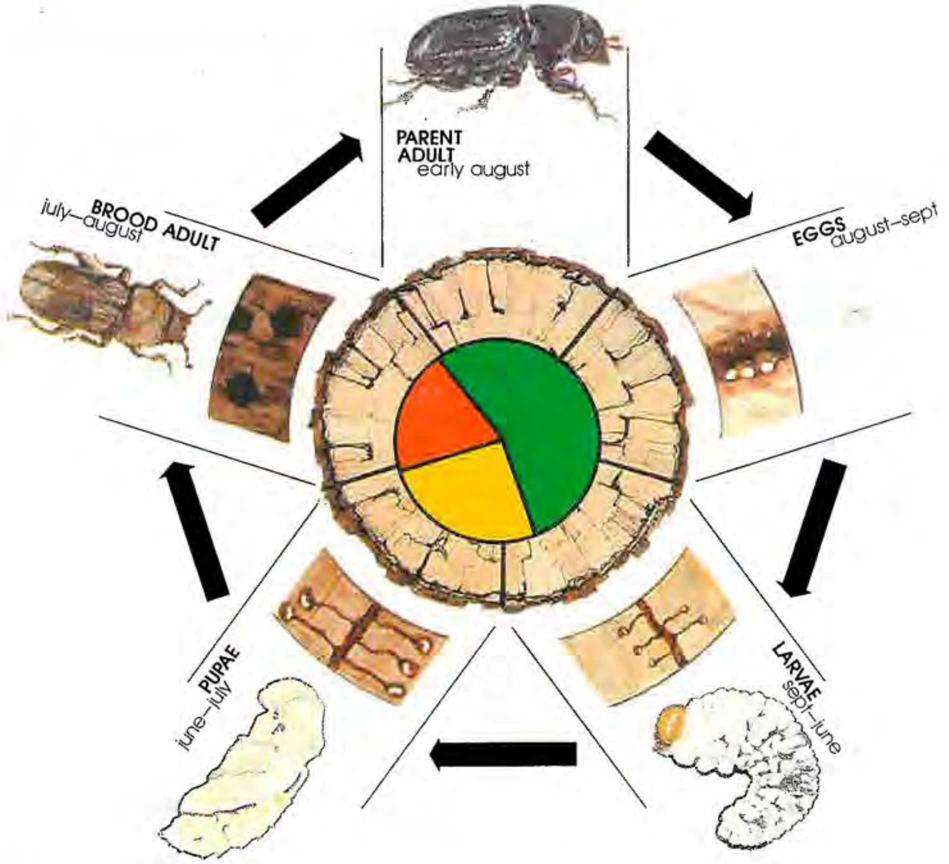

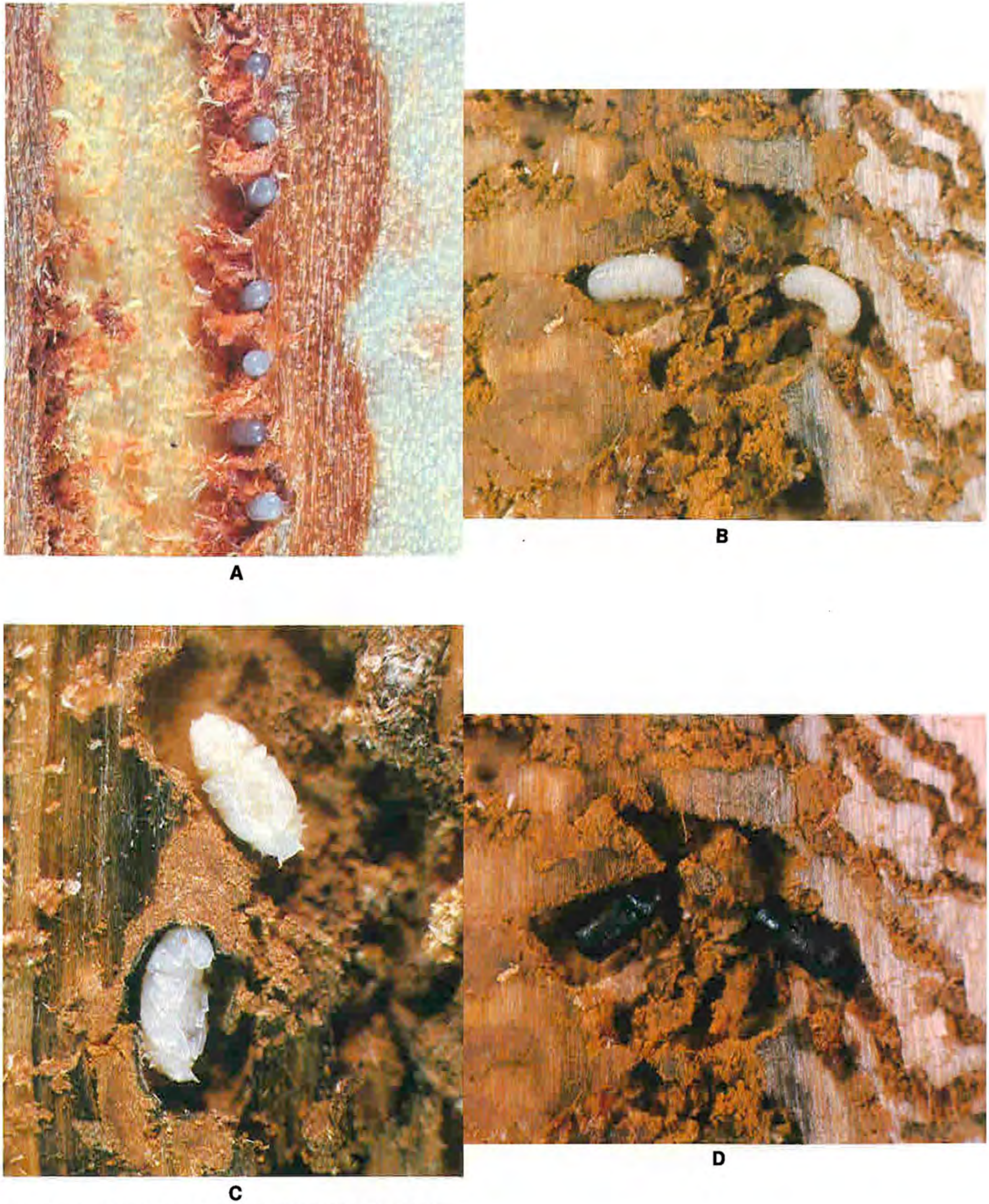

Figure 2.—Life stages of the mountain pine beetle: A. egg; B. larva; C. pupa; D. adult. (Photo A courtsey of Pacific Forest Research Centre, Canadian Forestry Service, Victoria, B.C.)

Cover photo: Generalized drawing of mountain pine beetle life cycle. Circle in the center shows color changes in tree foliage following infestation by beetles.

THE AUTHORS

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RESEARCH SUMMARY

Much of this work is original research by the authors. However, published literature on the taxonomy, biology, and population dynamics of the beetle are reviewed primarily as they occur in epidemic beetle populations in lodgepole pine forests. Lodgepole pine tree characteristics such as size and phloem thickness have a strong influence on beetle survival, size, sex ratio, and genotype. Of the many mortality factors acting upon the beetle population alone or in combination, none regulate the population before severe damage occurs to stands of lodgepole pine. These findings demonstrate that the mountain pine beetle is food regulated.

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PREFACE

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins, is a native bark beetle whose depredations cause various effects upon the lodgepole pine, *Pinus contorta* Douglas var. *latifolia* Engelmann, ecosystem. Historically, the beetle kills millions of trees each year in the United States and Canada. During epidemics, a single National Forest may lose more than a million trees in a single year; for example, 3.6 million lodgepole pines were killed on the Targhee National Forest, Idaho, in 1976 (Klein and others 1979). The mountain pine beetle has killed an estimated average of 2 billion bd.ft. per year since 1895 (Wood 1963). In 1970, volume loss of growing stock to all mortality causes totaled some 613 million ft^3 (17.4 million m^3) within the Rocky Mountain States; this is equivalent to nearly 75 percent of the volume that went into roundwood products. Sawtimber volume losses approximated 208 million ft^3 (5.9 million m^3)—equivalent to almost 50 percent of the roundwood products output from sawtimber (Green and Setzer 1974). The mountain pine beetle in lodgepole and ponderosa pines accounted for about 473.3 million ft^3 (13.4 million m^3) or 77 percent of this timber loss. Similar losses could be expected in the West Coast States. In western Canada, losses of lodgepole pine to the mountain pine beetle were estimated to be 1.3 million ft^3 (36 900 m^3) per year between 1950 and 1970 (Safranyik and others 1975). This impact places the mountain pine beetle as the prime insect agent affecting the lodgepole pine ecosystem. The effects of beetle infestations change the entire lodgepole pine environment and, depending on subsequent occurrence or exclusion of fire, largely determine the nature of successional dynamics—to lodgepole pine renewal in the case of fire, or to succession of more shade-tolerant species in the absence of fire.

Tree mortality in pine stands can occur as scattered individual trees, but more often entire groups of trees are killed. Unchecked, these groups expand with succeeding beetle generations, and eventually large areas may suffer extreme losses of their forest cover. This may or may not be a catastrophic situation, depending on landowner objective. Some landowners, for example, favor grassland over timberland, and a bark beetle outbreak may in fact be no disaster in their eyes. On the other hand, the value of a mountain home may be severely reduced by the death of high-value shade trees, and the owner may view this loss as highly undesirable. From the timber-producer standpoint, the beetle can disrupt management plans and cause an unwelcomed impact on local, regional, and national economies.

This treatise represents much original research by the authors, but also is a review of other published literature about the mountain pine beetle, with particular reference to epidemic infestations. Much research remains to be done in testing and applying management strategies indicated by this research. Also in need of study are the dynamics of mountain pine beetle populations during endemic periods. During periods of low beetle activity, we believe significant "keys" exist that will permit more effective management of stands to prevent population increases.

Our research approach first addressed the recognition and determination of relationships between the insect and its associated environmental factors. These relationships were based on biological functions, and they were studied to determine their biological effect upon the insect. Secondly, quantification of these relationships was based upon measurement units relative to beetle behavior. The host variable was considered as an integral unit within the ecosystem.

We intend to lead readers through this maze of interactive relationships to the extent of their interest and existing knowledge. With this in mind, we will have three parts published as separate general technical reports:

I. **Course of an Infestation**—including beetle impact on the lodgepole pine stand, how the beetle "moves through" the stand, expected timber mortality, and management alternatives. (See Intermountain Forest and Range Experiment Station publication General Technical Report INT-89, published in 1980.)

II. **Mountain Pine Beetle Population Dynamics**—including bionomics, analyses of mortality factors, entomological relationships, and the "inner workings" of a mountain pine beetle population. (This current volume.)

III. **Sampling and Modeling of Mountain Pine Beetle Populations**—including methods of sampling and modeling both lodgepole pine and mountain pine beetle populations. (In preparation.)

Mountain Pine Beetle Dynamics in Lodgepole Pine Forests

Part II: Population Dynamics

BIONOMICS

Taxonomy

Hopkins (1902) named *Dendroctonus ponderosae* the "pine destroying beetle of the Black Hills" from specimens collected from ponderosa pine, *Pinus ponderosa* Lawson, in the Black Hills of South Dakota. Three years later, Hopkins (1905) gave more details about *D. ponderosae* and shortened the common name to Black Hills beetle. This beetle was found in Arizona, Colorado, New Mexico, Utah, and Wyoming. Host trees were ponderosa pine; limber pine, *Pinus flexilis* James; white spruce, *Picea glauca* Moench Voss (Hopkins used *P. canadensis*); and Engelmann spruce, *P. engelmanni* Parry. However, Hopkins said the beetle was not destructive to Engelmann spruce.

The mountain pine beetle[1] *Dendroctonus monticolae*, was described by Hopkins (1909). The following were host trees: sugar pine, *Pinus lambertiana* Douglas; western white pine, *P. monticola* Douglas; lodgepole pine, *P. contorta* Douglas; and ponderosa pine. The mountain pine beetle was found in California, Idaho, Montana, Oregon, Washington, and Wyoming. Also, Hopkins (1909) described *Dendroctonus jeffreyi*, the Jeffrey pine beetle, from *Pinus jeffreyi* Greville and Balfour. He listed ponderosa pine as a host.

Blackman[2] thought that *D. monticolae* and *D. ponderosae* constituted a single species that varied according to host, food supply, and region. Blackman's contention was supported by experimental mating of *D. ponderosae* and *D. monticolae*, the progeny of which made successful attacks and produced fertile offspring (Hay 1956).

In a comprehensive treatment of the genus *Dendroctonus*, Wood (1963) combined *monticolae, ponderosae*, and *jeffreyi*. This synonymy was corroborated by studies of larvae and pupae (Thomas 1965). The scientific name, *D. ponderosae*, and common name, mountain pine beetle, were retained. However, some forest entomologists doubted that *jeffreyi* should be synonymized with *ponderosae*. Some reported that the Jeffrey pine beetle is limited to Jeffrey pine (Keen 1952; Eaton 1956). Vapor toxicity studies (Smith 1963, 1965) demonstrated Jeffrey pine beetles tolerated saturated resin vapors of Jeffrey pine, but not those of ponderosa pine, whereas mountain pine beetles tolerated vapors of ponderosa pine resin, but not those of Jeffrey pine. Additional evidence for the synonymy of *ponderosae* and *monticolae* and the distinctiveness of *jeffreyi* was obtained through laboratory matings and comparison of developmental rates, karyology, and morphology (Lanier and Wood 1968).

Recent pheromone studies further support maintaining the two species. One-heptanol, produced by oxidation of the terpene heptane in Jeffrey pine, is a pheromone involved in aggregation of *D. jeffreyi* (Renwick and Pitman 1979). *Trans*-verbenol, produced by oxidation of the host terpene alpha-pinene, appears to be the principal pheromone involved in aggregation of *D. ponderosae* in western white and ponderosa pines (Pitman and others 1968). Heptane constitutes about 90 percent of the volatile fraction of resin from Jeffrey pine, whereas alpha-pinene constitutes 32 to 60 percent of the volatile resin fraction from western white pine, but varies from 1 to 45 percent in ponderosa pine (Mirov 1961).

A genetic comparison of mountain pine beetles and Jeffrey pine beetles from northern California supports their separate species designations. Two loci are fixed for different alleles in the two species, strongly suggesting the absence of interbreeding (Higby[3]). These findings support the separation into two species—*D. ponderosae* and *D. jeffreyi*.

Genetic studies of mountain pine beetles also demonstrate differences between populations in *Pinus contorta* var. *murrayana* and *P. contorta* var. *latifolia*, probably related to longtime geographic isolation of populations in the two hosts (Stock and others 1978). Genetic analysis of several widely separated beetle populations in Idaho and Montana further suggests that genetic differentiation within this species is generally associated with geography (Stock and Guenther 1979); however, genetic differentiation among beetle subgroups in local areas is at least partly related to host tree species (Stock and Amman 1980).

Distribution and Host Trees

The beetle is found from the Pacific Ocean eastward through the Black Hills of South Dakota, and from about 56° north latitude in northern British Columbia southward to northwestern Mexico. The beetle occurs from about sea level in British Columbia to 11,000 ft (3 333 m) in Colorado (McCambridge and Trostle 1972; Safranyik 1978) (fig. 1).

The most important hosts of the mountain pine beetle from the standpoint of timber production are ponderosa, western white, sugar, and lodgepole pines. In addition, Coulter (*P. coulteri* D. Don), whitebark (*P. albicaulis* Engelmann), limber, pinyon (*P. edulis* Engelmann), bristlecone (*P. aristata* Engelmann), and foxtail (*P. balfouriana* Greville and Balfour) pines can be infested (Wood 1963). Brood is not usually produced in the occasionally infested nonhost tree—Engelmann spruce, grand fir (*Abies grandis* Lindl.), and incense-cedar (*Libocedrus decurrens* Torrey) (Evenden and others 1943). However, successful brood production by mountain pine beetles occurred in fairly widespread killing of mature and

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[1] "Beetle" refers to mountain pine beetle throughout this report unless otherwise noted.

[2] Blackman, M. W. Report on an examination of *Dentroctonus ponderosae* and *D. monticolae*. Washington, DC: U.S. Bureau of Entomology and Plant Quarantine, Forest Insect Investigations; 1938. 6 p. Unpublished report.

[3] Higby, Pamela K. Genetic relationships between two sibling bark beetle species, Jeffrey pine beetle (*Dentroctonus jeffreyi* Hopkins) and mountain pine beetle (*D. ponderosae* Hopkins), in northern California. Moscow, ID: University of Idaho; 1981. 50 p. Thesis.

overmature Engelmann spruce in the Flathead River Drainage and in three locales on the Gallatin National Forest of Montana (Mark D. McGregor, Forest Service, Missoula, Mont., personal communication, December 11, 1979). Brood is seldom produced in blue spruce, *P. pungens* Engelmann (Beal 1939). In addition to infesting native trees, a few beetles were produced from infested Norway spruce (*Picea abies* [Linnaeus] Karsten) in a University of Idaho arboretum (Furniss and Schenk 1969). Other exotics infested and killed included Scots pine, *P. sylvestris* L.; eastern white pine, *P. strobus* L.; red pine, *P. resinosa* Aiton; jack pine, *P. banksiana* Lambert; Austrian pine, *P. nigra* Arnold; and pitch pine, *P. rigida* Miller (Furniss and Schenk 1969). The mountain pine beetle apparently showed preference for exotic species of pine over native species, because neither *P. ponderosa* nor *P. monticola* was infested in the arboretum.

Ornamental Scots pines also were killed by the mountain pine beetle in Fort Collins, Colo., with beetles probably flying from infested ponderosa pine forests 7 or more miles away (McCambridge 1975). The beetles showed preference for Scots pine over adjacent Austrian and ponderosa pines, none of which were infested. Additional exotic or hybrid pines killed by mountain pine beetles at the Institute of Forest Genetics in California were cher pine, *P. roxburghii* Sargent; bishop pine, *P. muricata* D. Don; Japanese red pine, *P. densiflora* Sieb. and Zucc.; shortleaf-loblolly hybrid, *P. echinata* Mill. x *taeda* L.; and loblolly-slash hybrid, *P. taeda* x *elliottii* Engelmann var. *elliottii*. Adjacent ponderosa pine, as in Idaho and Colorado, were not attacked (Smith and others 1981).

The ability to attack and kill and even produce brood in some of the usually regarded nonhost trees, particularly climax species, would appear to aid the mountain pine beetle in maintaining forests of preferred species consisting of lodgepole, ponderosa, and western white pines.

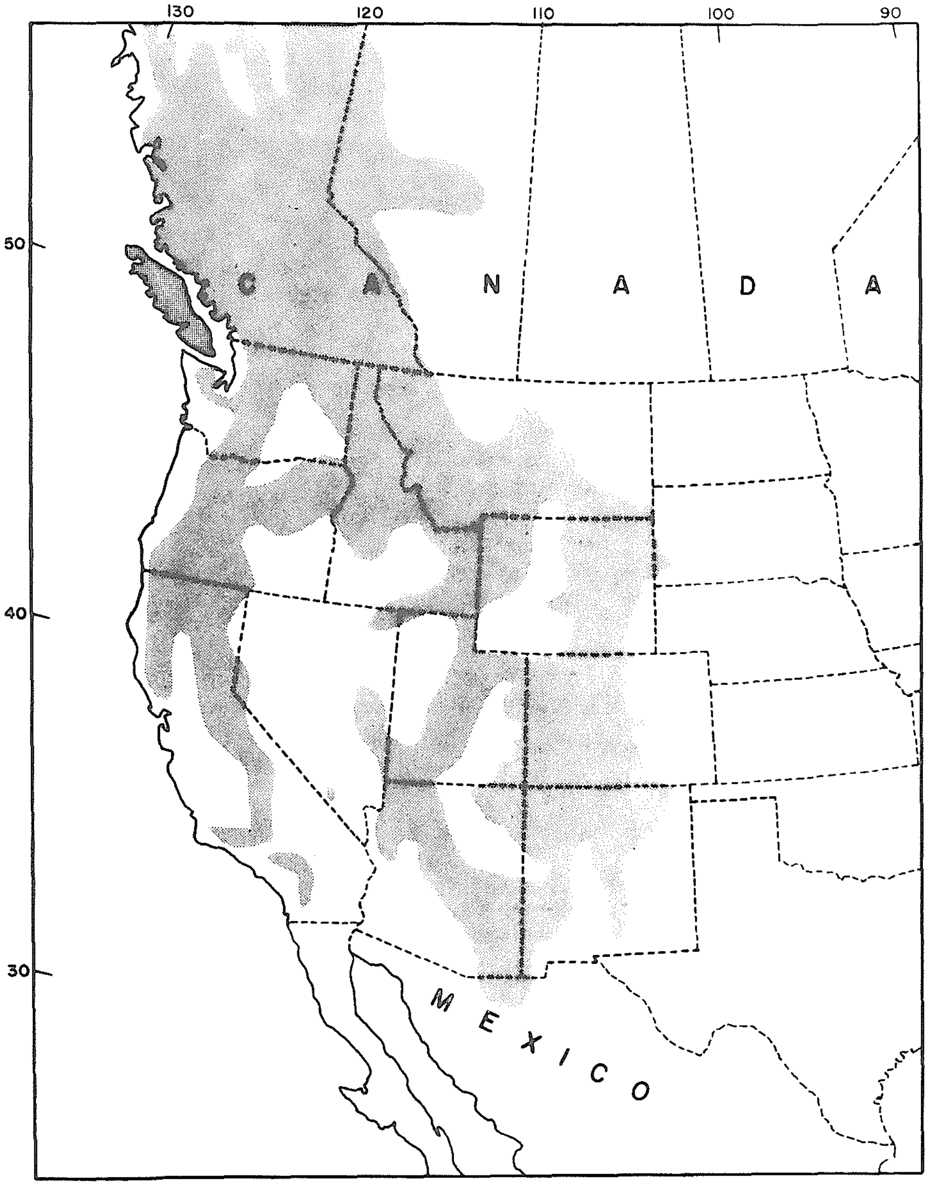

Figure 1.—Approximate distribution of the mountain pine beetle in North America (McCambridge and Trostle 1972).

Description

The egg is ovoid, white to cream colored, as shown in figure 2a. (Figure 2 is on the inside front cover). A sample of 20 eggs from lodgepole pine in northern Utah averaged 0.04 inch long (1.02 mm; sd = 0.10 mm) and 0.02 inch wide (0.51 mm; sd = 0.02 mm). However, cross-sectional area and weight of eggs are significantly related to beetle size, with the largest beetles producing the largest eggs (McGhehey 1971). Unfertilized eggs remain a uniform color, whereas fertilized eggs develop a clear area in one end during early embryogenesis.

The mountain pine beetle has four larval instars (fig. 2b). Larvae are white to cream colored, with amber head capsules. Head capsules are between 0.014 inch (0.36 mm) and 0.065 inch (1.64 mm) (fig. 3). Average head capsule width for the four instars from lodgepole pine are: I = 0.019 inch (0.493 mm; sd = 0.037 mm); II = 0.026 inch (0.653 mm; sd = 0.041 mm); III = 0.037 inch (0.950 mm; sd = 0.075 mm); and IV = 0.049 inch (1.240 mm; sd = 0.081 mm).

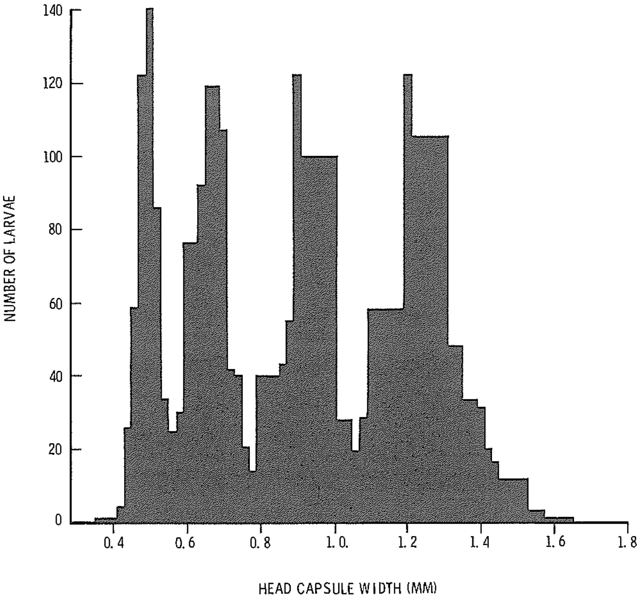

Figure 3.—Head capsule distribution of mountain pine beetle larvae.

The pupa is white to cream colored and of the general form and size of the adult. Legs and wing pads are folded beneath the body, and the abdominal segments are exposed (fig. 2c). The pupa is the earliest stage in which the sexes can be readily differentiated. Females have a protruding lobe between the eighth sternite and ninth tergite (fig. 4); the lobe is lacking in males (Schofer and Lanier 1970).

Adults are light tan and soft at first (commonly called teneral or callow adult), becoming dark brown to black and hard prior to emergence. Adults are stout, cylindrical, and average about 0.20 inch (5 mm) long (fig. 2d). Females are usually longer than males. For example, for beetles caught in cages during the 1973 flight on the Wasatch-Cache National Forest in Utah, the average length of females was 0.20 inch ($\bar{x}$ = 5.13 mm; sd = 0.42 mm; N = 426), and that of males was 0.19 inch ($\bar{x}$ = 4.73 mm; sd = 0.36 mm; N = 186).

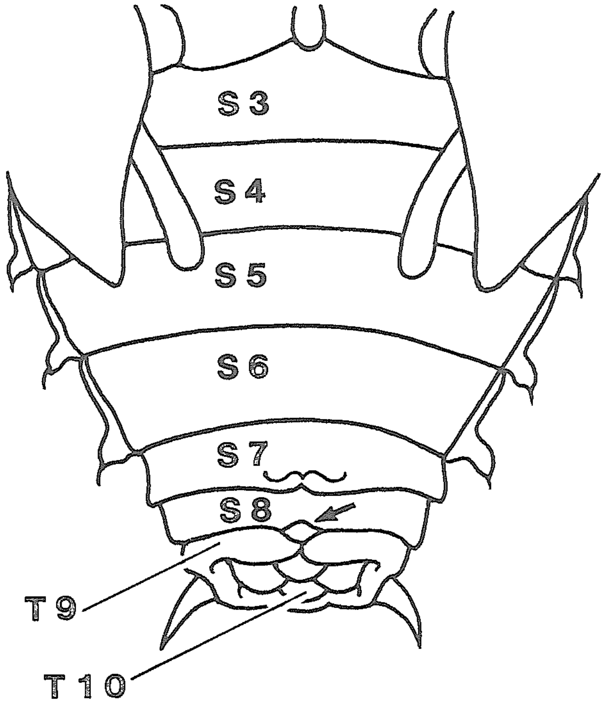

Figure 4.—Ventral aspect of female *Dendroctonus* pupa. Lobe indicated by arrow is a character of females; the lobe is absent in males (Schofer and Lanier 1970).

Sexual dimorphism of the seventh abdominal tergite in adult beetles permits easy separation of the sexes (Hopkins 1909; Lyon 1958). In males, the posterior margin of the tergite forms an angle of about 150° pointing to the rear; in females, the margin is gently rounded to the rear (fig. 5). The pointed margin of the male is used for stridulation (sound production used in communication) when the tergal plectrum is pulled across the file located on the underside of the elytra. Electron micrographs of the file and oscillograms of typical male chirps were made by Michael and Rudinsky (1972). The sound can be used to separate the sexes because males usually make a more continuous and audible sound than females (McCambridge 1962).

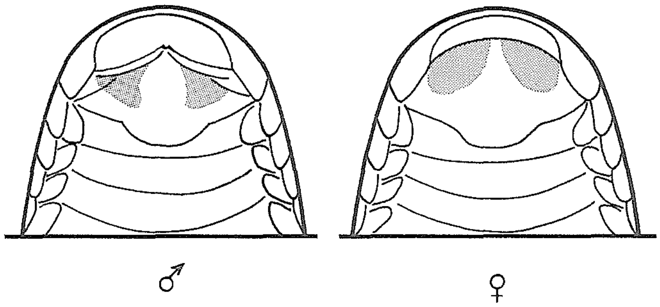

Figure 5.—Schematic, dorsal view of exposed, rear part of adult *Dendroctonus* abdomen. Left: male with angular rear margin of enlarged seventh tergite. Right: female with gently curved rearward margin (Lyon 1958).

Life Cycle

The typical 1-year beetle life cycle starts with emergence of new adults in middle to late July and early August, as shown in figure 6. (Figure 6 is on the front cover). Adults select and infest green trees, then construct vertical egg galleries. Eggs are laid in niches arranged singly in alternate groups along the sides of the gallery. Eggs hatch within a week or so, and the larvae feed in the phloem, usually making tunnels at right angles to the egg gallery. Larvae may reach the third and early fourth stages before cold weather in late October and November when they become dormant. They resume feeding in April, completing larval development in June. Larvae pupate within cells excavated in the bark and sapwood. Pupae transform into adults during the latter part of June to mid-July. New adults feed within the bark prior to emergence.

Several notable exceptions to the typical life cycle are created primarily by climatic differences and varying weather. New adults that mature and emerge early in a warm year may make two galleries (Reid 1962a). After infesting one tree and completing egg galleries, they emerge and infest a second tree. This phenomenon has been relatively uncommon in lodgepole pine forests south of Montana. Trees along Hell Roaring Creek in the Gallatin Canyon of Montana showed a high rate of parent reemergence in 1973. Although these parents then attacked and killed additional trees, it is doubtful that many progeny were produced because attacks came so late in the fall that few eggs hatched. Insufficient heat units occur for all eggs to hatch when beetles infest trees in late August (Reid and Gates 1970). All eggs and many small larvae that enter the winter are killed by the cold (Amman 1973). Eggs freeze at minus 0.6° F (-18° C) (Reid and Gates 1970).

A high proportion of parent beetles may survive mild winters within egg galleries they constructed during late summer and fall of the previous year. Only a few of these beetles appear to emerge and infest trees before their progeny emerge. Most often, early emerging parents will construct a gallery in green phloem on trees that had only a vertical strip of the bark infested previously (strip attack), or trees that resisted attack with a copious flow of resin (pitchout) that forced the beetles to abandon their galleries the previous year (Rasmussen 1974). Most parents that survive the winter probably emerge the same time as their progeny. This parental behavior is indicated by few or no parent emergence holes (those originating from egg galleries) and the few to no trees infested prior to emergence of progeny.

Parent beetles may extend their galleries and continue oviposition in the spring in green phloem tissue or tissue that has not deteriorated from micro-organisms introduced by the beetles.

Beetles may require 2 years to complete a generation at high elevations such as in western Montana and central Idaho (Evenden and others 1943; Gibson 1943), as well as at elevations above 8,000 ft (2 400 m) at 43° N latitude, 110° W longitude in northwestern Wyoming (Amman 1973). The beetle required 2 years to complete a generation in Banff National Park, Alberta, in 1956 (Reid 1962a). Previously, a generation had been completed in a single year in the park. The delaying effect that cool temperatures have on development and emergence of beetles is largely responsible. The life cycle of the beetle thus varies from year to year and place to place according to elevation, latitude, longitude, and weather differences.

BIOLOGY AND BEHAVIOR

Preemergence, Emergence, and Flight

Prior to emergence, new adults feed within the bark to complete maturation. During this feeding period, flight muscles increase in size and can be used to forecast when beetles are physiologically ready to emerge (McCambridge and Mata 1969). While feeding, adults also obtain fungal and yeast spores (Shifrine and Phaff 1956) and probably bacteria in the maxillary mycangium (a special structure for transporting spores) for inoculating fresh host material (Whitney and Farris 1970). A limited amount of mating may occur prior to emergence; 2 percent of newly emerged females contained sperm (McCambridge 1970).

When the density of new adults is high, their feeding chambers may coalesce. Then when a beetle chews an exit hole through the bark to emerge, all beetles within the common chamber emerge through the single hole (Reid 1963; Amman 1969). New adult densities of 1 to 20 beetles/ft^2 (930 cm^2) of bark surface average 1 beetle per emergence hole. At greater densities, the number of beetles emerging per hole increases geometrically, with an average of about 2 beetles per hole at densities of 200 beetles/ft^2 (930 cm^2) of bark surface (fig. 7).

Emergence and flight of new adults usually begin after relatively high temperatures and abundant sunshine (Reid 1962a; Rasmussen 1974). Emergence occurs only during the warm part of the day, starting when temperatures reach about 60° F (15.5° C), and ceasing in the afternoon when temperatures drop to about the same level (Reid 1962a; Rasmussen 1974). When beetles emerge, they are positively phototactic (Schonherr 1971; Shepherd 1966). Maximum flight activity generally occurs from 4 p.m. to 6 p.m. (mountain daylight time) in the mountains of Arizona, Colorado, Idaho, and Utah, in both lodgepole and ponderosa pine forests (Blackman 1931; McCambridge 1967, 1971; Rasmussen 1974) (table 1). Maximum flight activity farther north in Washington and British Columbia is earlier—from 11 a.m. to 4 p.m. in both ponderosa and lodgepole pine forests (Gray and others 1972; Reid 1962a). Flight may begin earlier in Washington and British Columbia because the threshold temperature may occur earlier in the day.

Emergence may be controlled, at least partially, by factors other than temperature. Watson (1970) found that a rhythmic and possibly circadian emergence cycle occurred for mountain pine beetles from lodgepole pine in Canada when reared in total darkness and at a constant temperature. Emergence was greatest between 9 a.m. and 3 p.m., which was similar to field results (Reid 1962a). A circadian emergence rhythm has also been suggested for mountain pine beetles in ponderosa pine (Billings and Gara 1975).

Beetles flying late in the day to green lodgepole pine trees remain in bark crevices and under bark scales until the following day (Rasmussen 1974). These beetles then either bore into the tree or take flight after air temperature reaches about 63° F (17° C) the following day. However, some beetles bore into ponderosa pine during the night (McCambridge 1974). This difference in behavior is probably related to generally warmer night temperatures in ponderosa stands, which are usually at lower elevations than lodgepole pine stands.

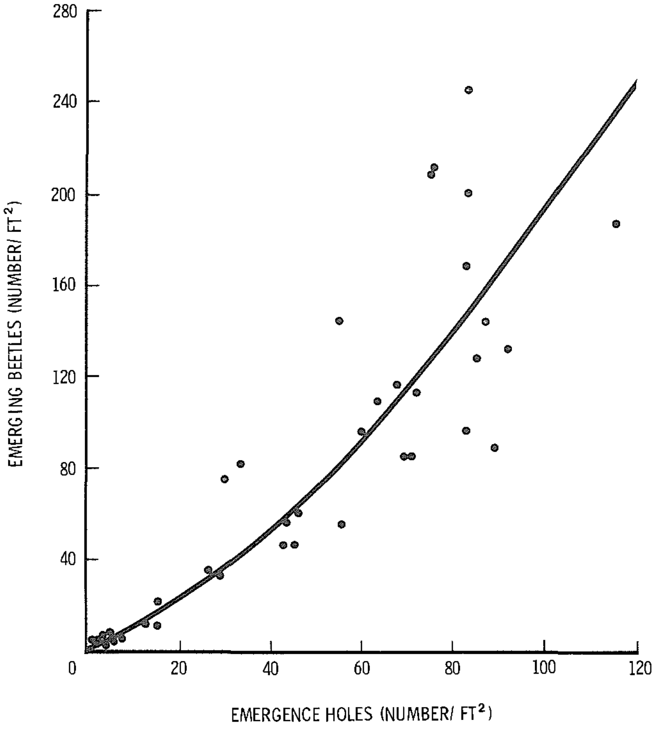

Figure 7.—The number of mountain pine beetles emerging per emergence hole increases as the density of beetles increases. (See regression statistics in appendix.)

Table 1.—Peak emergence and flight of mountain pine beetles in different portions of the beetles' range

Observer	Temperature	Time	Host	Locality
	°C			
Rasmussen (1974)	23	4 p.m.-6 p.m.	Lodgepole	Utah, Idaho
Reid (1962a)	22	1 p.m.-4 p.m.	Lodgepole	British Columbia
Shepherd (1966)	22	—	Lodgepole	British Columbia
Blackman (1931)	—	4 p.m.-dusk	Ponderosa	Arizona
Gray and others (1972)	20	11 a.m.-2 p.m.	Ponderosa	Washington
McCambridge (1971)	20	4 p.m.-6 a.m.	Ponderosa	Colorado

Beetles emerge at a greater relative rate from south than north aspects of trees, and at a greater rate low than high on the stem (Safranyik and Jahren 1970a). Temperature probably is responsible for the differences among aspects, since subcortical temperatures are usually higher on south than north aspects of the tree (Powell 1967). However, it does not explain the greater rate of emergence lower on the bole because temperatures in a lodgepole stand tend to increase with tree height (Bergen 1974).

Emergence and flight may be diminished when temperatures are too high. Gray and others (1972) and Rasmussen (1974) found that activity was reduced on days when air temperature reached or exceeded 90° F (32° C). In laboratory studies, adult beetles became photonegative between 95° and 99.5° F (35° and 37.5° C) (Shepherd 1966).

Emergence may last several weeks, with only a few beetles emerging at the beginning and end. After a period of sparse, sporadic emergence, the majority of beetles usually emerge and attack in about 1 week (fig. 8) (Rasmussen 1974). Emergence period varies from year to year as a result of rate of beetle development (McCambridge 1964) and weather during the emergence cycle.

In northern Utah, peak numbers emerged during 7 days in 1970, 9 days in 1971, and 7 days in 1972. Frequent light thunderstorms may have lengthened peak emergence in 1971 because beetles remain in the trees during such weather (Rasmussen 1974). The rapid emergence of most of the population is essential to the success of the mountain pine beetle in attacking and killing the most vigorous trees in lodgepole pine stands.

Males and females emerge in about equal numbers during the early and late portions of the emergence cycle, but females predominate during midcycle (Rasmussen 1974, 1980) (fig. 9). Similar results were obtained from laboratory rearings (fig. 10). Females emerging during the first half of the emergence cycle are larger than those emerging later (Safranyik and Jahren 1970a; Rasmussen 1980) (fig. 11).

Emergence of beetles from thin phloem is delayed and at a slower rate than emergence from thick phloem in the laboratory. Approximately 50 percent of the population emerged after 6 days from thick phloem, whereas it took 16 days for that proportion to emerge from thin phloem (fig. 12). Delayed emergence is critical because time of attack and oviposition determines how far larvae will develop prior to winter. Eggs and many small larvae are killed by cold (Amman 1973).

Safranyik and Jahren (1970b) investigated the relation of mountain pine beetle size to tree diameter, height and aspect on the stem, bark thickness, moisture content of the outer sapwood, and brood density. Generally the average pronotal widths of emerging males and females were inversely related to height on the stem, with the largest beetles occurring at 4 to 6 ft (1.2 to 1.8 m) above ground. Beetle size was not related to north or south aspects, but sizes of both sexes were positively correlated with tree diameter. In addition, size was correlated with bark thickness and moisture content of the outer sapwood in 1 of the 2 years of the investigations.

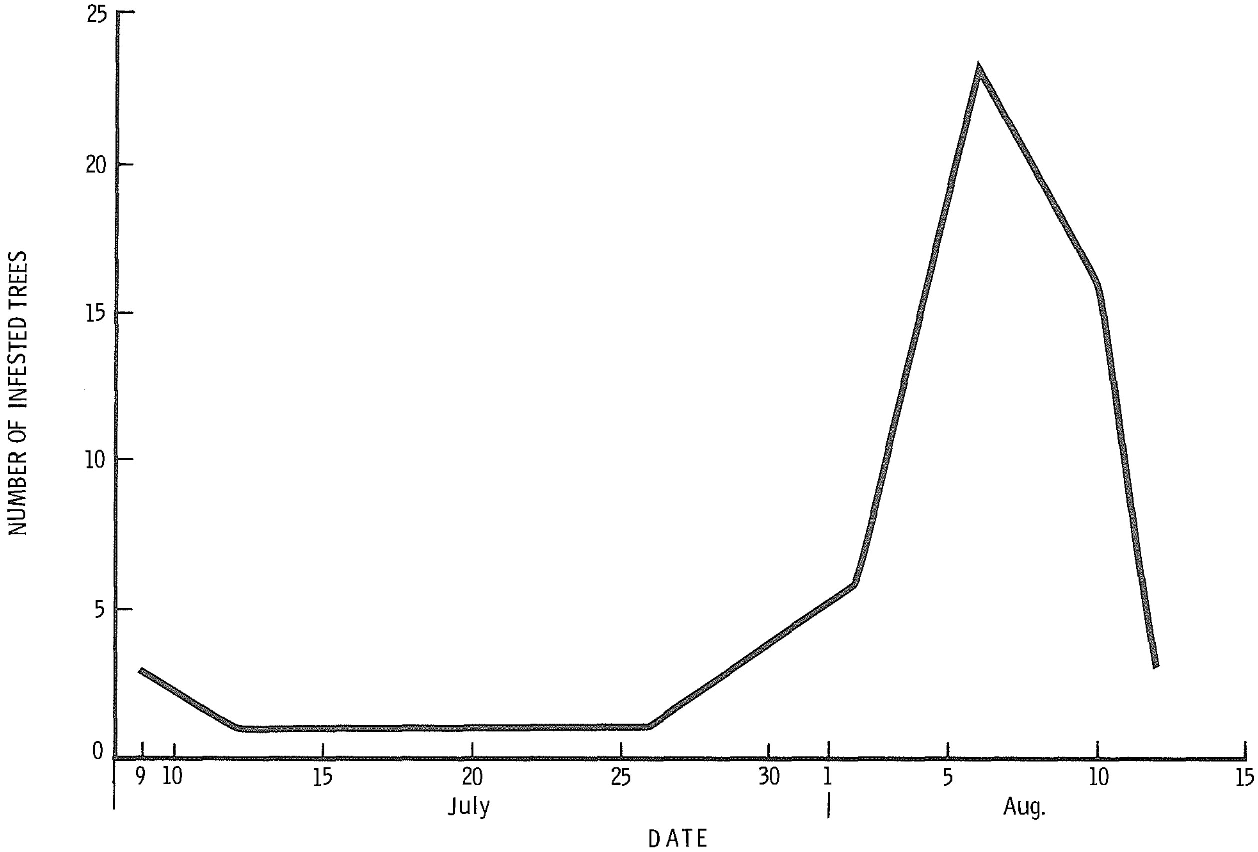

Figure 8.—Numbers of trees attacked by date during the 1971 flight period, Wasatch National Forest, Utah.

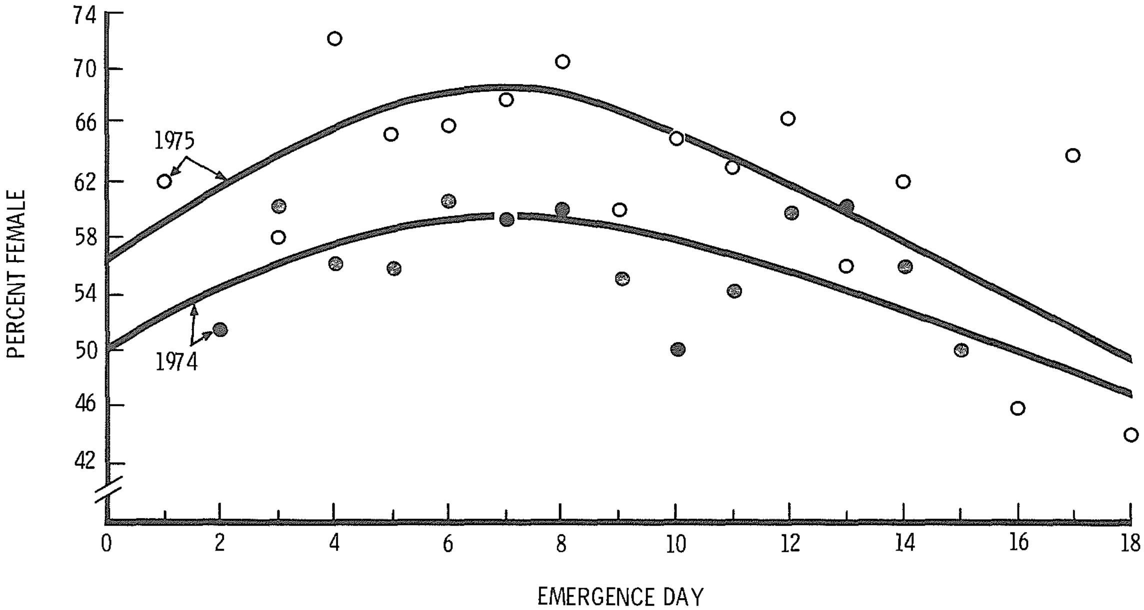

Figure 9.—Percent of emerging mountain pine beetles that were female in relation to day of emergence for 1974 and 1975 (Rasmussen 1980). (See regression statistics in appendix.)

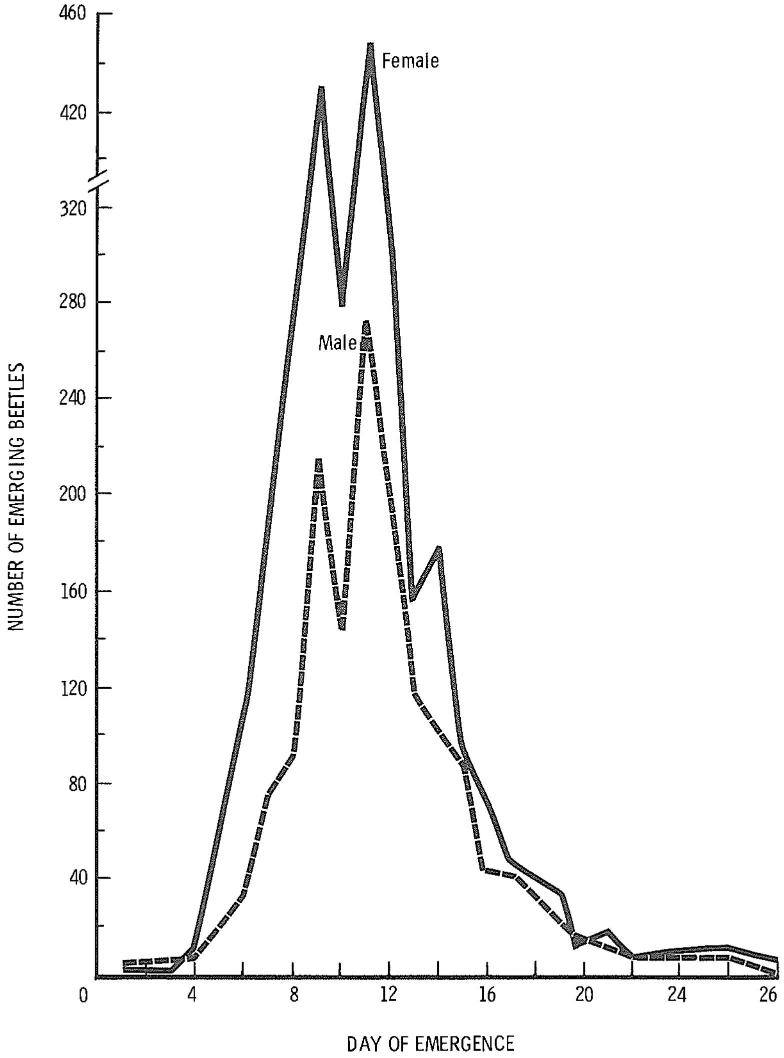

Figure 10.—Emergence cycle of male and female mountain pine beetles in a laboratory population.

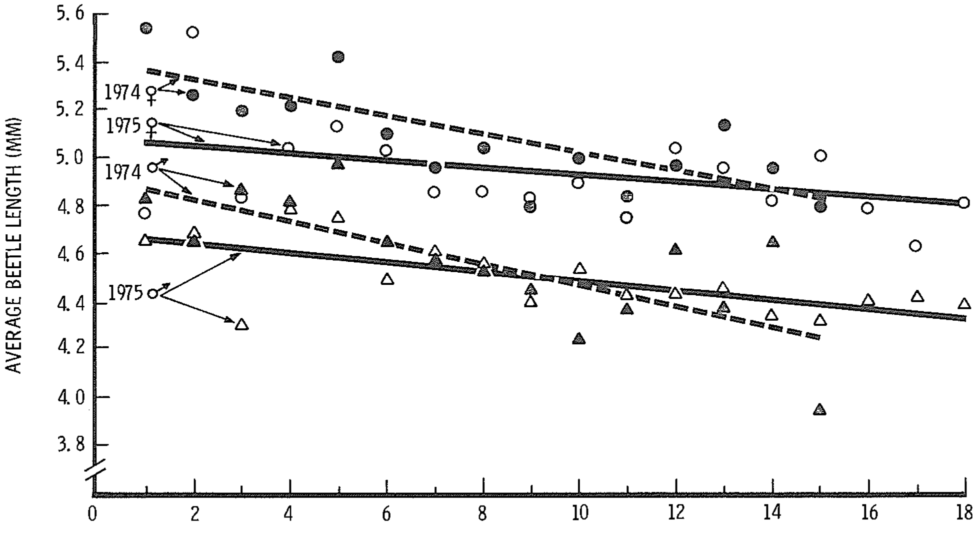

Figure 11.—Comparison of female and male mountain pine beetle size in relation to emergence day for 1974 and 1975, Logan Canyon plot, Wasatch-Cache National Forest, Utah (Rasmussen 1980). (See regression statistics in appendix.)

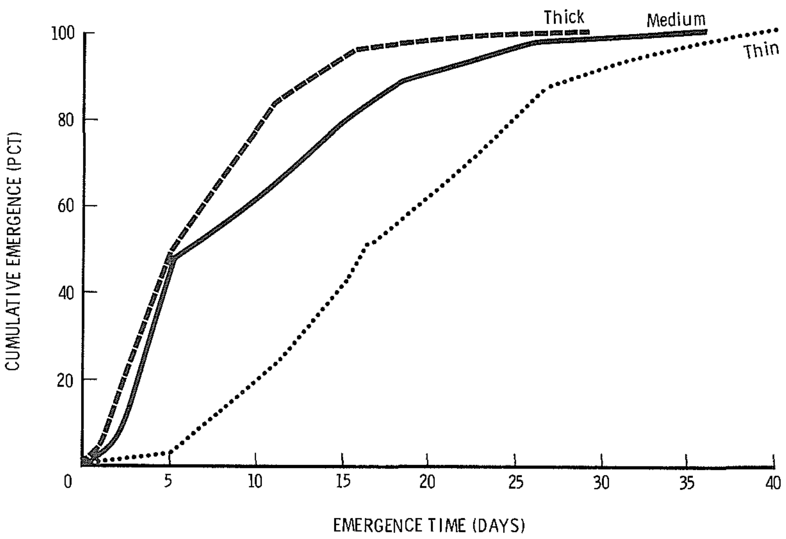

Figure 12.—Rate of mountain pine beetle emergence from three phloem thickness categories in a laboratory population.

Beetle size differed according to rearing temperature in the laboratory (table 2). Females reared at a constant 77° F (25° C) were significantly ($P \leq 0.001$) smaller than those reared at 59° or 68° F (15° or 20° C). However, this was not the case with males, which were smaller when reared at both 68° and 77° F (20° and 25° C) than when they were reared at 59° F (15° C). There was no significant difference in size of males reared at 68° and 77° F (20° and 25° C).

Table 2.—Length of new adult mountain pine beetles reared at three constant temperatures

Temperature	Male length			Female length		
	$\bar{x}$[1]	sd	n	$\bar{x}$	sd	n[1]
°C	*--- mm ---*			*--- mm ---*		
15	4.55	0.32	30[2,1,]	5.19	0.37	61[1]
20	4.53	.34	99[1]	5.01	.37	202[2]
25	4.28	.34	26[2]	4.95	.30	90[2,1]

[1] Means having the same number are significantly different at the 0.001 level of probability.

In a second study, parents were introduced in logs from a single tree, and the logs then placed at different elevations on the north slope of the Uinta Mountains in Utah. New adults completing development in cooler temperature regimes were larger (table 3).

The larger size of Douglas-fir beetles, *D. pseudotsugae* Hopkins, reared at cool, in contrast to warm, temperature was shown by Atkins (1967). In addition, Atkins found that beetles reared at cool temperatures had proportionately greater lipid content than those reared at warmer temperatures.

Table 3.—Length of new adult mountain pine beetles reared at four elevations in northern Utah

Elevation		Male length[1]			Female length[1]		
		$\bar{x}$	sd	n	$\bar{x}$	sd	n
Feet	*m*	*--- mm ---*			*--- mm ---*		
8,600	(2,621)	4.66	0.40	43	5.21	0.44	79
9,000	(2,743)	4.83	.33	38	5.40	.46	109
9,400	(2,865)	4.94	.35	60	5.48	.38	200
9,800	(2,987)	5.20	.39	121	5.70	.41	194

[1] All means were significantly different from one another at the 0.001 level.

Beetle size also has been related to phloem thickness. Beetles reared in thick phloem were significantly larger than those reared in thin phloem (table 4, $P \leq 0.001$) at all egg gallery densities ($P \leq 0.005$) (fig. 13) (Amman and Pace 1976). A difference in beetle size among tree diameters is apparent throughout most of an infestation cycle (table 5); both males and females from the largest trees are almost always larger (fig. 14). The principal reason probably is the greater thickness of phloem as food for developing larvae, and possibly greater nutritional value found in large than in small trees (Amman 1969, 1975b, 1978).

Table 4.—Length of new adult mountain pine beetles reared in lodgepole pine billets having thin or thick phloem

Phloem thickness	Male length			Female length		
	$\bar{x}$	sd	n	$\bar{x}$	sd	n
	---- mm ----			*---- mm ----*		
Thin	4.45[1]	0.381	26	4.98[1]	0.344	33
Thick	4.71	.272	81	5.25	.354	85

[1] Means for thin and thick phloem are significantly different for both sexes at the 0.001 level of probability.

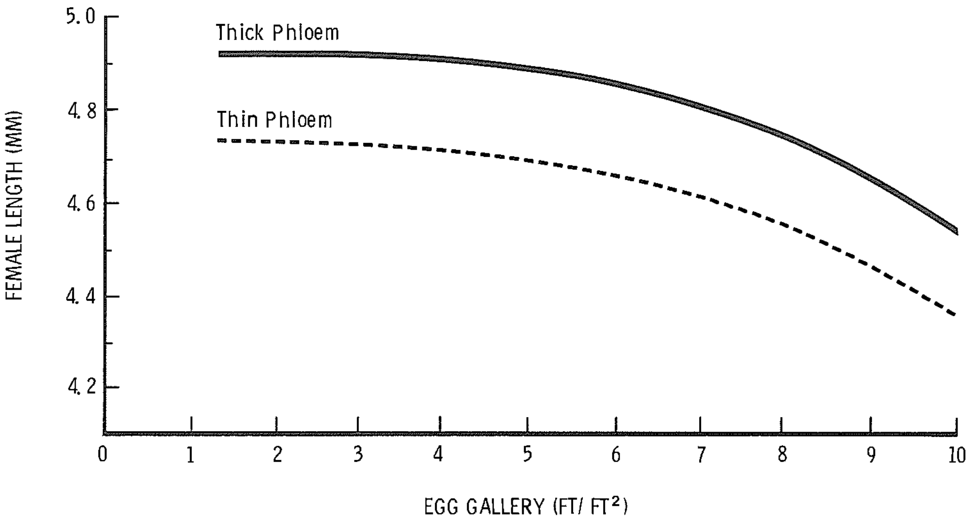

Figure 13.—Length of mountain pine beetle females in relation to egg gallery density for two phloem thickness categories (Amman and Pace 1976). (See regression statistics in appendix.)

Table 5.—Average lengths of male and female mountain pine beetles from different lodgepole pine diameter classes and years, Wasatch-Cache National Forest

	<8.9 inches (22.6 cm)		**9.0-10.9 inches (23-27.7 cm)**		**11.0-13.9 inches (27.9-35.3 cm)**		**>14 inches (35.6 cm)**	
Year	♂	♀	♂	♀	♂	♀	♂	♀
	mm							
				Stillwater Plot				
1968	--	--	--	--	--	--	4.77	5.26
1969	--	--	3.72	4.02	--	--	4.02	4.39
1970	--	--	4.11	5.05	4.75	5.15	5.01	5.23
1971	--	--	4.59	5.11	4.65	5.45	4.83	5.36
1972	--	--	4.58	5.26	4.50	5.15	4.71	5.31
1973	--	--	4.69	5.10	4.62	5.15	4.84	5.31
1974	4.52	4.55	4.48	5.08	4.72	5.12	4.89	5.18
1975	4.56	4.92	4.76	5.02	4.46	4.98	4.46	5.10
1976	--	--	4.60	5.17	4.56	5.17	4.56	5.10
1977	4.49	4.93	4.81	4.85	4.47	4.98	--	--
1978	4.41	4.38	4.58	4.89	4.49	4.91	4.50	4.92
1979	4.23	--	--	4.49	4.58	4.84	4.34	4.23
Grand average	*4.44*	*4.59*	*4.49*	*4.91*	*4.58*	*5.07*	*4.63*	*5.04*
				Logan Canyon Plot				
1971	4.20	4.18	--	4.92	4.56	4.43	--	--
1972	4.20	4.67	4.52	4.95	4.59	5.18	4.82	5.24
1973	--	--	4.40	4.87	4.47	4.86	4.53	5.10
1974	--	4.48	4.35	4.73	4.47	5.02	4.78	5.19
1975	4.25	4.76	4.37	4.78	4.20	4.57	4.39	4.75
1976	4.25	4.68	4.44	4.76	4.41	4.81	4.47	4.86
1977	--	--	--	--	4.49	5.13	4.60	5.09
1979	3.77	4.49	4.53	4.85	4.70	5.19	4.73	5.11
Grand average	*4.13*	*4.57*	*4.44*	*4.84*	*4.49*	*4.90*	*4.62*	*5.05*

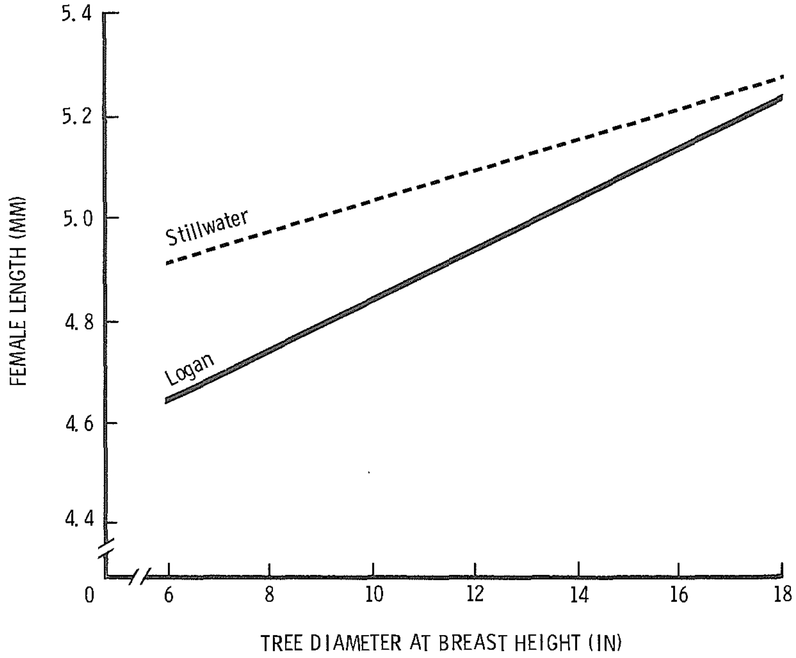

Figure 14.—Length of female mountain pine beetles increased with diameter at breast height of lodgepole pine in the Logan Canyon and Stillwater plots, Wasatch-Cache National Forest for years 1971-78 and 1968-79 respectively. (See regression statistics in appendix.)

Most mountain pine beetles fly at a level corresponding to the midbole of lodgepole pine in both thinned and unthinned stands. Beetle catches in nondirectional barrier traps revealed that, overall, 35 percent of beetles were caught at a height of 6 ft (1.8 m) above ground; 48 percent at midbole height, about 25 ft (7.6 m); and 17 percent at midcrown height, about 45 ft (13.7 m) (Schmitz and others 1980). Greater catches at midbole may result from less understory vegetation and tree branches than at the other two levels.

Flight tests showed that newly emerged beetles generally flew with the wind when pheromones were absent. However, in the presence of synthetic *trans*-verbenol and freshly cut host material, flight was toward the attraction source and against the wind (Gray and others 1972).

Host Selection and Infestation

The mountain pine beetle usually selects the largest trees in the stand to infest, at least during the few years preceding and during a major epidemic (Cole and Amman 1969; Evenden and Gibson 1940; Hopping and Beale 1948). Beetles use both visual and chemical cues when infesting these trees. In laboratory studies, the mountain pine beetle was attracted to large dark objects (simulating the large diameter trees) against a light background as shown by Shepherd (1966). He suggested that the beetle uses vision in selecting trees to infest. Further evidence of this is furnished by Rasmussen (1972), who attempted to attract mountain pine beetles to small diameter trees by baiting them with *trans*-verbenol and alpha-pinene. Beetles were attracted into the area of the baited tree, but usually selected a nearby tree of large diameter. Among trees of similar diameter, beetles infested those that had the thickest phloem (Roe and Amman 1970). This suggests that the beetle may also use chemical cues from the tree in selecting its host when little difference in tree size exists. Terpenes occur in greater quantity in thick than in thin phloem (fig. 15), and, because of the volatility of the monoterpenes, could be the olfactory stimulus used by beetles to locate trees having thick phloem (Cole and others 1981).

A random landing (Hynum and Berryman 1980) and attack pattern (Burnell 1977) have been proposed. Hynum and Berryman (1980) trapped landing beetles on both living and dead lodgepole pines and on live Douglas-fir trees. Catches among the three types of trees were not significantly different; therefore, they concluded the mountain pine beetle landed at random on trees. However, Hynum and Berryman's data show a high mean catch with low numbers of observations on nonhost trees compared to low mean catch and large numbers of observations on lodgepole pine. This suggests that increased sample size may have demonstrated a significant difference in catch, with a preference shown for landing on Douglas-fir, a nonhost tree. The sizes of Douglas-fir on which traps were placed were given only as medium and large. Large Douglas-fir trees may have served as large dark objects that laboratory studies demonstrated to be more attractive to mountain pine beetles than are small dark objects (Schonherr 1976; Shepherd 1966). In addition, dark-colored bark (Schonherr 1971) and texture (Shepherd 1965) may have been factors that further influenced initial landing rates of mountain pine beetles.

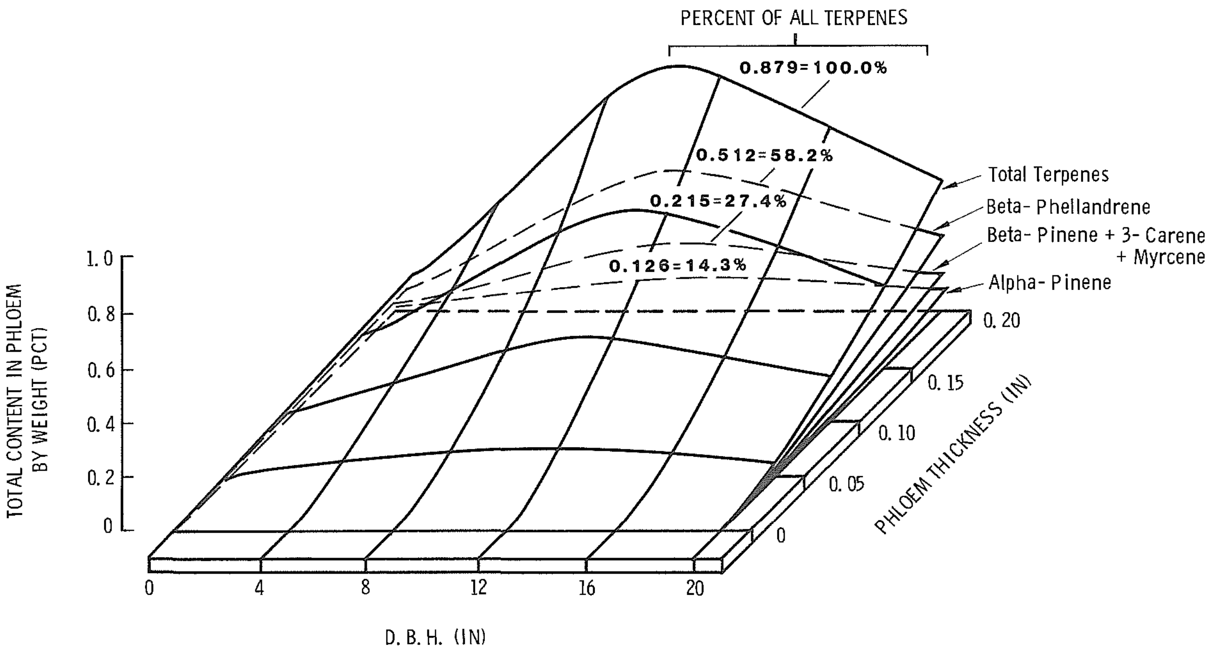

Figure 15.—Monoterpenes in lodgepole pine increase with phloem thickness and diameter.

Random landing, however, does not necessarily mean random attack, but possibly only a necessary resting or shelter spot for the night when temperatures or light conditions fall below the threshold required for flight. Beetles do spend the night on some trees without boring into them (Rasmussen 1974). The next day, they take flight when the temperature threshold is reached.

Hynum and Berryman (1980) further postulate that beetles determine suitable hosts by first nibbling the bark to detect a compound that induces gallery initiation. They state that gallery initiation stimulants appear to be the controlling factor in the host selection process, and these are unrelated to diameter. However, Raffa and Berryman (1982) were unable to demonstrate feeding differences on extracts from trees they considered resistant or susceptible to mountain pine beetle attack.

The idea of beetles being attracted visually to trees on the basis of size (Shepherd 1966) and perhaps olfactorily to higher proportions of terpenes found in large trees (Cole and others 1981) is consistent with most studies of lodgepole pine mortality, losses being highest in the large diameters (Cole and Amman 1969; Evenden and Gibson 1940; Hopping and Beale 1948; Klein and others 1978; Parker 1973; Roe and Amman 1970; Safranyik and others 1974).

The response to large diameter trees is probably related to the greater chance of encountering thick phloem, and hence greater brood survival (Amman 1969, 1975b). Ratios of emerging brood adults to attacking parent adults are much higher in large than in small diameter lodgepole pines (Cole and Amman 1969; Klein and others 1978; Safranyik and others 1974).

After alighting on a lodgepole pine, most female beetles move upward, often obliquely (Rasmussen 1974). They examine many bark scales and crevices before initiating an egg gallery. Beetles avoid smooth areas and burrow into the bark under scales and crevices (Rasmussen 1974). Initial attacks occurred under bark scales 61 percent of the time, and in bark crevices 39 percent of the time. When beetles fail to find an acceptable niche, even on attacked trees, they may take flight after searching less than 30 minutes.

The female that has completed flight and just initiated her gallery has large flight muscles, expanded fat body, reduced reproductive system, and the digestive tract is empty, characteristics necessary for flight (Reid 1958b; 1962b). Following initiation of the egg gallery and mating, the flight muscles and fat body atrophy, and the reproductive and digestive systems increase in size (Reid 1958b; 1962b). The sequence of increase and decrease in organ size is reversed when a beetle prepares to fly to another tree and start a second egg gallery.

The female aggregating pheromone, *trans*-verbenol (Pitman and others 1968), is synergized by a small amount of another pheromone, *exo*-brevicomin (Rudinsky and others 1974). *Trans*-verbenol is an oxidation product of alpha-pinene, one of the terpenes found in small quantity in lodgepole pine. The pheromones, in conjunction with terpenes from the tree, guide other beetles to the tree and serve as a signal for mass invasion of the host (Vité and Pitman 1968). The observation that pheromone release can occur prior to initiation of feeding on the tree led to the hypothesis that females naturally release pheromones in response to stimuli from other females on the same tree (Rudinsky and others 1974). Terpenes in lodgepole pine consists mostly of beta-phellandrene, with small amounts of alpha-pinene, beta-pinene, 3-carene, myrcene, and camphene (Smith 1964). The proportions of these terpenes differ according to geographical location (Smith 1964; Lotan and Joye 1970; Shrimpton 1974). The terpene of particular interest is alpha-pinene, because it rapidly initiates and increases the biosynthesis of *trans*-verbenol by mountain pine beetles (Hughes 1973).

Although a combination of *trans*-verbenol and alpha-pinene was most attractive to mountain pine beetles from western white pine (Pitman and Vité 1969), a combination of *trans*-verbenol and myrcene or terpinolene was considered more attractive to beetles in ponderosa pine (Billings and others 1976). The large amount of beta-phellandrene, and particularly its increase with diameter and phloem thickness in lodgepole pine, suggests that this terpene in combination with *trans*-verbenol may prove to be the most attractive to mountain pine beetles in lodgepole pine (Cole and others 1981).

If a tree is mass attacked (that is, attacked by many beetles within a day or two), pitch ceases to flow from holes where beetles have entered the bark, thus insuring success of beetle reproduction in the tree. Evidence of beetle infestation usually consists of pitch tubes where beetles have entered the tree and boring dust in cracks and at the base of the tree. Some trees have few pitch tubes because of rapid mass attack. Although pitch tubes may be absent or small, orangish-brown boring dust around the base of the tree is a sure sign that the tree has been invaded by a sufficient number of beetles to kill the tree. The size of pitch tubes is dependent upon the number and rate of beetle attacks and amount of moisture available to the tree. Physiological processes by which lodgepole pine resists mountain pine beetle infestation have been described by Shrimpton (1978).

Trees not mass attacked within 48 hours of initial attack were not successfully attacked that year (Rasmussen 1974). This is probably due to lack of sufficient beetles to generate a mass attack, or perhaps the quantity of terpenes and/or beetle pheromones may not be competitive with surrounding sources of attractants. Female beetles in many trees that were not mass attacked abandoned their galleries (Amman 1975a, 1980). Most females abandoned their galleries after constructing up to 2 inches (5 cm) of egg gallery. However, in these same trees, some females constructed gallery and oviposited regardless of the number of attacks on the tree. One notable extreme was a single attack on a tree with construction of 7 inches (17.8 cm) of gallery and oviposition throughout. However, resinosis as described by Reid and others (1967) would prevent egg hatch and/or larval development.

The average height of initial attack is 4.7 ft (1.4 m) (Rasmussen 1974). Initial attacks occurred between 4 and 6.9 ft (1.2 and 2.1 m) above ground level 79 percent of the time, and between 4 and 7.9 ft (1.2 and 2.4 m) 93 percent of the time. The remaining initial attacks occurred below the 4-ft (1.2-m) level. Succeeding attacks spread up, down, and around the bole.

Attack density did not change with height in trees in northern Utah and northwestern Wyoming (Carlson and Cole 1965); however, fewer attacks occurred with increased height in British Columbia (Shepherd 1965). Density of attacks increased with tree diameter (Carlson and Cole 1965). The length of the bole that is infested is partially related to both size of the beetle population and to tree diameter. Most trees 8 to 9 inches (20 to 23 cm) diameter at breast height (d.b.h.) are infested to a height of about 20 ft (6 m) or less, compared to an infested height of 30 to 40 ft (9 to 12 m) for trees 20 inches (51 cm) d.b.h. and larger (Cahill 1960). Differences in infested height occur between areas, with trees on the best sites being infested to a greater height.[4] This difference is related to the greater bole length on good sites. Klein and others (1978) noted that as an outbreak subsides there is a decline in infested height, which probably is related to lower beetle density since beetles attack the base first and then proceed to attack higher.

The number of attacks on the tree differs significantly with respect to cardinal direction, with the greatest density on the north aspect (Reid 1963). During a 2-year study, Rasmussen (1974) recorded 36 percent of initial attacks on the north aspect, 25 percent on the west, 21 percent on the east, and 18 percent on the south. Total attacks were distributed similarly to that of initial attacks. North aspects received the most, east and west aspects had intermediate numbers of attacks, and the south aspect had the least (Shepherd 1965). The distribution of attacks by aspect suggests beetles prefer cooler temperatures. Maximum bark surface temperatures on the north side of the tree were 1.8° F (1° C) cooler than air temperatures, whereas on the south side they were 11° F (6° C) higher than air temperatures (Powell 1967). Light may also influence attack behavior by aspect because beetles that are ready to initiate galleries are negatively phototactic (Schonherr 1971). In addition, the adult reverses its photopositive response at temperatures between 95° and 99.5° F (35° and 37.5° C) and becomes photonegative (Shepherd 1966).

Density of attacks is greater on rough than on smooth bark (Shepherd 1965; Safranyik and Vithayasai 1971). The number of niches available to females for starting galleries may influence attack density (Safranyik and Vithayasai 1971). Pheromones and tree vigor are also important factors. Attack density on individual trees is regulated by host condition (oleoresin and exudation) (Renwick and Vité 1970). Attacks stop when the tree no longer exudes resin at the sites of attack. Differences in attack densities on lodgepole pine trees of different size in any given year suggest that host condition is a factor in lodgepole pine, with the most vigorous trees attacked heaviest (Carlson and Cole 1965; Cole and others 1976). The work of Rudinsky and others (1974) indicates that antiaggregative pheromones, *exo*-brevicomin and *endo*-brevicomin, are involved in regulating attack densities. The amount and rapidity with which pheromones are produced are probably related to the sex ratio of the attacking population. Cole and others (1976) hypothesized that the change in attack density over the life of an infestation is related to sex ratio of the population.

Sex ratio differs among mountain pine beetle broods, but is almost always in favor of females. Any factor that stresses the population reduces male survival. Reduced male survival has been attributed to crowding (W. Cole 1973), to length of cold storage (Safranyik 1976; Watson 1971), and to thin phloem (Amman and Pace 1976) in laboratory studies; and to drying (Amman and Rasmussen 1974) or a combination of drying and thin phloem (Cole and others 1976) in field studies.

In laboratory studies, some broods consist entirely of females. This phenomenon raises the possibility of differential survival of X and Y sperm. Another possible consideration is the presence of a lethal cytoplasmic factor that causes death of the males during embryonic development (Lanier and Oliver 1966; Lanier and Wood 1968).

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[4] Johnson, Philip C. Height of broods as a factor affecting the treatment of standing lodgepole pine trees infested by the mountain pine beetle. Coeur d'Alene, ID: U.S. Department of Agriculture, Agricultural Research Service, Bureau of Entomology and Plant Quarantine, Forest Insect Laboratory; 1951. 8 p. Unpublished report.

Sex ratios of beetle populations change somewhat from year to year as a result of population stress. Sex ratio shows a fairly strong association to tree diameter (Cole and others 1976) and changes by year of infestation (fig. 16).

During the initial years of an infestation, there was either no relation to tree diameter or only a slight tendency for small diameter trees to produce fewer females than large trees. For example, in 1970, beetles from 6-inch (15-cm) trees averaged 63 percent female compared to 70 percent female from 20-inch (50-cm) trees. However, as the infestation progressed, small diameter trees produced higher percentages of females than did large trees. In fact, during the middle years of the infestation, large diameter trees produced more males than early or late in the infestation. For example, at the height of the infestation (1975), brood from 6-inch (15 cm) d.b.h. trees averaged 85 percent female, compared to only 55 percent female from 20-inch (50-cm) d.b.h. trees (fig. 17).

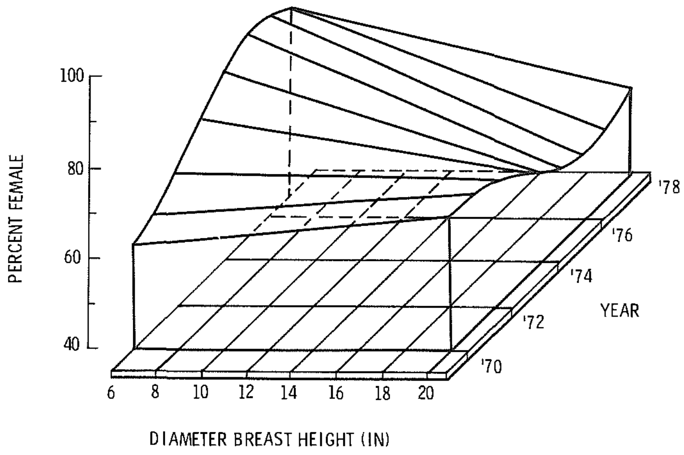

Figure 16.—Percent female in mountain pine beetle populations differed by diameter of lodgepole pine and year of infestation, Wasatch-Cache National Forest, Utah.

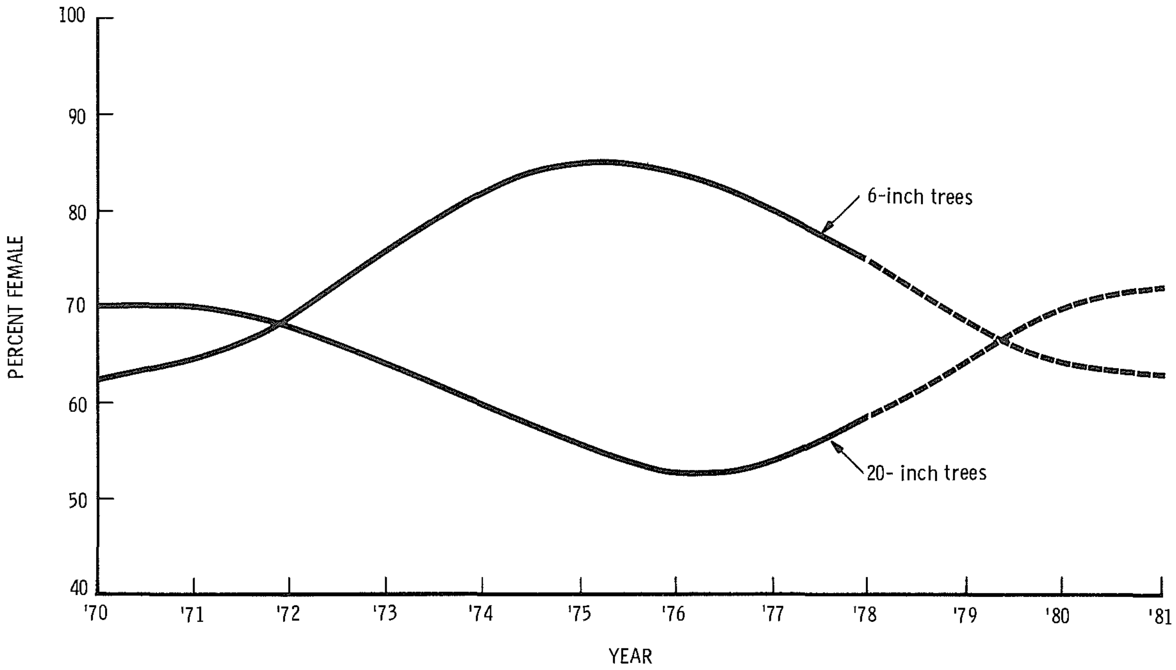

Figure 17.—Change in percent female of mountain pine beetle populations for the two extremes in lodgepole pine diameter classes during the life of an infestation, Wasatch-Cache National Forest, Utah.

An increase in the proportion of females emerging from small trees appears to occur almost from the beginning of the infestation. This suggests that conditions within the small trees are at their best at this time for male survival. As the infestation progresses, gallery density increases; thus intraspecific competition increases and, in addition, drying as a result of increased beetle activity under the bark increases. These factors are adverse to male survival and shift the sex ratio in favor of females. However, the decline in the proportion of females emerging from small trees toward the end of the infestation is difficult to explain. Conditions associated with less egg gallery possibly are beginning to shift more toward those that existed at the beginning of the infestation.

In the large diameter trees, survival may be impeded by the light gallery densities and conditions associated with them; for example, more resinous conditions in the phloem at the beginning of the infestation. In addition, the benefit of close association of larvae observed by W. Cole (1973) in laboratory rearings may be missing. As the infestation progresses and gallery density increases, conditions for survival of males apparently improve. Following the peak of the infestation, gallery density continues to increase, resulting in increased intraspecific competition and drying due to excessive amounts of egg gallery and to opening of the bark by large numbers of feeding larvae. These factors are adverse to male survival, resulting in the sex ratio shifting more toward females.

Because of the shift in sex ratio in field populations after the year of peak emergence, insufficient males probably exist to mate most females in a relatively short time. Hence, unmated females continue to produce the aggregative pheromone that attracts additional females and increases attack density. Attacks probably stop when enough males arrive to produce sufficient concentration of the antiaggregative pheromones. Therefore, the mountain pine beetle appears to regulate attack density by the pheromone system (Rudinsky and others 1974), but the differences noted in attack density among trees of different diameter appear to be related to host condition (Renwick and Vité 1970).

The strip attack is another strategy that helps the mountain pine beetle survive when their numbers are low. Only a strip of bark on a portion of the tree trunk is infested without killing the tree. These strips can contain extremely high brood production. For example, the central portion of a strip attack involving less than 25 percent of the circumference of a 16-inch (41-cm) d.b.h. lodgepole on the Wasatch-Cache National Forest had 180 brood emergence holes/ft^2 (930 cm^2) of bark surface. Egg gallery and larval mines along the edges of strip attacks are inundated with resin, and no brood survives. The bark from strip attacks eventually sloughs off, leaving the egg gallery etchings exposed on the sapwood surface. Previous mountain pine beetle infestations can be dated by comparing tree age with age of the strip attack.

In addition to the effect of attacking beetles on the tree, blue-stain fungi (*Ceratocystis montia* [Rumbold 1941] and *Europhium clavigerum* [Robinson-Jeffrey and Davidson 1968]) introduced by adult beetles play an important role in causing tree death (Safranyik and others 1975). Fungal spores, which are picked up during maturation feeding by new adults prior to leaving the tree, are carried in a maxillary mycangium (Whitney and Farris 1970). This association suggests a true symbiosis. Spores are introduced into a live tree as beetles attack and start constructing egg galleries. Blue-stain fungi invade the phloem, and especially the sapwood, where they help to reduce resin flow and disrupt the vascular system (Nelson 1934). An initial rapid reduction in moisture occurs in the sapwood (Reid 1961). Therefore, one benefit to the beetle appears to be regulation of moisture in the tree during beetle development. Blue-stain fungi do not appear to be necessary to mountain pine beetle nutrition (Whitney 1971).

Mating and Oviposition

Almost all mating occurs after the female starts her egg gallery. Less than 1 percent of females were mated in lodgepole pine prior to emergence (Reid 1958a). Only 2 percent of the females removed from ponderosa pine bark prior to emergence contained spermatozoa (McCambridge 1970). In males, quantity of mature spermatozoa increases within vasa deferentia and vasa efferentia for several days following emergence and mating (Cerezke 1964).

After the female starts an egg gallery she usually is soon joined by a male. Acoustic signals are an important part of attack and mating behavior. Males stridulate prior to entering the gallery. Several reasons for this have been proposed. Both attractant and stress stridulations were identified (Michael and Rudinsky 1972). Stridulation stopped production of aggregation pheromone by the Douglas-fir beetle, *D. pseudotsugae* Hopkins (Rudinsky 1968). In addition, stridulation may be part of territorial behavior by discouraging males from entering occupied territory, thus distributing the frequently scarce male population more efficiently (McGhehey 1968). Male stridulation also notifies the female that a male and not a female is entering her gallery (Ryker and Rudinsky 1976). Females usually repel other females that attempt to enter their galleries.

Beetles may mate at the entrance or within the gallery. Within the gallery, males and females turn in opposite directions with abdomens towards each other, male posterior to the female (Reid 1958a). An average of 11 minutes elapsed from male-female contact until copulation, which lasted 3.5 to 5 minutes (Ryker and Rudinsky 1976). Copulation may occur several times during egg gallery construction (Reid 1958a). After copulation, the male may either leave the gallery and seek another female to mate, or he may stay in the gallery with the female. Should the male stay, he pushes boring dust (that the female chews away in the process of making the gallery) and resin out of or into the bottom of the gallery. The boring dust plug packed in the entrance of the gallery probably prevents other mountain pine beetles and enemies from entering. If a male gets in the way of the female, she kills him and packs him along with the boring dust into the bottom of the gallery. Mated females elongate their egg galleries at a rate faster than unmated females, presumably because of assistance by the male (if he stays) in moving and packing boring dust (fig. 18) (Amman 1980; Reid 1958a; Rasmussen 1974). The female usually cuts horizontally or obliquely across the grain of the wood for about 0.25 inch (6 mm) when she initates the gallery, then tunnels upward through the phloem and the outer surface of the sapwood, following the grain of the wood even when it is spiral-grained. This behavior, coupled with the original spacing of galleries, does much to reduce intraspecific competition among the developing brood.

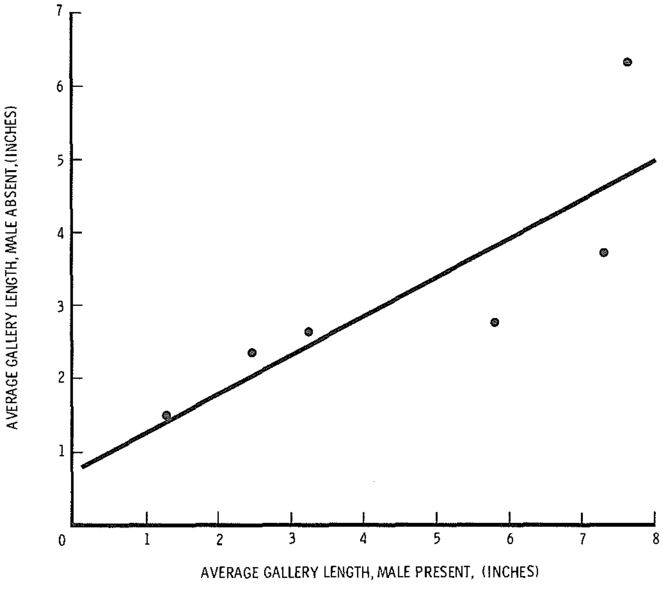

Figure 18.—Average lengths for mountain pine beetle galleries that contained males, compared to those that did not contain males (only those plots were used that had both categories represented) (Amman 1980).

Ventilation tunnels are placed at irregular intervals along the egg gallery. These extend from the egg gallery to near the outer surface of the bark and appear related to stage of gallery construction, thickness of bark, and beetle activity (Wood 1963). In thin-barked lodgepole pine, 18 of 35 egg galleries contained ventilation chambers, and only 3 had more than 1 chamber (Wood 1963).

Eggs are laid in individual niches cut in the phloem in groups that alternate irregularly between the two sides of the gallery. The average number of eggs laid in an inch of gallery ranges between 4.2 and 5.9 (1.7 and 2.3/cm). However, as many as 15 eggs/inch (5.9/cm) have been laid (Amman 1972a; Reid 1962b). More than 200 eggs were deposited in some individual galleries that were more than 50 inches (127 cm) long (Reid 1962b). Heavy egg production occurs during early gallery construction, then gradually declines (fig. 19). Several factors affect oviposition. Oviposition differs with the proximity of adjacent egg galleries. The average number of eggs laid on sides of adjacent galleries ranged from 1.7/inch (0.7/cm) for galleries spaced 0.12 inch (3 mm) apart to 3.6/inch (1.4/cm) for galleries spaced 0.88 inch (21 mm) apart (fig. 20). Oviposition reaches a plateau where galleries are 1 inch (25 mm) apart. Therefore, the activities of adjacent parent beetles would have little effect at distances greater than 1 inch when females are boring simultaneously. Stridulation by females probably serves a territorial function (Rudinsky and Michael 1973) and helps to maintain distance between galleries or causes reduced oviposition. However, when one beetle bores ahead of its neighbor, previous gallery construction might be sensed from drying of phloem and presence of fungi, bacteria, and yeasts, and thus the beetle reduces oviposition.

Large beetles lay more eggs than small beetles (Amman 1973; McGhehey 1971; Reid 1962b). The average number of eggs laid per inch of gallery ranged from 3.2 (1.3/cm) for a beetle 0.17 inch (4.3 mm) long to 7.9 (3.1/cm) for a beetle 0.21 inch (5.4 mm) long (fig. 21). The average number of eggs laid per day ranged from 3.4 for a beetle 0.17 inch (4.3 mm) long to 8.2 for a beetle 0.23 inch (5.9 mm) long (fig. 21). Although these differences are significant, much variation in egg-laying capacity exists among beetles of a similar size, even when they are held under similar conditions of food, temperature, and egg-laying substrate. Average length of gallery constructed per day also was significantly related to beetle length.

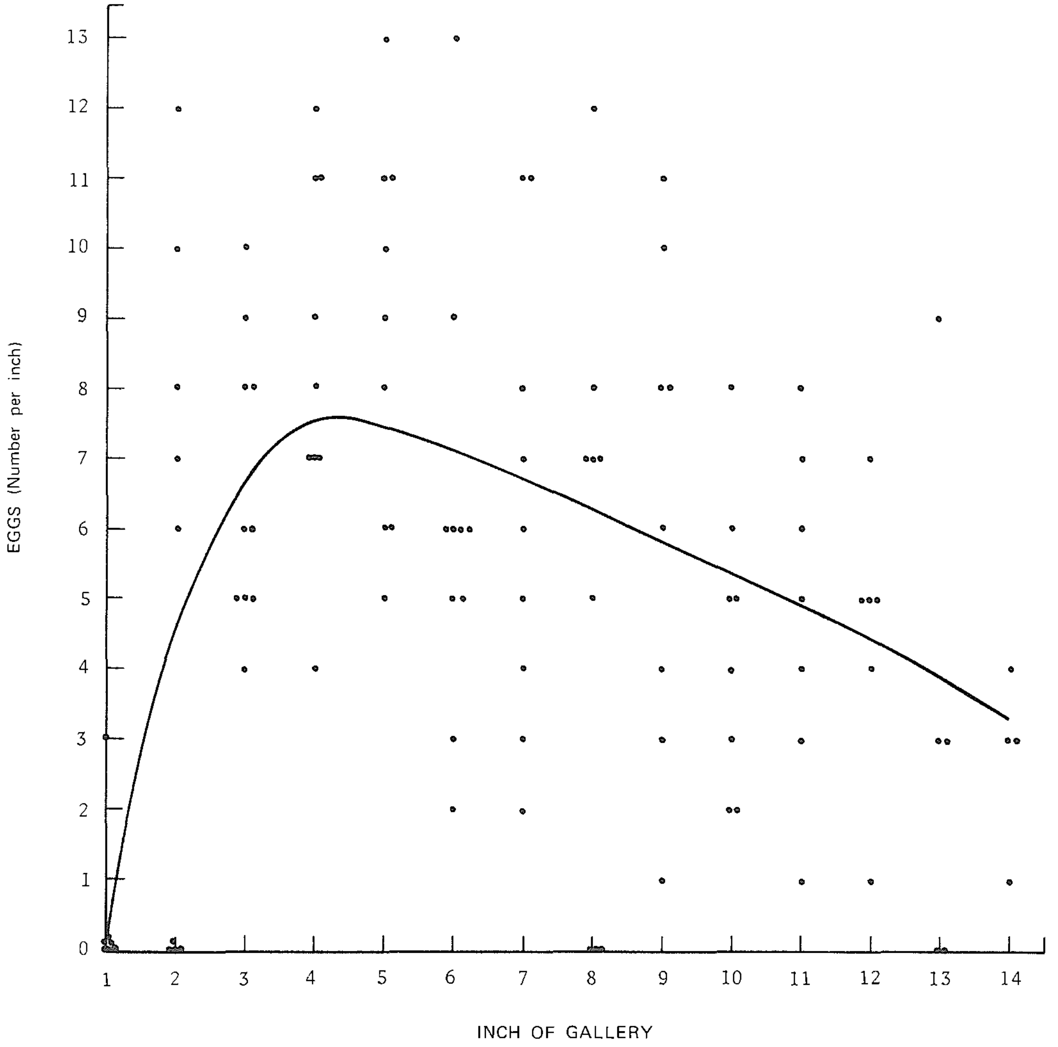

Figure 19.—Numbers of mountain pine beetle eggs laid per inch of gallery (46 galleries 6-14 inches [15-36 cm] long). (See regression statistics in appendix.)

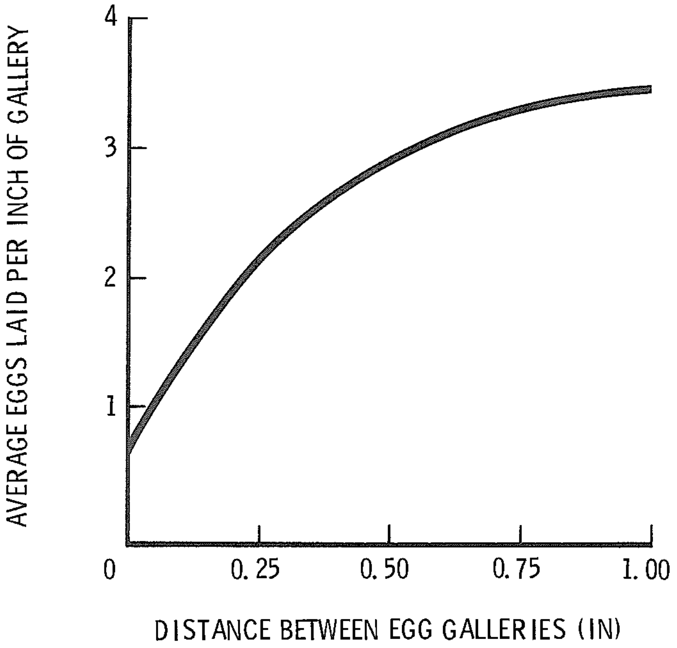

Figure 20.—Average number of eggs laid per inch of egg gallery in relation to distance between galleries.

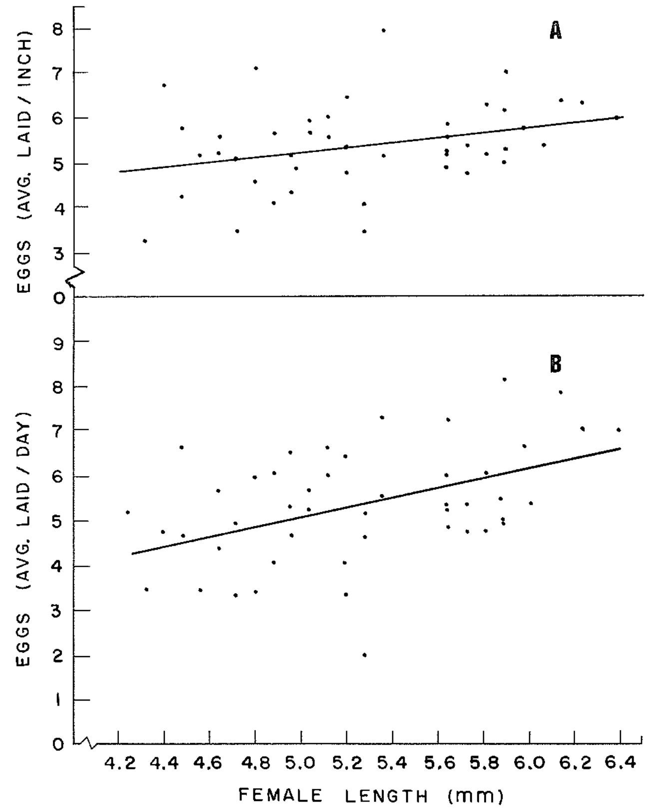

Figure 21.—The relation of oviposition behavior to length of female mountain pine beetle. (See regression statistics in appendix.)

Oviposition differed in relation to phloem thickness, with greater numbers of eggs laid in thick than in thin phloem (fig. 22). The average number of eggs ranged from 3.5/inch (1.4/cm) in phloem 0.06 inch (1.5 mm) thick to 9.6/inch (3.8/cm) in phloem 0.18 inch (4.6 mm) thick. Average number of eggs laid per day ranged from 1.7 in phloem 0.06 inch (1.5 mm) thick to 7.7 in phloem 0.20 inch (5.1 mm) thick. The relation between rate of gallery construction and phloem thickness was not significant. This is surprising because a beetle in thin phloem constructs more of its gallery in the sapwood (which should be harder to chew) than a beetle in thick phloem. Average depth of excavation into the sapwood ranged from 0.045 inch (1.1 mm) in phloem 0.04 inch (1.0 mm) thick to 0.01 inch (2.8 mm) where phloem was thicker than 0.12 inch (2.8 mm). A possible explanation for differences in rates of oviposition and numbers of eggs laid between thin and thick phloem might be related to lower nutritional quality of thin phloem. Another explanation is that beetles expended more energy in constructing galleries where they chewed deep into the sapwood, thus leaving less energy for egg production.

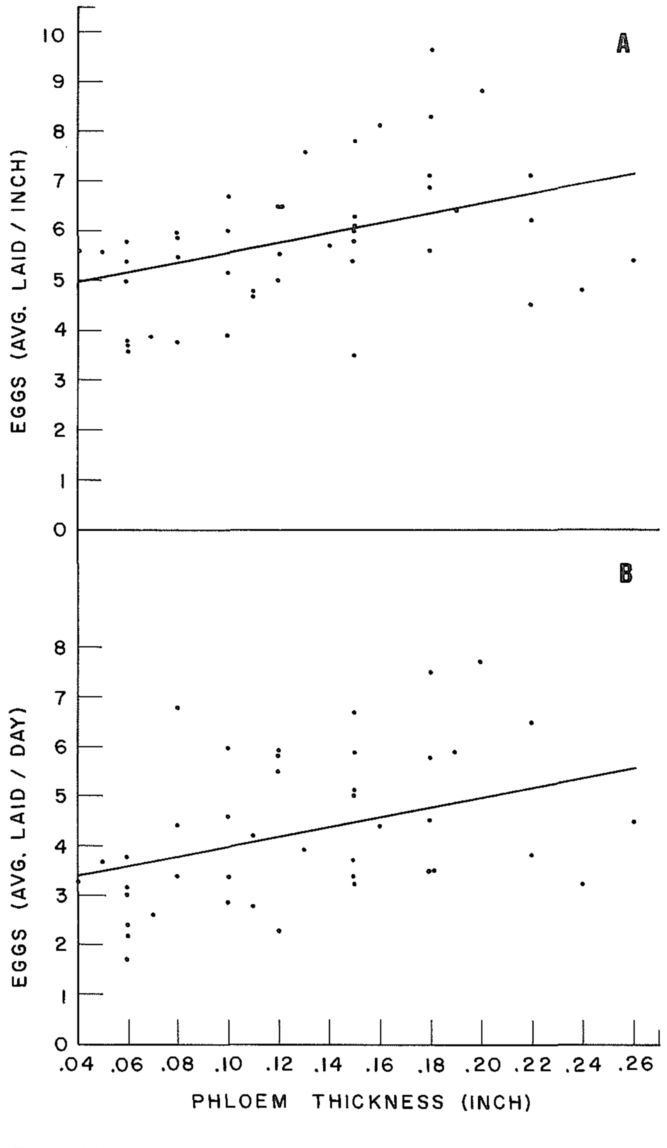

Figure 22.—The relation of oviposition behavior of the mountain pine beetle to thickness of lodgepole pine phloem. (See regression statistics in appendix.)

Both rate of gallery construction and number of eggs laid are strongly related to temperature (fig. 23). Some oviposition occurs as low as 35° F (1.7° C) (Reid 1962b). However, both functions increase substantially when temperatures exceed 59° F (15° C) (Amman 1972a). Average number of eggs laid per inch of gallery ranged from 1.3 (0.5/cm) at 44.6° F (7° C), to 8.3 (3.3/cm) at 59° F (15° C). The number of eggs laid per day ranged from an average of 0.23 at 44.6° F (7° C) to 6.6 at 68° F (20° C). A curvilinear relation is indicated, with a big increase in oviposition occurring at 68° F (20° C). Peak oviposition is almost reached at 68° F (20° C); consequently, numbers of eggs would not be expected to increase significantly at higher temperatures. However, the curves for both length of gallery constructed per day and number of eggs deposited per day continue to rise and could be expected to peak at temperatures higher then 68° F (20° C).

Crowding during larval development affected oviposition by the resultant new adults (Cole 1973). Adults very crowded as larvae laid fewer eggs and constructed fewer inches of gallery than adults much less crowded as larvae. Likewise, adults crowded at medium levels as larvae laid fewer eggs than adults least crowded as larvae.

Egg Hatch

Embryonating eggs were classified into four stages of development. Stage I eggs were homogeneously opaque in appearance. Stage II eggs were clear at one end. Stage III eggs were clear at both ends. And stage IV eggs possessed a clearly defined head capsule (Reid and Gates 1970).

Several factors are important to egg hatch. Reid and Gates (1970) established 40° F (4.4° C) as minimum and about 95° F (35° C) as maximum temperatures at which eggs could hatch. An average of 5,113 degree-hours (a degree-hour is 1 degree of temperature sustained for 1 hour above the threshold of development) above 40° F (2,841 degree-hours above 4.4° C) was required for 50 percent of eggs to hatch under field conditions. Optimum temperatures for hatch in the laboratory range from 69° to 77° F (21° to 25° C) (Reid and Gates 1970). We observed that hatching occurred between 36.6 days at a constant 50° F (10° C) and 8.4 days at a constant 68° F (20° C), the range of temperatures used (fig. 24).

In addition to suitable temperature, 90 percent or greater relative humidity is required for successful embryogenesis and hatch (Reid 1969). Egg survival was only slightly affected by resin vapors (3 percent mortality), but an envelope of resin caused almost complete mortality (Reid and Gates 1970). Mortality was about 40 percent when eggs were only half covered by resin.

Larval Behavior and Development

After hatching, larvae feed individually in the inner bark (phloem). Larval galleries usually extend at right angles from the egg galleries of the parents. Consequently, feeding larvae eventually girdle the tree.

W. Cole (1973) studied larval behavior under several levels of crowding in an artificial medium. He found that initial feeding and survival rates of larvae increased as crowding increased. Also, he noted that stadial length (duration between molts) decreased with increased crowding during the first and second stadia, but increased during the third and fourth stadia. Decreased survival to the adult stage occurred with prolonged crowding at high levels.

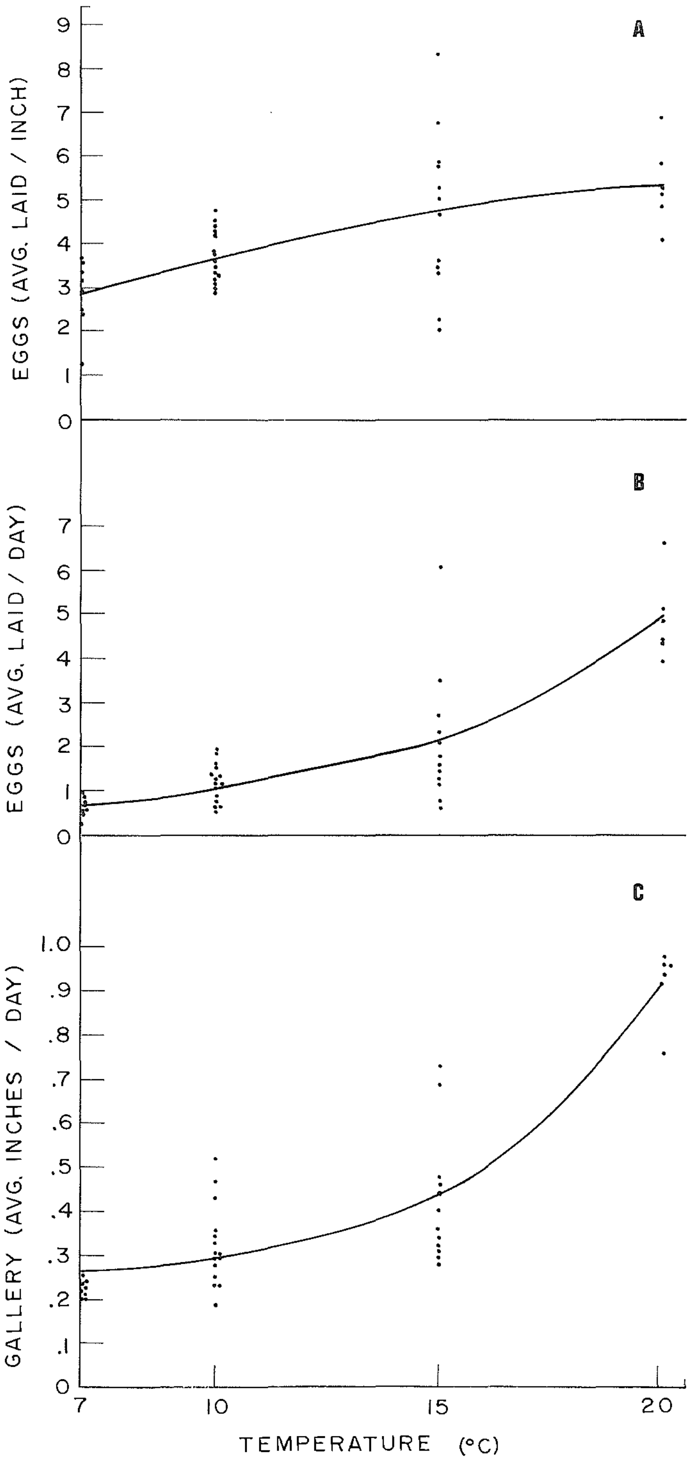

Figure 23.—The relation of oviposition behavior of the mountain pine beetle to temperature. (See regression statistics in appendix.)

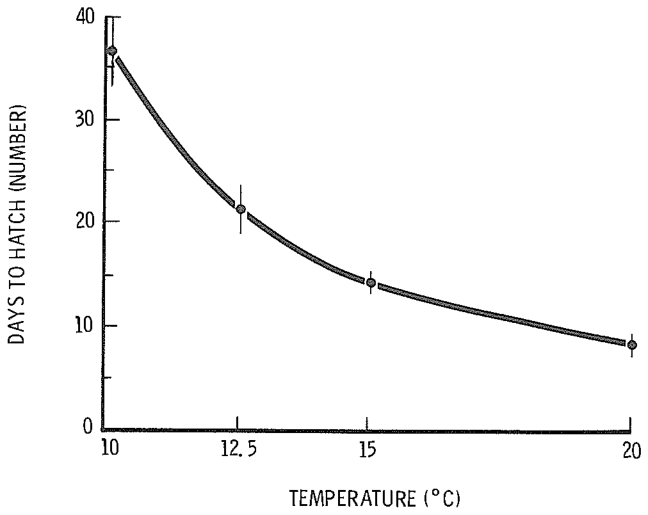

Figure 24.—Average number of days for mountain pine beetle eggs to hatch at different constant temperatures. Vertical line through each data point represents ± one standard deviation.

Larval behavior differs in thick and thin phloem. In thick phloem, a double layer of larvae may occur while larvae are small. Some feed near the surface of the sapwood, whereas the remainder near the inner surface of the dead outer bark. This behavior initially reduces competition for food and space.

In both thick and thin phloem when larval mines and egg galleries are encountered, some larvae may cross them while other larvae may mine toward the egg gallery. Still others submerge into the phloem to mine under galleries. Larvae do not necessarily keep extending their mines away from the parent egg gallery. Some back down their mines, then commence to feed again and fill the area behind them with boring dust. Others feed along the edges of their mines, making the mines three to four times the width of the larva and up to 0.5 inch (1.27 cm) long.

Larvae in thin phloem mined faster than those in thick phloem for the first 2 weeks ($P < 0.02$), but at the end of the third week, galleries were of similar length ($P > 0.05$) (fig. 25a). The close proximity of larvae in thin phloem may have stimulated more rapid feeding (W. Cole 1973) than in thick phloem where two layers of larvae may occur. Possible nutritional differences between thick and thin phloem would influence larval feeding rate. Larvae in thin phloem possibly needed to mine farther to obtain the same nutritional requirements acquired with a short gallery in thick phloem. The increased feeding rate by large larvae in thick phloem may disperse larvae before pupation. Physical encounters among larvae frequently result in death either by cannibalism or entomocide, which W. Cole (1973) defines as killing of one larva by another but not necessarily for food as with cannibalism. Dispersion of larvae prior to pupation would reduce the chances of pupae being cannibalized by late developing larvae, and would reduce competition for food by new adults during maturation feeding when they consume up to 0.5 inch^2 (1.6 cm^2) of phloem each during maturation feeding prior to flight.

As expected, first instars in both thin and thick phloem were the same size. However, larvae feeding in thin phloem had significantly wider head capsules during the second and third instars than larvae in thick phloem ($P < 0.001$), but fourth instars from thick phloem had larger head capsules than larvae in thin phloem ($P < 0.001$) (fig. 25b). The larger second and third instars in thin phloem may be related to close association and faster feeding rate of larvae (indicated by longer larval mines) (W. Cole 1973). The larger size of fourth instars in thick phloem may be related to better overall nutrition and an appar-

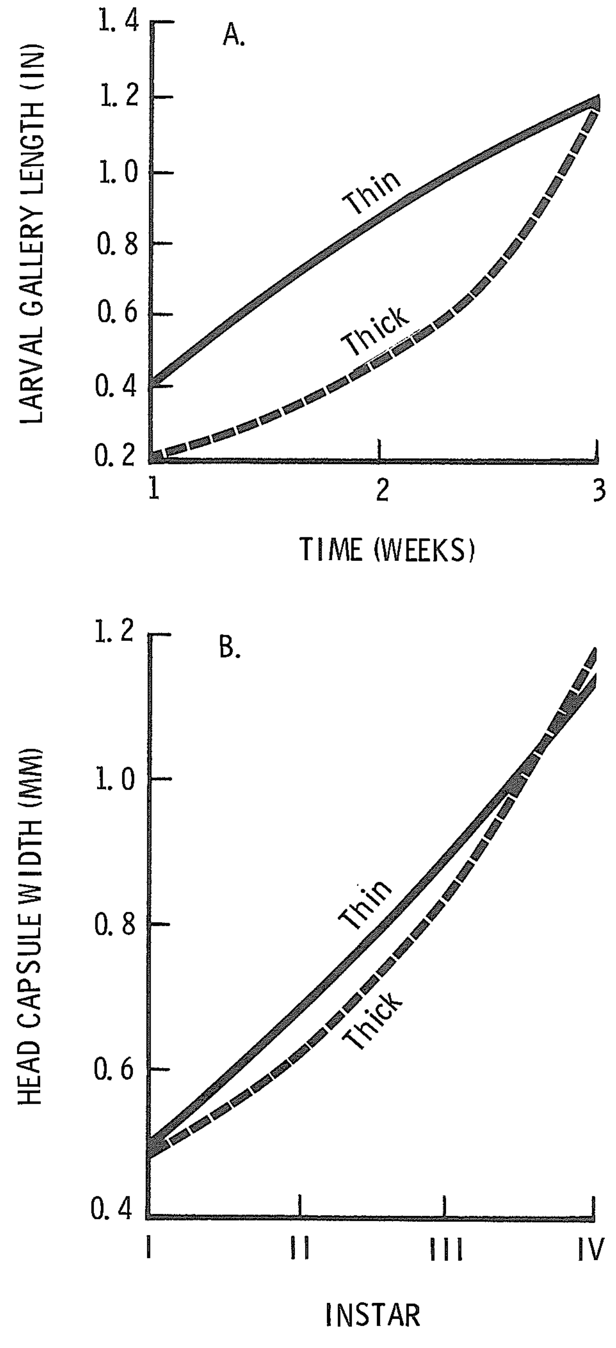

Figure 25.—A. Rate of larval gallery construction in thin and thick phloem; B. head capsule width of larvae reared in thin and thick phloem.

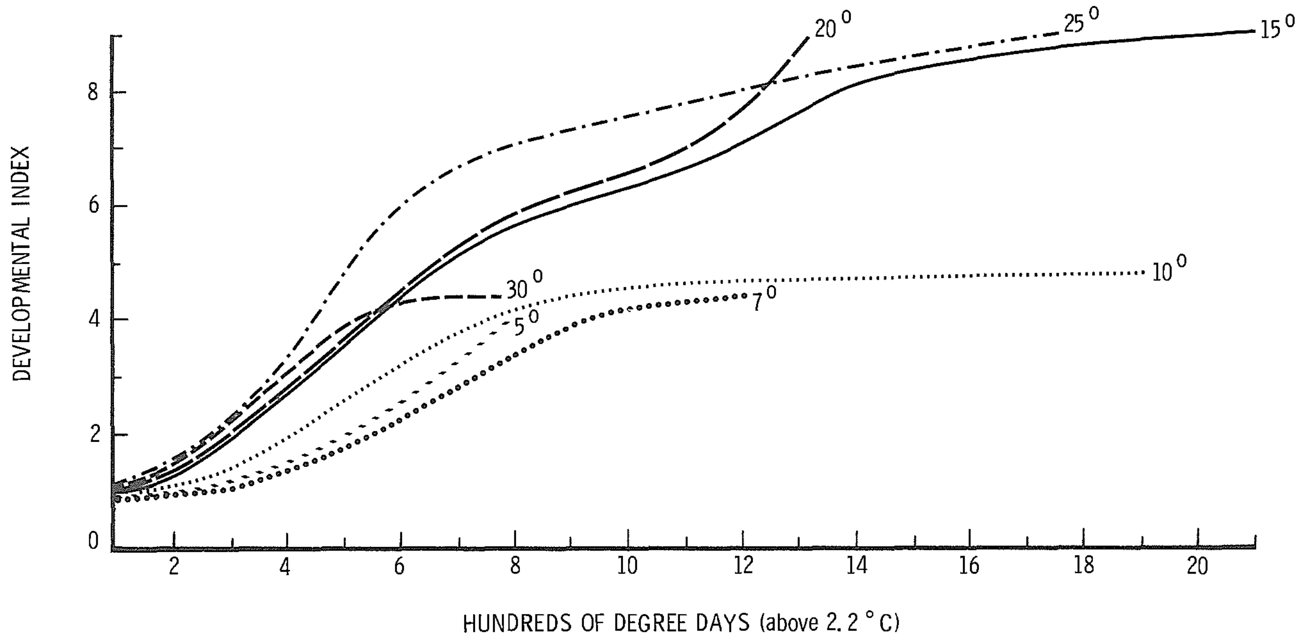

Figure 26.—Mountain pine beetle development at seven constant temperatures. Developmental Index: 1 = egg; 2-5 = I-IV larval instars; 6 = pupa; 7 = teneral adult; 8 = new adult; 9 = new emerged adult.

ent rapid feeding rate (or mining rate) in this instar. Adults from larvae feeding in thick phloem were significantly larger than those resulting from larvae feeding in thin phloem, as previously noted by Amman and Pace (1976).

Beetle development from egg to teneral adult required about 626 degree-days (a degree-day is 1 degree above the threshold for 24 hours) above 50° F (348 degree-days above 10° C) threshold in the subcortical zone of the tree (Powell 1967), and about 500 degree-days above 50° F (278 degree-days above 10° C) air temperature (Reid 1962a). We found the beetle required about 675 degree-days above 50° F (375 degree-days above 10° C) to reach the teneral adult stage at a constant 59° F (15° C), our lowest temperature at which development was completed. Degree-days required for development at 59° F (15° C) approximates the estimate given for the subcortical region by Powell (1967). Beetle rearing was unsuccessful at 59° F (15° C) at Victoria (L. Safranyik, Canadian Forestry Service, Victoria, B.C., personal communication, May 5, 1981), suggesting differences in beetle subpopulations.

In laboratory studies, the threshold for larval development is near 36° F (2.2° C) (McCambridge 1974). Growth rate increases with temperature from 40° to 55° F (4.4° to 12.8° C) and was similar at each test temperature regardless of individual larval size (McCambridge 1974).

We conducted studies on rate of beetle development at constant temperatures from 41° to 86° F (5° to 30° C). The rate of development was very slow at temperatures of 41° and 44.6° F (5° and 7° C), but much of this was attributed to very slow egg development. Even though the slabs were held at room temperature of 76° F (24.4° C) for 8 days and received 320 degree-days above 36° F threshold (178 degree-days above 2.2° C), an additional 250 and 427 degree-days above 36° F (139 and 237 degree-days above 2.2° C) at 41° and 44.6° F (5° and 7° C), respectively, were required before larvae were first detected. The apparent greater heat requirements at 44.6° F (7° C) than 41° F (5° C) are an artifact probably related to time of initial oviposition. First and second instars seem to develop moderately fast at these low temperatures. However, development begins to slow when larvae reach the third instar (fig. 26). Development of third instars is slower than in earlier instars, even at 50° F (10° C). Slowing of development is even more pronounced in the fourth instar at these low temperatures, and pupation requires more degree-days (or possibly a much higher threshold temperature) than for temperatures exceeding 50° F (10° C). It appears that the threshold for pupation is near 50° F (10° C).

Larval growth is not linear at temperatures below 59° F (15° C) (fig. 26). Higher temperatures are required to maintain the growth rate of earlier instars, and apparently a higher threshold temperature is needed for development to proceed to the next stage. Only 11 percent of larvae held at 50° F (10° C) reached the pupal stage after 2,245 degree-days above 36° F (2.2° C) threshold, whereas beetles held at 59° F (15° C) contained 14 percent pupae after only 819 degree-days. Overall development was most efficient (required the fewest degree-days) at 68° F (20° C), with some beetles completing development and emerging after 895 degree-days above 36° F (2.2° C) threshold. Slightly more degree-days were required at 59° and 77° F (15° and 25° C)—1,150 and 1,300 respectively—before emergence. Both temperatures appear somewhat inhibitory to later stages beginning with the pupa at 50° F (10° C) and teneral adult at 77° F (25° C). At a constant 86° F (30° C), beetles died before completing the pupal stage.

Certain advantages accrue to the mountain pine beetle because of the greater heat requirements of advanced stages. First, in the fall the greater heat requirements prevent most beetles from progressing to the pupal and teneral adult stages, which are highly susceptible to winter killing by cold temperatures (Amman 1973; Reid 1963). Second, the greater heat requirements (or higher threshold temperature for development) of late stages help to keep the population together by allowing late-hatching larvae to catch up in development. Synchrony is accomplished when the early instars keep developing after temperatures are too cool for development in later instars. Synchrony of the population is important if the beetles are to emerge en masse to infest and kill the largest, most vigorous trees in the forest.

When fully developed in late spring, larvae excavate oval cells in the bark (these may extend slightly into the sapwood) where they pupate and later become adults.

BEETLE SURVIVAL AND MORTALITY

Phloem Thickness Effect

The principal factor determining brood survival and production in lodgepole pine is quantity of phloem, the food of developing larvae (Amman 1969; 1972b). Phloem in a sample of lodgepole pines had accumulated for an average of 21.7 years (Cabrera 1978). Phloem thickness is positively correlated with tree diameter (Amman 1969) and to characteristics of good tree vigor (D. Cole 1973). Brood production of the mountain pine beetle was found to increase with total bark thickness (Amman 1969; Reid 1963). Phloem thickness was considered the causal factor (Amman 1969). Subsequent laboratory studies (Amman 1972b) and field studies (Berryman 1976) demonstrated brood production to be positively correlated with phloem thickness. In the laboratory, brood production ranged from an average of 23 beetles/ft² (930 cm²) for phloem 0.05 inch (1.27 mm) thick to an average of 138 beetles/ft² (930 cm²) for phloem 0.17 inch (4.32 mm) thick (fig. 27). Brood production also shows a positive increase with egg gallery length (Amman and Pace 1976) and number of attacks (Berryman 1976; Schmid 1972) forming an asymptote that extends out to the highest densities observed. This suggests that brood production will be governed by phloem quantity, regardless of intraspecific competition.

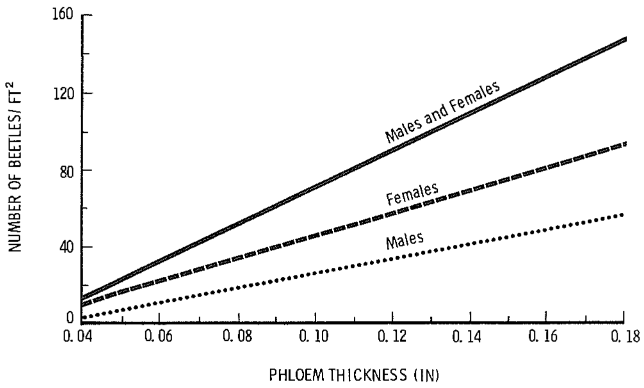

Figure 27.—Mountain pine beetle brood production in relation to phloem thickness of lodgepole pine. (See regression statistics in appendix.)

Phloem of young trees or younger portions of older trees (upper portions of the boles) has more and larger cortical resin ducts than that of older portions of trees (Berryman 1976). However, numbers and sizes of cortical resin ducts vary considerably (Cabrera 1978). As the number of resin ducts increases in the phloem, less food is available for larvae (Amman 1972b). Mountain pine beetles produce large numbers of new adults in phloem of young trees or younger portions of older trees in the laboratory (table 6). However, beetles don't do well in young trees in the field because of excessive drying following tree death (Cole and others 1976). Drying may be related to the interaction of the resinous bark of young trees and the blue-staining fungi that appear to be moisture regulators of the beetle-infested tree. Resin could adversely affect survival of the fungi (Shrimpton 1973) and its penetration into the sapwood (Ballard and others 1980) where the rate of transpiration and hence drying of the wood might be slowed.

Table 6.—Mountain pine beetle production, percent female and length in billets from different aged portions of three lodgepole pine trees 50-59 years old

	Age class							
	19-29 (n = 15)		30-39 (n = 20)		40-49 (n = 12)		50-59 (n = 13)	
	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd	$\bar{x}$	sd
Beetles/ft² (930 cm²)	162.34	28.94	172.45	34.14	156.51	35.35	174.32	30.95
Percent female	63.40	9.69	64.04	8.37	68.27	10.22	61.88	7.36
Beetle length (mm)								
Male	4.37	.09	4.34	.15	4.40	.13	4.39	.16
Female	4.96	.10	4.94	.09	4.99	.08	4.97	.08

Factors of Mortality

A mortality factor, in order to be effective, must cause a departure from expected survival and emergence as predicted from phloem thickness. The mortality factor then would either cause the infestation to decline with less overall tree killing or cause the rate of tree killing to slow. In the latter case, the eventual loss of trees could be about the same as where the mortality factor was not operating. An example is the effect of insecticide treatment of mountain pine beetles, which was shown to extend the length of the infestation in a case or two but did not save trees since tree losses were the same in treated and untreated stands (Amman and Baker 1972).

A variety of mortality factors affect mountain pine beetle populations, and their influence in several geographic areas was investigated during many years of life table sampling. Two earlier papers (Cole 1974, 1975) detailed portions of these investigations.

Parasites and predators.—A long list of parasites and predators of the mountain pine beetle has accumulated starting with DeLeon's (1934) study; a few additional ones have been added since then (table 7). The most numerous insect parasites and predators in lodgepole pine have been presented in a field key (Rasmussen 1976).

Table 7.—Parasites and predators of the mountain pine beetle; all species were reported by DeLeon (1934) unless otherwise noted

- Class Insecta
  - Order Hemiptera
    - Family Anthocoridae
      - Several species
  - Order Coleoptera
    - Family Staphylinidae
      - *Nudobius* sp.
      - *Quedius longipennis* Mann.
    - Family Histeridae
      - *Isolomalus mancus* Csy.
      - *Platysoma punctigerum* Lec.
    - Family Cleridae
      - *Enoclerus lecontei* (Wolc.)
      - *Enoclerus sphegeus* (Fabr.)
      - *Thanasimus undatulus* Say.
    - Family Pythidae
      - *Pytho planus* Herbst.
    - Family Trogositidae
      - *Temnochila virescens* (Fab.) var. chlorodea (Mann.)
    - Family Nitidulidae
      - *Glischrochilus vittatus* (Say)
      - *Epirea linearis* Makl.
    - Family Rhizophagidae
      - *Rhizophagus procerus* Csy.
    - Family Cucujidae
      - *Cucujus clavipes* Fabr. var. *puniceus* Mann.
    - Family Colydiidae
      - *Lasconotus complex* Lec.
    - Family Tenebrionidae
      - *Corticeus parallelus* (Melsheimer)
      - *Corticeus substriatus* (LeConte) (Parker and Davis 1971)
  - Order Diptera
    - Family Xylophagidae
      - *Xylophagus abdominalis* Loew.
    - Family Dolichopodidae
      - *Medetera aldrichii* Wheeler
    - Family Lonchaeidae
      - *Lonchaea viridana* Meigen
    - Family Asilidae
      - *Laphria gilva* (Linnaeus) (Schmid 1969)
  - Order Hymenoptera
    - Family Braconidae
      - *Coeloides dendroctoni* Cush.
    - Family Pteromalidae
      - *Pachyceras eccoptogastri* Ratz.
      - *Dinotiscus* (= *Cecidostiba*) *dendroctoni* Ashm.
      - *Dinotiscus* (= *Cecidostiba*) *acutus* (Prov.)
      - *Dinotiscus burkei* (Crawford)
      - *Rhopalicus pulchripennis* Cwfd. (Dahlsten and Stephen 1974; Rasmussen 1976)
    - Family Eurytomidae
      - *Eurytoma cleri* Ashmead
- Class Nematoda
  - Family Rhabditidae
    - *Aphelenchoides conurus* Steiner (Steiner 1932)
    - *Aphelenchoides acroposthion* Steiner (Steiner 1932)
    - *Contortylenchus reversus* (Thorne) (Thorne 1935)
    - *Mikoletzkya pinicola* (Thorne) (Thorne 1935; Reid 1958c)
    - *Cryptaphelenchus latus* (Thorne) (Thorne 1935)
    - *Ektaphelenchus tenuidens* (Thorne) (Thorne 1935; Reid 1958c)
    - *Panagrodontus dentatus* Thorne (Thorne 1935; Reid 1958c)
    - *Sphaerularia hastata* Khan (Reid 1958c)
    - *Aphelenchoides brachycephalus* Thorne (Reid 1958c)
    - *Aphelenchoides talonus* Thorne (Reid 1958c)
- Class Aves
  - Family Caprimulgidae
    - prob. *Chordeiles minor* (Forster) (Rust[1])
  - Family Picidae
    - *Picoides tridactylus* (Linnaeus) (Rust[1])
    - *Picoides pubescens* (Linnaeus) (Amman 1973)
    - *Picoides villosus* (Linnaeus) (Rust[1])
  - Family Tyrannidae
    - *Contopus sordidulus* Sclater (Stallcup[2])
    - *Contopus borealis* (Swainson) (Stallcup[2])
    - *Empidonax* sp. (Stallcup[2])
  - Family Corvidae
    - *Nucifraga columbiana* (Wilson) (Stallcup[2])
  - Family Paridae
    - *Parus gambeli* Ridgeway (Stallcup[2])
  - Family Sittidae
    - *Sitta pygmaea* Vigors (Stallcup[2])
    - *Sitta carolinensis* Latham (Stallcup[2])
    - prob. *Sitta canadensis* Linnaeus (Blackman 1931; Rust[1])
  - Family Certhiidae
    - *Certhia americana* Bonaparte (Stallcup[2])
  - Family Muscicapidae
    - *Turdus migratorius* Linnaeus (Stallcup[2])
    - *Mydaestes townsendi* (Audubon) (Stallcup[2])
    - prob. *Sialia currucoides* (Bechstein) (Beal 1939; Blackman 1931)
  - Family Emberizidae
    - *Dendroica coronata* (Linnaeus) (Stallcup[2])

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[1] See footnote 6 in text.

[2] See footnote 7 in text.

Egg parasites and predators were studied in the laboratory during four seasons. Egg mortality ranged between 2.5 and 6.5 percent for the four seasons (table 8). The greatest loss was attributed to nematodes (1.13 to 4.06 percent), which are known to have considerable influence on bark beetles (Massey 1966). *Mikoletzkya pinicola* (Thorne) was identified in pure culture (C. L. Massey, letter dated March 16, 1971) from our earlier beetle rearing studies. Loss to nematodes occurred somewhat evenly throughout the galleries (fig. 28). Unidentified fungi caused the second greatest loss of eggs (0.76 to 1.80 percent), with most usually occurring in the first few inches of the gallery (fig. 28). Other factors causing small egg losses were: cannibalism or entomocide by early hatching larvae (0.0 to 1.25 percent), unknown causes (0.0 to 0.31 percent), and infertility (0.18 to 0.89 percent). Unidentified mites accounted for only two eggs (0.06 percent) during one season. Most mites must have been saprophytic or fungus feeders, or were predacious on other organisms under the bark. Predatory mites of the mountain pine beetle were not found during a study of Colorado and South Dakota beetles (Boss and Thatcher 1970).

Although not included in the previous tests, *Medetera aldrichii* may destroy 40 to 50 percent of beetle eggs (DeLeon 1935b). Schmid (1971) reported *Medetera* larvae preyed on beetles eggs in the first few inches of egg gallery and consumed from 12 to 25 eggs each during 15 days of laboratory rearing.

The most important predator of mountain pine beetle larvae is *Medetera aldrichii* Wheeler (DeLeon 1935b). *Medetera* fed on almost any species of larva, including its own, and DeLeon (1935b) believed that cannibalism was important in reducing *Medetera* populations. However, in its favor, *Medetera* had no natural enemies of the immature forms, and it may feed on a pine beetle larva for only a short time, abandon the larva (which later dies), and then search for another prey (DeLeon 1935b). This predatory behavior greatly increases the number of prey destroyed per predator, compared to those predators consuming all of a prey before killing another. However, this behavior appears to be density dependent (Nagel and Fitzgerald 1975). When prey are scarce, *Medetera* consumes most of each prey before seeking another.

The most important parasite is a brachonid, *Coeloides dendroctoni* Cushman (DeLeon 1935a). *Coeloides* was considered the most important natural enemy of the mountain pine beetle because most larvae parasitized by it were fully grown and almost ready to pupate. Bark beetle larvae that have reached this stage have a high probability of reaching the adult stage unless parasitized (DeLeon 1935a). *Medetera* was considered overall to be a less effective natural enemy than *Coeloides* because many of the beetle larvae that *Medetera* destroyed in the fall, when both predator and prey were most abundant, would have died from other causes before maturing.

Laboratory studies of some insect predators have established their potential effect on beetle numbers. Each *Enoclerus sphegeus* Fabricius adult killed one mountain pine beetle adult per day (Schmid 1970a). *Enoclerus sphegeus* larvae consumed an average of 16 large or 38 small mountain pine beetle larvae while completing development (Amman 1970). Larvae of another clerid, *Thanasimus undatulus* Say, consumed an average of 18 large or 35 small mountain pine beetle larvae to complete development (Amman 1972c). Completion of larval development by *Medetera* required an average of 14.7 Douglas-fir beetle larvae (*D. pseudotsugae* Hopkins), but only 6.2 when fed exclusively large larvae (Nagel and Fitzgerald 1975).

Attempts have been made to evaluate the impact of parasites and predators on mountain pine beetle populations in the field. Bedard[5] found that 54 percent of the brood in windfelled trees were parasitized, and that parasitism averaged 65 percent in standing trees. He recommended against chemical treatment of

Table 8.—Mountain pine beetle egg mortality by specific factors and infertility, Wasatch-Cache National Forest, Utah

Year	Eggs examined	Mortality factors						Total egg loss
		Nematodes	Fungi	Entomocide	Mites	Unknown	Infertile	
	No.	*Percent*						
1972	2,093	4.06	0.76	1.25	0.00	0.05	0.38	6.50
1974	3,581	2.85	1.51	.06	.06	.31	.89	5.68
1975	3,563	1.23	1.80	.00	.00	.00	.87	3.90
1976	3,811	1.13	1.13	.00	.00	.08	.18	2.52

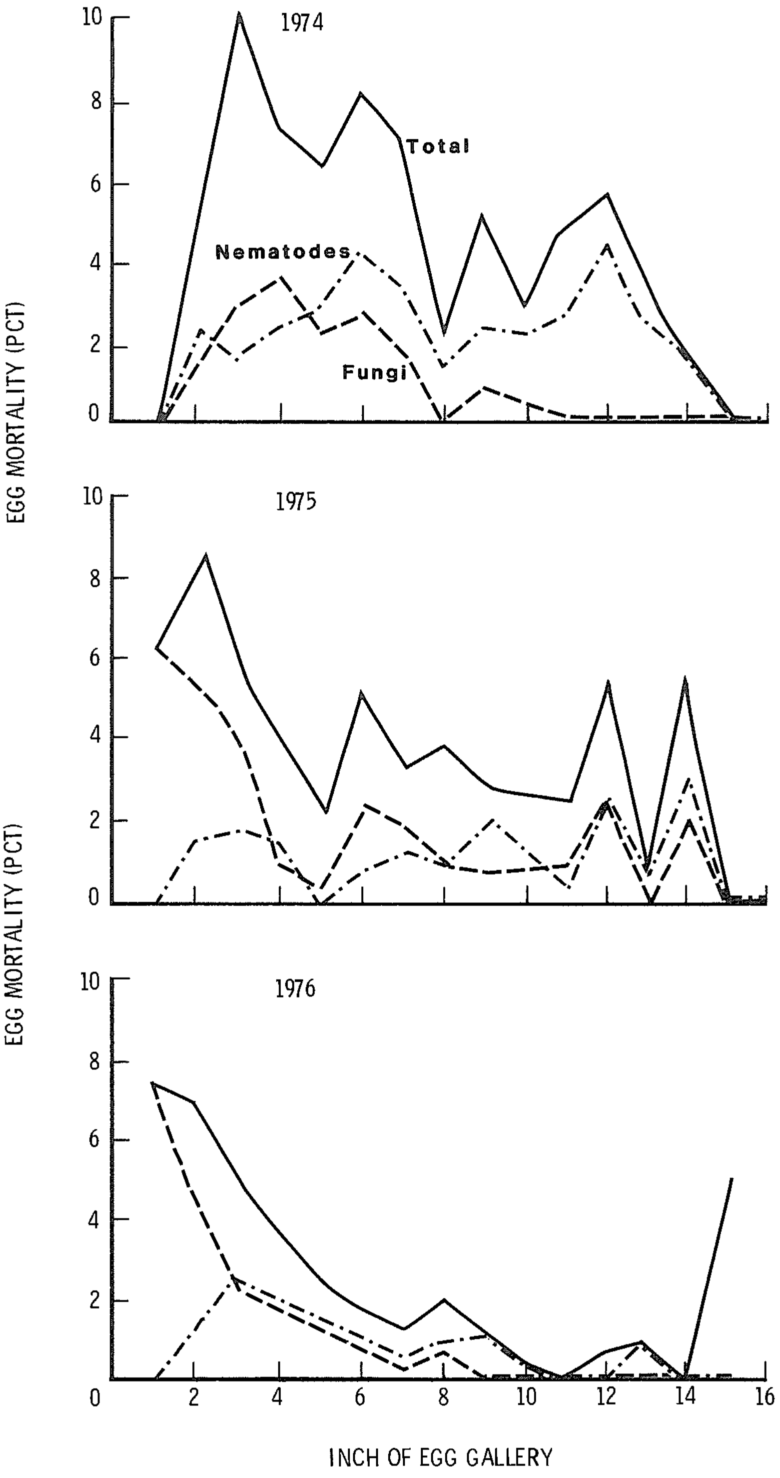

Figure 28.—Total mountain pine beetle egg mortality and mortality due to nematodes and fungi during laboratory studies in 3 years: 1974, 1975, 1976.

windfalls with parasitism of 30 percent or more, and standing trees with parasites in the base. When 21 or more parasites and predators per ft^2 (930 cm^2) of bark surface were present, mountain pine beetle populations were reduced (Bedard[5]).

Woodpeckers consume large numbers of beetles and cause the death of many more from desiccation when the birds open the bark. Prey size is an important factor affecting predation by woodpeckers (Koplin and Baldwin 1970). Trees containing small larvae tend to be avoided and woodpeckers concentrate on trees containing large larvae. At high elevations in northwest Wyoming, woodpeckers preyed mostly on parent beetles because of the small size of larvae (Amman 1973). During epidemics, woodpeckers are believed to have an insignificant effect on mountain pine beetle production (Berryman 1976). However, during endemic periods, they may play an important role in keeping a beetle population in check.

Several factors limit the effectiveness of insect parasites and predators. For *Coeloides* (DeLeon 1935a), these factors include:

1. It is found generally in *Ips*-infested material and is insufficient in number during the first few years of a mountain pine beetle infestation to destroy many of the larvae.
2. The main generation of *Coeloides* stays in the tree almost a year after the host beetle has been killed. Then, instead of catching up with the outlying groups of mountain pine beetles, the parasites stay within the original epicenter.
3. It increases in numbers slowly.
4. *Coeloides* is parasitized by *Eurytoma* sp. (Eurytomidae) and *Gelis* sp. (Ichneumonidae).
5. Thick bark limits parasitism by *Coeloides*.[5]

The thick bark of sugar pine excludes most parasites and predators except predacious beetles (Struble 1942). The bark of ponderosa pine is even more limiting to parasites and predators than the bark of sugar pine (Dahlsten and Stephen 1974).

The effect of predators on flying beetles is difficult to measure. The robber fly, *Laphria gilva* (L.), killed about 1 percent of flying mountain pine beetles in ponderosa pine stands of the Black Hills (Schmid 1969). Large numbers of robber flies were captured in passive traps in lodgepole pine stands (R. F. Schmitz, personal communication, January 1981).

The impact of birds on mountain pine beetle populations during the flight period can be substantial. Stomach content analysis of 18 birds revealed 15 with mountain pine beetle adults ranging in numbers between 1 and 289, and up to 20 percent of the food volume (Rust[6]). Nighthawks contained the most beetles, averaging 76 ($n = 10$), while the three-toed and hairy woodpeckers averaged only 2 beetles ($n = 5$). However, the following year, quantities of beetles taken by these birds was reversed—nighthawks averaged 5 beetles ($n = 14$), and woodpeckers averaged 33 ($n = 8$). Rust[6] pointed out that the heavy concentration of mountain pine beetles had shifted to another area the second year. Because the nighthawks stayed within their established breeding grounds, they had fewer beetles to prey upon the second year. Woodpeckers, on the other hand, moved to the area with the greater beetle population.

Stallcup[7] estimated from bird censuses and stomach analyses that birds consumed 8.5 percent of adult beetles during the beetles' flight period in a ponderosa pine stand of Colorado. A number of birds not previously reported as predators of the beetle were observed (table 7).

These observations suggest that birds could have a substantial impact on flying mountain pine beetle populations.

Intraspecific competition.—Competition has long been regarded as one of the principal density-dependent mortality factors of insect populations. Laboratory populations of mountain pine beetles under attack densities of 3, 9, and 18/ft^2 (930 cm^2) of bark surface in lodgepole pine billets produced 3.8, 2.2, and 0.6 adults/attack, respectively (Cole 1962). Under similar conditions, beetle production increased to the apparent capacity of the space and food, and then did not change throughout the higher gallery densities (Amman and Pace 1976) (fig. 29). In a laboratory study using artificial media for larval food, initially dense larval populations stimulated larval feeding; but as larvae matured they killed siblings without consuming them (entomocide) (W. Cole 1973). Entomocide and cannibalism reduce larval density and bring the population into equilibrium with food quantity and space (phloem volume). Another effect of competition (crowding) during larval development is reduced oviposition by the resulting new adults (W. Cole 1973), with egg production varying inversely with crowding density.

Low attack densities (Berryman 1976; Klein and others 1978) or low gallery densities (Amman and Pace 1976) result in high brood per parent ratios (fig. 30). But both attack and gallery densities must be high enough to assure that resinosis does not kill the brood.

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[5] Bedard, W. D. The relation of parasites to mountain pine beetle control in western white pine. Washington, DC: U.S. Department of Agriculture, Bureau of Entomology; 1933. 7 p. Unpublished report.

Bedard, W. D. Preliminary report relative to biological factors in the control of the mountain pine beetle 1937 investigations. Washington, DC: U.S. Department of Agriculture, Bureau of Entomology; 1938. 23 p. Unpublished report.

Bedard, W. D. Biological factors in the control of the mountain pine beetle. Washington, DC: U.S. Department of Agriculture, Bureau of Entomology; 1939. 19 p. Unpublished report.

[6] Rust, Henry J. Relation of insectivorous birds to the mortality of the mountain pine beetle during the flight period. Couer d'Alene, ID: U.S. Department of Agriculture, Bureau of Entomology, Forest Insect Field Station; 1929. 5 p. Unpublished report.

Rust, Henry J. Relation of insectivorous birds to the mortality of the mountain pine beetle during the flight period. Couer d'Alene, ID: U.S. Department of Agriculture, Bureau of Entomology, Forest Insect Field Station; 1930. 11 p. Unpublished report.

[7] Stallcup, Patrick L. A method for investigating avian predation on the adult Black Hills beetle. Fort Collins, CO: Colorado State University; 1963. 60 p. Thesis.

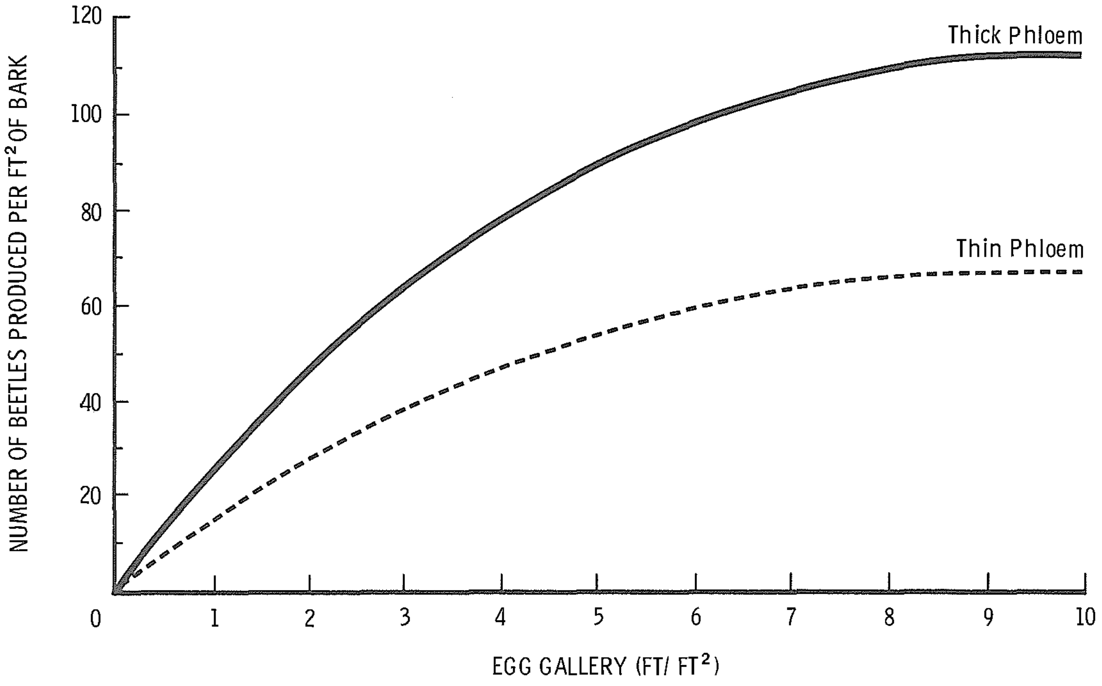

Figure 29.—Mountain pine beetle production per unit area of bark in relation to egg gallery density for two phloem thickness categories (Amman and Pace 1976). (See regression statistics in appendix.)

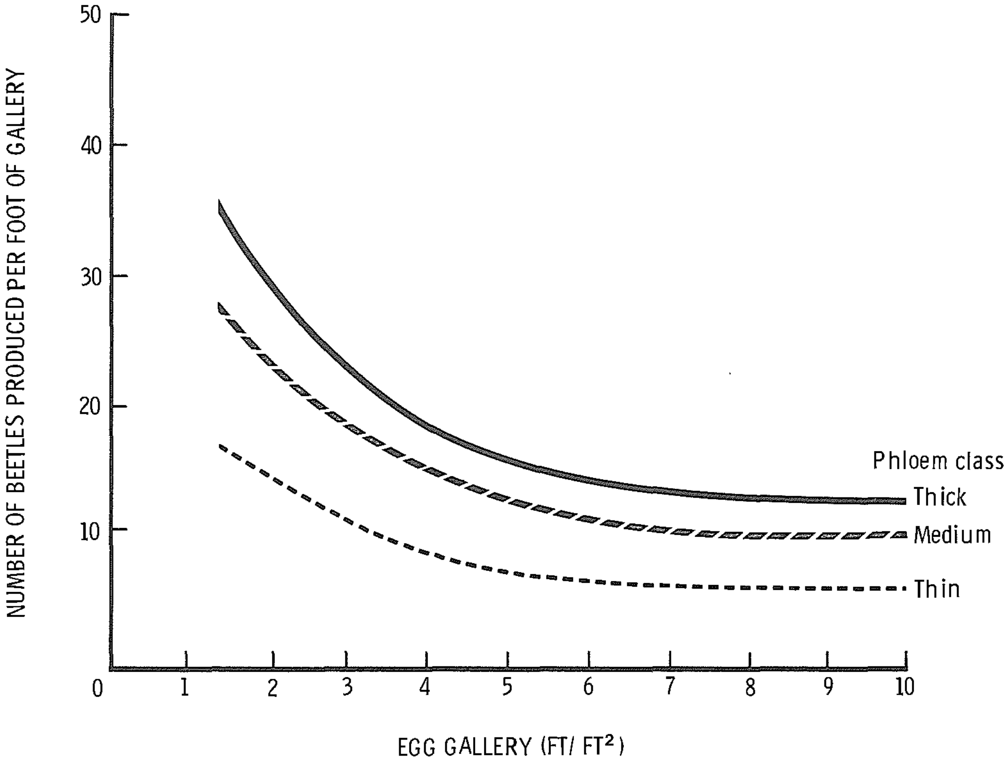

Figure 30.—Mountain pine beetle production per unit length of egg gallery for three phloem thickness categories. (See regression statistics in appendix.)

Interspecific competition.—Interspecific competition has little impact on epidemic mountain pine beetle populations in lodgepole pine (Berryman 1976). Competitors generally use smaller trees and portions of large trees unoccupied by mountain pine beetles. However, in ponderosa pine, wood borer larvae (Cerambycidae) impact mountain pine beetle populations by destroying mountain pine beetle larvae while both are feeding in the phloem (McCambridge and others 1979; Blackman 1931).

Resin.—The resinous response of lodgepole pine to mountain pine beetle infestation occurs when the beetle chews through resin ducts (Shrimpton 1978). The rate and density of attacks greatly influence the amount of resin available for flushing out ("pitching out" is the common term) beetles and hence success of attacks. A few attacks, or many attacks that occur over many days, usually are pitched out or beetles abandon the tree (Amman 1975a, 1980). Even when egg gallery is constructed and eggs are laid at low attack or gallery densities, the galleries are inundated by resin, thus killing eggs and larvae (Reid and Gates 1970). Low larval survival has been reported for bark with dense cortical resin canals (Berryman 1976). However, overall, studies over many years show losses to resin are minimal (Cole 1975, 1981).

Drying.—Host drying following infestation by mountain pine beetles is an important factor in mortality of beetle brood (Blackman 1931; Cole 1975), and probably is one of the deciding factors causing beetle populations to return endemic before killing most of the small diameter trees in a stand (Cole and others 1976). Excessive drying of the phloem deprives developing brood of necessary moisture. Larvae cease feeding and shrivel as they desiccate. Drying is usually more severe in small diameter lodgepole pine (Amman 1977) (fig. 31), and is believed partially related to sapwood depth (Amman 1978). Sapwood contains more moisture then heartwood (Reid 1961) and is usually thinner in small trees than in large ones (fig. 32). Harvey (1979) found that 6-inch (15-cm) d.b.h. lodgepole pines contained proportionately only one-half the sapwood of trees 8 inches (20 cm) d.b.h. and larger. Rate of lodgepole pine drying also is affected by blue-stain fungi (Reid 1961). Trees drying most rapidly following beetle infestation contained more moisture at time of brood emergence (Amman 1977). These trees had profuse growth of blue-stain fungi throughout the sapwood as shown in figure 33a. (Figure 33 is on the inside back cover). Trees with sporadic and sparse growth of fungi in the sapwood dried excessively (fig. 33b). In addition to tree and blue-stain fungi, drying is also influenced by beetle attack behavior. As attack and gallery densities increase, drying also increases, probably because of greater opening of the bark (Cole and others 1976).

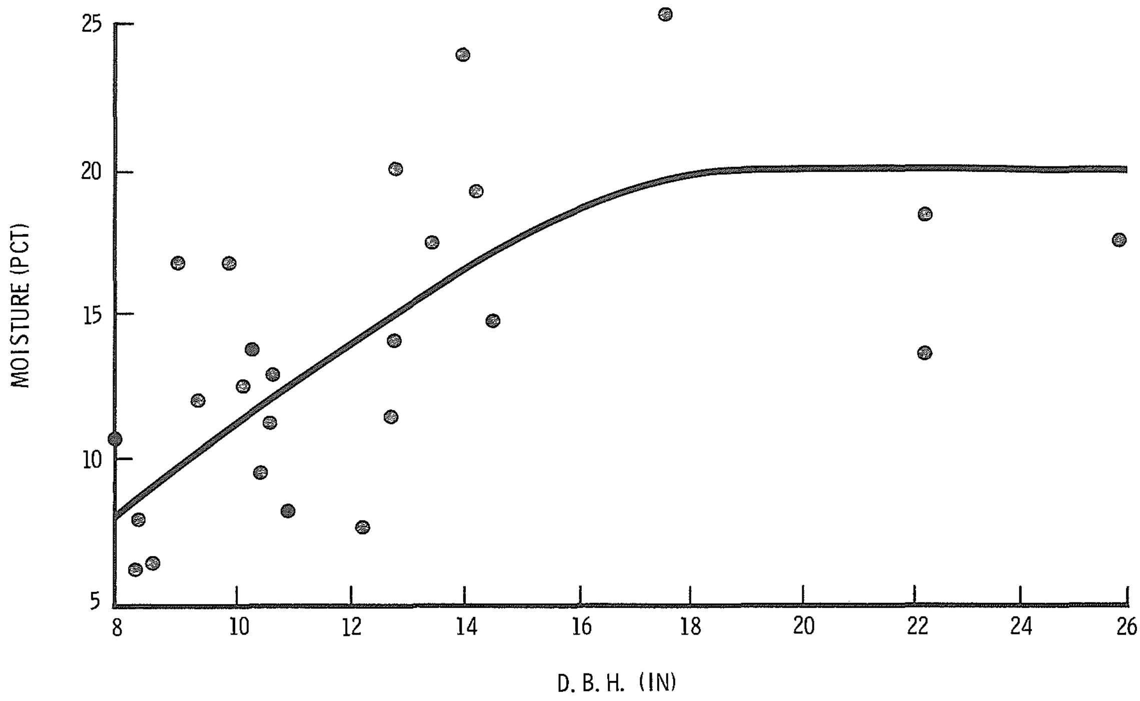

Figure 31.—Moisture content of the sapwood of infested trees 3 weeks prior to emergence of mountain pine beetle brood adults, Wasatch-Cache National Forest, Utah (Amman 1976).

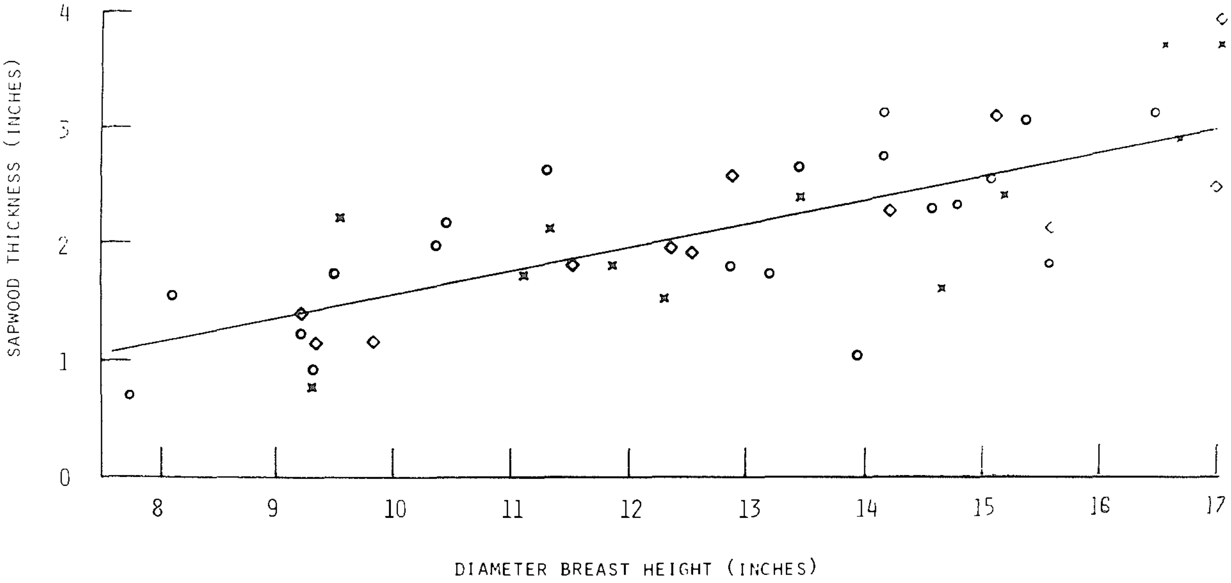

Figure 32.—Sapwood thickness of infested lodgepole pine in relation to diameter at breast height for 3 years, 1971-73, Wasatch-Cache National Forest, Utah (Amman 1978). (See regression statistics in appendix.)

Temperature.—Cold winter temperatures also kill many beetles (Cole 1975). Losses to freezing temperatures are influenced by an interaction of temperature and time. Because there is a lag of subcortical temperature behind air temperatures, very cold temperatures for a brief period do not kill as many beetles as somewhat warmer temperatures that persist for a longer time (Beal 1934). For example, temperatures dipped to -44° F (-40° C) at Moran, Wyo., briefly in January 1963 (U.S. Weather Bureau 1963). Much of the population was killed, but pockets of infested trees and thick-barked portions of others escaped freezing. Mountain pine beetles can increase or decrease their cold hardiness at any time of the year, depending upon existing temperatures (Yuill 1941). Cold hardiness varies by host species; beetles from lodgepole and ponderosa pines are more cold hardy than those from sugar pine in California (Yuill 1941).

Even temperatures occurring during an average winter may interact with the stage of overwintering brood to cause extensive mortality (fig. 34). Eggs and small larvae are more susceptible to winterkill than large larvae (Amman 1973; Reid 1962a), even though the first three larval stages contain proportionately the same amount of glycerol, an alcohol that protects against freezing (Sômme 1964). As the beetle disposes of water, thereby increasing the proportion of glycerol, it can tolerate colder temperatures without freezing. All eggs and pupae die during the winter. Young brood resulting from late August and September attacks, young brood occurring toward the end of long galleries, and young brood of occasional second attacks by parents will usually be affected more adversely than the older brood occurring from early attacks and short galleries. Large beetle larvae are most susceptible to cold temperatures in the early spring after feeding is resumed. Sudden freezing temperatures can cause much larval mortality at this time.

High temperatures in lodgepole forests of most of the Rocky Mountains are not likely to cause beetle mortality. Solar heat was tested as a means of destroying brood under the bark of lodgepole pine (Patterson 1930). Beetle brood safely endured temperatures of 100° F (37° C). However, temperatures between 110° and 120° F (43° and 49° C) killed the brood, requiring only 20 to 30 minutes of exposure to 120° F.

Distribution of mortality.—Most beetle mortality factors are unevenly distributed among trees and bark samples, although the effect of abiotic factors, as expected, tends to be more evenly distributed among trees and samples (table 9). These differences in distribution of mortality factors among and within trees and by stage of infestation (endemic, epidemic, and postepidemic) can greatly influence their overall effect on mountain pine beetle populations.

Within trees, parasites are more commonly found in the upper portions, and predators in the lower portions of western white pine trees in northern Idaho (Bedard[5]), in lodgepole pine trees in northwestern Wyoming (Bean[8]), and in sugar pine trees in California (Dahlsten and Stephen 1974). Almost all *Coeloides* were in the middle third of the tree, while the predator *Medetera* was primarily in the basal third in lodgepole pine. Trees infested early in the flight period tend to contain more *Medetera* than those infested later (Schmid 1970b).

Losses of beetles to different mortality agents also varied according to stage of infestation in 1973-74: endemic (Hyalite Canyon, Gallatin National Forest, Mont.; Upper Salmon River, Sawtooth National Forest, Idaho); epidemic (Logan Canyon, Wasatch-Cache National Forest, Utah; Warm River, Targhee National Forest, Idaho); and postepidemic (Elkhart Park, Bridger-Teton National Forest, Wyo.; Turpin Meadows, Bridger-Teton National Forest, Wyo.).

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[8] Bean, James L. The effects of control measures on the mountain pine beetle (*Dendroctonus monticolae* Hopkins) in lodgepole pine, Teton National Forest, Jackson, Wyoming. About 1949. Unpublished report. 22 p., plus figures and tables.

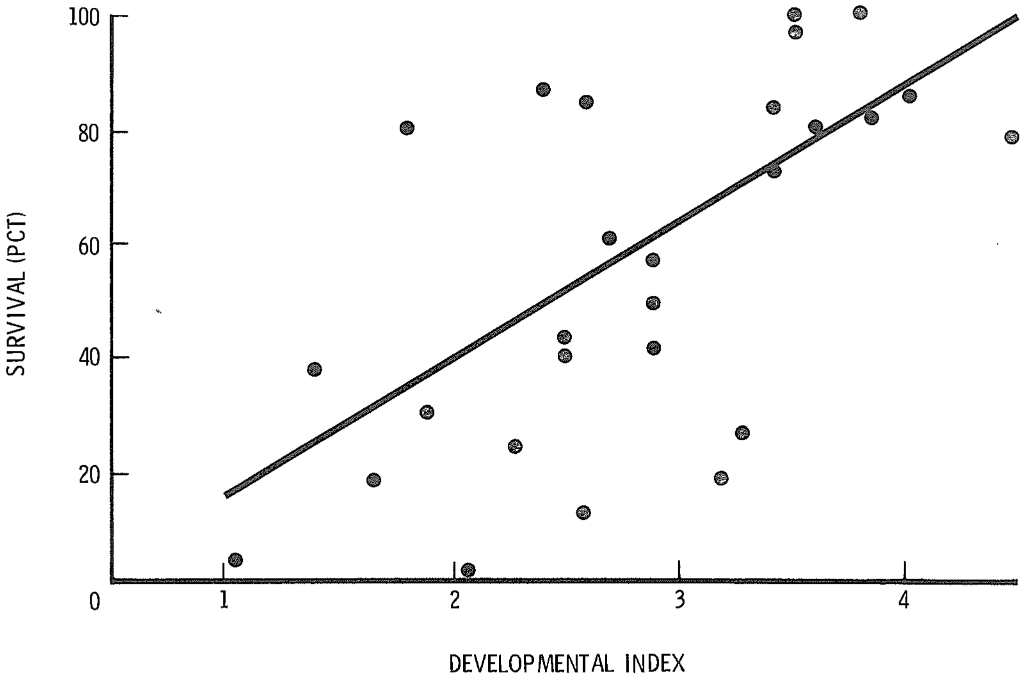

Figure 34.—Survival of mountain pine beetle brood during the winter is related to how advanced larval development is in the fall. Developmental Index: 1 = egg; 2 = first instar; 3 = second instar; 4 = third instar.

Table 9.—Percent of trees (Tr.) and samples (Sa.) in which losses of mountain pine beetle to specific mortality factors[1] were observed, Wasatch-Cache National Forest, Utah

Year	Number		WC		BC		PA		T		PI		CL		MD		WP		UNK	
	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.
	Percent																			
Fall sample																				
Trees ≤8.9 in (22.6 cm) d.b.h.																				
1974-75	2	4							50.0	25.0									50.0	25.0
1975-76	5	10							100.0	70.0					20.0	10.0				
1977-78	1	2							100.0	50.0	100.0	50.0								
1978-79	1	2							100.0	50.0										
Trees 9.0-11.9 in (22.9-30.2 cm) d.b.h.																				
1970-71	1	22			9.1	4.5			18.2	9.1			9.1	4.5	36.4	18.2			9.1	4.5
1971-72	8	16	50.0	31.2	62.5	50.0	25.0	12.5	37.5	18.8	25.0	12.5			62.5	43.8			87.5	68.8
1972-73	4	8	25.0	25.0	25.0	25.0			50.0	37.5	25.0	12.5			25.0	12.5			25.0	12.5
1973-74	11	22	81.8	68.2	18.2	18.2	9.1	9.1			9.1	4.5	9.1	4.5	72.7	54.5	18.2	13.6	9.1	4.5
1974-75	8	16	37.5	18.8	75.0	56.2			50.0	43.8					25.0	18.8			37.5	37.5
1975-76	8	16							62.5	37.5										
1976-77	4	8			25.0	12.5	25.0	12.5	75.0	37.5					25.0	25.0				
1977-78	4	8	25.0	25.0	25.0	25.0	50.0	25.0	50.0	37.5			25.0	12.5	100.0	75.0				
1978-79	6	12	33.3	25.0	33.3	25.0	16.7	8.3	33.3	16.7					16.7	16.7				
Trees 12.0-14.9 in (30.5-37.9 cm) d.b.h.																				
1970-71	1	2																100.0	50.0	
1971-72	3	6	33.3	16.7	66.7	33.3			33.3	16.7					66.7	33.3			100.0	83.3
1972-73	6	12	66.7	41.7	50.0	33.3			50.0	33.3	50.0	33.3			50.0	33.3			66.7	33.3
1973-74	6	12	83.3	75.0			16.7	16.7							83.3	66.7		16.7	16.7	16.7
1974-75	8	16	50.0	25.0	50.0	31.2	12.5	6.2	37.5	31.2					37.5	31.2			25.0	25.0
1975-76	5	10							80.0	70.0					20.0	10.0				
1976-77	7	14			14.3	7.1	14.3	7.1	14.3	7.1					57.1	35.7				
1977-78	3	6	33.3	33.3	66.7	33.3	33.3	16.7	66.7	50.0	33.3	16.7			100.0	50.0				
1978-79	4	8	25.0	12.5	50.0	25.0			75.0	50.0	25.0	12.5			100.0	62.5				
Trees 15.0 + in (38.1 cm) d.b.h.																				
1971-72	1	2	100.0	100.0	100.0	100.0													100.0	50.0
1972-73	2	4	100.0	50.0	100.0	50.0			50.0	25.0					50.0	50.0			50.0	25.0
1973-74	3	6	66.7	50.0	33.3	33.3									66.7	50.0				
1974-75	2	4			50.0	25.0			50.0	50.0	50.0	25.0			50.0	50.0				
1975-76	2	4							50.0	25.0										
1976-77	7	14					14.3	14.3	42.8	21.					57.1	50.0				
1977-78	6	12	33.3	25.0	50.0	41.7	16.7	16.7	33.3	16.7					100.0	83.3				
1978-79	1	2	100.0	100.0	100.0	50.0									100.0	100.0				
Spring sample																				
Trees ≤8.9 in (22.6 cm) d.b.h.																				
1974-75	2	4							100.0	100.0			50.0	25.0						
1975-76	5	10							100.0	90.0	40.0	20.0	20.0	10.0						
1977-78	1	2																		
1978-79	1	2							100.0	100.0										
1979-80	1	2							100.0	50.0										
Trees 9.0-11.9 in (22.9-30.2 cm) d.b.h.																				
1970-71	11	22			18.2	13.6			81.8	77.3	18.2	13.6	18.2	9.1	9.1	4.5				
1971-72	8	16			50.0	31.2			100.0	93.8			62.5	43.8			25.0	12.5		
1972-73	4	8					25.0	12.5	100.0	75.0	25.0	12.5					25.0	12.5		
1973-74	11	22			9.1	4.5			90.9	81.8	72.7	50.0	18.2	9.1			63.6	54.5	27.3	18.2
1974-75	8	16	25.0	12.5	12.5	6.2			87.5	81.2	25.0	18.8			12.5	6.2	50.0	37.5		
1975-76	8	16							100.0	93.8	25.0	25.0	37.5	18.8						
1976-77	4	8							75.0	62.5	50.0	37.5	50.0	37.5					25.0	12.5
1977-78	4	8			25.0	25.0			100.0	75.0	75.0	50.0	50.0	25.0			75.0	62.5		
1978-79	6	12	16.7	8.3					100.0	91.7	33.3	25.0					50.0	33.3		
1979-80	5	10	20.0	10.0			20.0	10.0	100.0	80.0			20.0	10.0			20.0	20.0		
Trees 12.0-14.9 in (30.5-37.9 cm) d.b.h.																				
1970-71	1	1	100.0	50.0					100.0	100.0			100.0	50.0						
1971-72	3	6	33.3	33.3	66.7	50.0			100.0	100.0			33.3	16.7						
1972-73	6	12	16.7	8.3			16.7	16.7	83.3	83.3	16.7	16.7	50.0	41.6						

(con.)

Table 9.—(con.)

Year	Number		WC		BC		PA		T		D		MD		CD		WP		UNK	
	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.	Tr.	Sa.
									Percent											
1973-74	6	12							66.7	50.0	16.7	16.7	50.0	50.0			16.7	16.7	16.7	16.7
1974-75	8	16	25.0	25.0	37.5	37.5	12.5	6.2	100.0	93.8	25.0	12.5	37.5	25.0	25.0	12.5	50.0	43.8		
1975-76	5	10	20.0	10.0	20.0	20.0	20.0	10.0	100.0	100.0	20.0	10.0	60.0	40.0						
1976-77	7	14							100.0	71.4	42.8	28.6	85.7	50.0					14.3	14.3
1977-78	3	6	33.3	16.7	66.7	33.3			66.7	66.7	66.7	33.3	100.0	66.7			66.7	33.3		
1978-79	4	8	50.0	37.5	50.0	25.0			100.0	100.0			25.0	25.0					25.0	12.5
1979-80	4	8			25.0	12.5			100.0	87.5	50.0	25.0					50.0	37.5		
									Trees 15.0 + in (38.1 cm) d.b.h.											
1971-72	1	2			100.0	50.0			100.0	100.0										
1972-73	2	4							100.0	75.0			50.0	25.0						
1973-74	3	6							100.0	83.3			33.3	33.3			33.3	33.3		
1974-75	2	4							100.0	100.0	50.0	50.0	100.0	75.0			50.0	50.0		
1975-76	2	4	50.0	25.0					100.0	75.0										
1976-77	7	14							71.4	64.3	42.8	35.7	42.8	28.6						
1977-78	6	12			33.3	16.7	16.7	8.3	100.0	91.7	33.3	25.0	100.0	83.3			16.7	16.7		
1978-79	1	2							100.0	100.0	100.0	50.0	100.0	50.0						
									Early summer sample											
									Trees ≤8.9 in (22.6 cm) d.b.h.											
1974-75	2	4	50.0	25.0			50.0	50.0												
1975-76	5	10									40.0	20.0	40.0	40.0	20.0	10.0				
1977-78	1	2											100.0	50.0						
1978-79	1	2					100.0	50.0									100.0	50.0		
1979-80	2	4					50.0	50.0			50.0	25.0								
									Trees 9.0-11.9 in (22.9-30.2 cm) d.b.h.											
1970-71	11	22	36.4	27.3	45.5	40.9	18.2	13.6	9.1	9.1	18.2	13.6	54.5	31.8			9.1	4.5		
1971-72	8	16					12.5	6.2			50.0	31.2			25.0	18.8	50.0	37.5		
1972-73	4	8			50.0	25.0	75.0	62.5												
1973-74	11	22					72.7	50.0	9.1	4.5	9.1	4.5	27.3	13.6						
1974-75	8	16	12.5	6.2			62.5	56.2	12.5	6.2	25.0	12.5			25.0	25.0				
1975-76	8	16					25.0	12.5	25.0	12.5	25.0	12.5	25.0	25.0						
1976-77	4	8	25.0	12.5			100.0	100.0							25.0	25.0				
1977-78	4	8					25.0	12.5	25.0	12.5	25.0	12.5	75.0	62.5	50.0	50.0				
1978-79	6	12	16.7	8.3			50.0	41.7			16.7	8.3			16.7	8.3	16.7	8.3		
1979-80	4	8			25.0	12.5									50.0	37.5				
									Trees 12.0-14.9 in (30.5-37.9 cm) d.b.h.											
1970-71	1	2	100.0	100.0	100.0	100.0					100.0	100.0								
1971-72	3	6	33.3	16.7			33.3	16.7			33.3	33.3					33.3	16.7		
1972-73	6	12			66.7	50.0	50.0	33.3			33.3	25.0								
1973-74	6	12					16.7	8.3	50.0	41.6	50.0	33.3								
1974-75	8	16			12.5	6.2	75.0	56.2			25.0	18.8	25.0	12.5	37.5	31.2				
1975-76	5	10	20.0	10.0			60.0	50.0			40.0	20.0	60.0	40.0						
1976-77	7	14					85.7	78.6					28.6	21.4						
1977-78	3	6	33.3	16.7					33.3	16.7	33.3	16.7	66.7	33.3	33.3	16.7				
1978-79	4	8					75.0	62.5			25.0	12.5			25.0	12.5	25.0	12.5		
1979-80	4	8			25.0	12.5	50.0	37.5							50.0	50.0				
									Trees 15.0 + in (38.1 cm) d.b.h.											
1971-72	1	2					100.0	100.0												
1972-73	2	4			50.0	50.0					50.0	25.0								
1973-74	3	6					33.3	33.3	66.7	50.0	66.7	50.0	33.3	16.7						
1974-75	2	4			50.0	25.0	100.0	100.0			50.0	25.0								
1975-76	2	4											50.0	25.0						
1976-77	7	14			14.3	7.1	85.7	71.4			42.8	21.4	42.8	21.4			14.3	14.3		
1977-78	6	12	33.3	33.3							33.3	16.7	33.3	25.0	16.7	8.3				
1978-79	1	2																		

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[1] Abbreviations of mortality factors are:
WC = competition within brood of an individual egg gallery
BC = competition among brood of several egg galleries
CL = clerid
CD = *Coeloides*
MD = *Medetera*
PA = pathogen
WP = woodpecker
T = temperature
D = drying
PI = pitch
UNK = unknown

Table 10.—Mountain pine beetle survival and mortality to specific causes in three classes of infestation (endemic, epidemic, and postepidemic) and three heights in lodgepole pine

Item		Height above ground and infestation class											
		4.5 ft (1.4 m)			12 ft (3.7 m)			20 ft (6.1 m)			Heights combined		
		End.	Epi.	Post.	End.	Epi.	Post.	End.	Epi.	Post.	End.	Epi.	Post.
Samples (232 cm²)	No.	16	20	24	16	20	24	8	14	8	40	54	56
Starting populations	No.	1,621	1,693	2,571	1,048	1,467	1,891	501	1,124	668	3,170	4,284	5,130
Emerging adults	No.	56	29	15	47	16	8	14	15	5	117	60	28
	%	3.5	1.7	.6	4.5	1.1	.4	2.8	1.3	.7	3.7	1.4	.5
Mortality factors:													
Within[1] competition	No.	48	72	1	64	17	10	0	112	0	112	201	11
	%	3.0	4.3	.05	6.1	1.2	.5	0	10.0	0	3.5	4.7	.2
Between[2] competition	No.	13	110	15	28	0	27	0	128	16	41	238	58
	%	.8	6.5	.6	2.7	0	1.4	0	11.4	2.4	1.3	5.6	1.1
Clerid	No.	19	6	4	9	4	4	1	7	0	29	17	8
	%	1.2	.4	.2	.9	.3	.2	.2	.6	0	.9	.4	.2
Coeloides	No.	17	26	1	5	17	0	0	31	0	22	74	1
	%	1.0	1.5	.05	.5	1.2	0	0	2.8	0	.7	1.7	.02
Medetera	No.	58	246	2	49	219	2	20	94	0	127	559	4
	%	3.6	14.5	.1	4.7	14.9	.1	4.0	8.4	0	4.0	13.0	.08
Pathogen	No.	0	35	5	15	88	0	0	0	0	15	123	5
	%	0	2.1	.2	1.4	6.0	0	0	0	0	.5	2.9	.1
Woodpecker	No.	35	142	33	25	354	88	0	153	75	60	649	196
	%	2.2	8.4	1.3	2.4	24.1	4.7	0	13.6	11.2	1.9	15.2	3.8
Temperature	No.	454	574	803	189	291	599	81	212	131	724	1,077	1,533
	%	28.0	33.9	31.2	18.0	19.8	31.7	16.2	18.9	19.6	22.8	25.1	29.9
Drying	No.	306	158	564	308	275	167	84	144	106	698	577	837
	%	18.9	9.3	21.9	29.4	18.7	8.8	16.8	12.8	15.9	22.0	13.5	16.3
Pitch	No.	0	12	11	0	35	24	0	2	3	0	49	38
	%	0	.7	.4	0	2.4	1.3	0	.2	.4	0	1.1	.7
Unknown	No.	615	283	1,117	309	151	962	301	226	332	1,225	660	2,411
	%	37.8	16.7	43.4	29.4	10.3	50.9	60.0	20.1	49.8	38.7	15.4	47.1

[1] Competition within brood of an individual egg gallery.

[2] Competition among brood of several egg galleries.

Predation by clerids, although usually light, was greater at 4.5 ft (1.4 m) above ground than higher in the trees in endemic populations, slightly higher at the 20-ft (6.1-m) level in epidemic populations, and about equal in 4.5- and 12-ft (1.4- and 3.7-m) levels during the postepidemic period (table 10). Overall, predation by clerids was greater in endemic infestations.

Coeloides parasitized more beetles at all three sample heights in epidemic infestation than in the other two infestation types. However, this accounted for a maximum of only 2.8 percent of the beetle population at any one height. The amount of parasitism was particularly low (0.02 percent) in the postepidemic infestations. This is probably partly related to the excessive drying of infested trees that occurs during the postepidemic period (Cole and others 1976), which may affect *Coeloides* as much or more than its mountain pine beetle host. Also, *Coeloides* may have switched to *Ips* species, which are commonly parasitized by *Coeloides* (DeLeon 1935a) and which are more abundant than mountain pine beetles in the postepidemic period (Evenden and Gibson 1940).

Medetera, the most important insect predator, caused greatest mortality in epidemic infestations, accounting for 13 percent of the beetles. Predation was about equal in the 4.5- and 12-ft (1.4- and 3.7-m) samples, but less in the 20-ft (6.1-m) sample. Schmid (1971) reported similar findings, with greatest numbers 5 to 10 ft (1.5 to 3.0 m) above ground in ponderosa pine. Predation was extremely light in the postepidemic infestations, and probably is related to excessive drying of host trees that either affected *Medetera* directly or indirectly by reducing the number of prey. *Medetera* larvae desiccate easily (Schmid 1971). Also, possible association of *Medetera* with the more numerous *Ips* would reduce *Medetera*'s effect on mountain pine beetles.

Woodpeckers accounted for greater predation in epidemic infestations than in endemic and postepidemic infestations. The low amount of woodpecker predation in endemic infestations may be due to sparse woodpecker populations during such periods. Most woodpecker predation occurred in the 12-ft (3.7-m) samples, with the least at 4.5-ft (1.4-m) samples. The smaller amount of predation at 4.5 ft (1.4 m) is probably related to thicker bark found at that height, compared to higher on the tree or to deep snow that prevented access. Dahlsten and Stephen (1974) observed that predation of mountain pine beetles by woodpeckers in sugar pine was greater in the upper half of the tree, which probably also was related to thinner bark in that portion. Woodpeckers tend to feed on beetles that are easiest to reach and are an acceptable size. Woodpeckers tend to avoid small larvae when larger prey are available (Koplin and Baldwin 1970; Amman 1973).

Beetle mortality attributable to pathogens—probably the fungus *Beauveria bassiana* (Balsamo) Vuillemin, a pathogen being investigated by Whitney and others (1978)—was low but occurred most commonly in epidemic infestations. The very low incidence of disease during postepidemic infestations may have been because of excessive drying of the trees during this phase of the infestation.

Evaluation of Mortality Factors

It is difficult to evaluate the relative importance of mortality factors that operate on any population for controlling or regulating influences. Previous work (Cole 1974, 1975) only evaluated mortality factors over a short time. Full evaluation requires simultaneous measuring of mortality attributable to all factors operating on several populations for a number of years, preferably throughout an infestation cycle. The following analysis covers such a period of sampling for mountain pine beetles in lodgepole pine.

Data Source.—Data were taken from infestations on three National Forests: Wasatch-Cache in northern Utah (Stillwater plot), Bridger-Teton in northwestern Wyoming, and Targhee in southeastern Idaho. Another infestation on the Wasatch-Cache National Forest (Logan Canyon plot) was followed as a special case because the population has remained at a "high endemic" level over 9 years and shows particularly interesting relationships between mortality factors and population fluctuations.

Mountain pine beetle populations were sampled between 1964 and 1977 by tree diameter and infestation stage (preepidemic, epidemic, and postepidemic). The infested tree was the sampling unit. To minimize between-tree variance, trees were stratified by diameter classes: 9-inch (23-cm) including trees 11.9 inches (30 cm) d.b.h. and less; 12-inch (30.5-cm) including trees 12 through 14.9 inches (30.5 to 37.8 cm) d.b.h.; and 15-inch (38-cm) d.b.h. and greater. The random sampling technique (Carlson and Cole 1965) focused on critical within-tree measurements and sampling efforts.

Two 6-inch by 6-inch (232-cm^2) samples were taken per tree each sample date. The samples were selected at random within an area ± 1 ft (30.5 cm) of breast height. Insects within the samples were recorded as individuals living and dead (by cause of death) within each developmental stage of the beetle. Previous work (Cole 1975) demonstrated that observations at five developmental intervals within a generation were sufficient to detect population mortality by cause of death among developmental stages. Pertinent developmental intervals within the life cycle for observations of mortality are as follows:

0. Base population—	The total of live and dead eggs and larvae from the late fall sample.
1. Late fall—	Number of live larvae entering winter.
2. Early spring—	Number of larvae that survived the winter.
3. Summer—	Number of mature larvae and pupae.
4. Late summer—	Number of emerging new adults, obtained by caging the sample area.

We used the abridged cohort life table, in which a generation of beetles is sampled at particular points in time. However, the abridged cohort life table was not strictly followed because of destructive sampling and because emergence of new adults was equated with the end of life for that particular cohort (that is, death of the last individual). Consequently, flight mortality was not considered. In addition, individuals within the sample were assumed to be subjected to the same risks, and the survival of one individual was assumed to be independent of the survival of any other individual (Chiang 1968).

Ten individual mortality factors (risks) were measured:

1. Within competition (WC)—mortality from crowding of larvae within the same brood or egg gallery.
2. Between competition (BC)—mortality from crowding of larvae from two or more separate or different broods or egg galleries.
3. A predacious fly, *Medetera aldrichii* (MD).
4. Predacious beetles, *Thanasimus undatulus* and *Enoclerus sphegeus* (CL).
5. Insect parasites, primarily *Coeloides dendroctoni* (CD).
6. Woodpeckers (WP).
7. Temperature (T)—mortality from low winter temperatures.
8. Drying of the phloem (D), recorded as desiccation of the larvae.
9. Pitch (PI), recorded as inundation of larval galleries with pitch and drowning of larvae.
10. Unknown (UNK)—cause of death could not be determined.

Due to inadequacy of measurement techniques, not all mortality is readily definable or measurable and therefore is attributable to unknown causes.

Data Analysis.—The competing risks analysis (Chiang 1968) was used in most cases. Some terms are:

Risk of dying—	A mortality factor present in a population prior to the death of an individual within that population.
Cause of dying—	A mortality factor causing death of an individual in that population.
Crude probability—	The probability of death from a specific risk in the presence of all other risks evident in the uncontrolled insect population and as measured for construction of life tables.
General probability—	Probability of death (or survival) when the cause of death is not specified.

The approach used was to determine the probability of death, using competing risks analysis of life tables to evaluate mortality factors, singly and in combination (Cole 1981). The probability of death due to a mortality factor is the probability proportional to the total loss from all mortality factors. For example, if the probability of loss from all factors was 0.50, and from a single mortality factor was 0.10, then that single factor was contributing 0.10 of 0.50, or taking 0.05 of the total population.

Probability of survival.—As expected from previous population studies (Reid 1963; Cole and others 1976; Klein and others 1978), the largest populations occurred in large trees except in the preepidemic period when populations in 12- and 15-inch (30- and 38-cm) tree classes were similar (table 11; fig. 35). The probability of an individual surviving the entire egg-to-adult period increased with tree size during the preepidemic period (table 12; fig. 36). During the epidemic and postepidemic periods, probability of survival was greatest in the 12-inch (30-cm) diameter class and was approximately equal in the 9- and 15-inch (23- and 38-cm) classes.

Table 11.—Mountain pine beetle survival and mortality[1] by cause in three lodgepole pine diameter classes and three stages of infestation

Infestation	Observation	No. alive	No. dead	Numbers per sample										
				WC	BC	CL	CD	MD	PA	WP	T	D	PI	UNK
				Tree diameter class: 23 cm										
	0	69.64	0	0	0	0	0	0	0	0	0	0	0	0
Pre-epidemic	1	55.37	14.27	1.10	1.08	0	0	.25	0	0	.26	0	0	11.58
	2	30.36	25.01	1.23	1.25	0.03	0	.70	0	0.58	13.78	1.00	0	6.44
	3	8.21	22.15	.71	1.11	.01	0.35	.26	.39	.63	7.07	0.31	.11	11.20
	4	3.33	4.88	0	0	0	0	0	0	0	0	0	0	4.88
	Sum		*66.31*	*3.04*	*3.44*	*.04*	*.35*	*1.21*	*.39*	*1.21*	*21.11*	*1.31*	*.11*	*34.10*
	0	93.60	0	0	0	0	0	0	0	0	0	0	0	0
	1	85.78	7.82	.75	.73	0	0	.48	0	.10	1.03	0	.20	4.53
Epidemic	2	27.38	58.40	1.30	2.33	0	0	.38	.05	1.15	37.02	8.61	0	7.56
	3	19.35	8.03	.15	.35	.03	.30	.13	.18	.20	.17	.67	.03	5.82
	4	15.21	4.14	0	0	0	0	0	0	0	0	0	0	4.14
	Sum		*78.39*	*2.20*	*3.41*	*.03*	*.30*	*.99*	*.23*	*1.45*	*38.22*	*9.28*	*.23*	*22.05*
	0	80.43	0	0	0	0	0	0	0	0	0	0	0	0
Post-epidemic	1	69.96	10.47	1.97	2.95	.15	.03	1.84	.20	.03	2.12	.11	.32	.75
	2	26.84	43.12	.20	.86	.04	.01	.85	.14	1.65	12.39	4.80	.45	21.73
	3	13.24	13.60	0	0	.08	1.08	.06	.08	.62	.46	4.34	.02	6.86
	4	6.00	7.24	0	0	0	.02	0	.02	0	0	.07	0	7.13
	Sum		*74.43*	*2.17*	*3.81*	*.27*	*1.14*	*2.75*	*.44*	*2.30*	*14.97*	*9.32*	*.79*	*36.47*
				Tree diameter class: 30 cm										
	0	83.68	0	0	0	0	0	0	0	0	0	0	0	0
Pre-epidemic	1	70.78	12.90	.33	.58	0	.02	1.11	.84	0	.03	0	0	9.99
	2	32.70	38.08	.51	2.00	0	0	1.35	.27	2.33	15.33	.35	.14	15.80
	3	15.46	17.24	.55	.41	.03	.36	.86	1.01	1.58	6.15	.07	0	6.22
	4	7.42	8.04	0	0	0	0	0	0	0	0	0	0	8.04
	Sum		*76.26*	*1.39*	*2.99*	*.03*	*.38*	*3.32*	*2.12*	*3.91*	*21.51*	*.42*	*.14*	*40.05*
	0	113.48	0	0	0	0	0	0	0	0	0	0	0	0
	1	103.65	9.83	1.63	2.10	0	0	1.65	0	.23	1.27	0	.15	2.80
Epidemic	2	49.48	54.17	0	3.25	0	0	.43	.70	1.38	29.80	6.70	0	11.91
	3	30.04	19.44	0	0	.10	.48	.15	.05	.68	.10	.93	0	16.95
	4	15.14	14.90	0	0	0	0	0	0	0	0	0	0	14.90
	Sum		*98.34*	*1.63*	*5.35*	*.10*	*.48*	*2.23*	*.75*	*2.29*	*31.17*	*7.63*	*.15*	*46.56*
	0	80.15	0	0	0	0	0	0	0	0	0	0	0	0
Post-epidemic	1	66.99	13.16	2.50	1.54	.03	.08	2.10	.10	.18	3.10	0	0	3.53
	2	34.21	32.78	.40	.69	.03	.17	1.68	.28	.72	12.15	3.01	.11	13.54
	3	16.78	17.43	0	0	.21	.35	.07	.78	.64	.41	3.52	0	11.45
	4	8.33	8.45	0	0	0	0	0	0	0	0	.03	0	8.42
	Sum		*71.82*	*2.90*	*2.23*	*.27*	*.60*	*3.85*	*1.16*	*1.54*	*15.66*	*6.56*	*.11*	*36.94*
				Tree diameter class: 38 cm										
	0	82.56	0	0	0	0	0	0	0	0	0	0	0	0
Pre-epidemic	1	69.98	12.58	.41	.50	.03	0	1.14	1.73	0	.24	0	0	8.53
	2	40.36	29.62	1.30	.08	0	0	1.90	0	.25	9.86	.07	0	16.16
	3	16.96	23.40	.30	2.46	.01	.14	.42	0	.30	4.88	.08	0	14.81
	4	8.25	8.71	0	0	0	0	0	0	0	0	0	0	8.71
	Sum		*74.31*	*2.01*	*3.04*	*.04*	*.14*	*3.46*	*1.73*	*.55*	*14.98*	*.15*	*0*	*48.21*
	0	128.88	0	0	0	0	0	0	0	0	0	0	0	0
	1	117.23	11.65	2.63	1.20	0	0	3.23	.15	.58	.48	0	0	3.38
Epidemic	2	51.18	66.05	.78	7.78	0	0	1.70	1.38	.33	30.20	14.13	0	9.75
	3	26.30	24.88	0	0	.10	.15	.28	.15	.25	0	.03	0	23.92
	4	17.08	9.22	0	0	0	0	0	0	0	0	0	0	9.22
	Sum		*111.80*	*3.41*	*8.98*	*.10*	*.15*	*5.21*	*1.68*	*1.16*	*30.68*	*14.16*	*0*	*46.27*
	0	100.20	0	0	0	0	0	0	0	0	0	0	0	0
Post-epidemic	1	82.49	17.71	1.53	1.51	.04	0	6.73	0	0	2.84	0	0	5.05
	2	34.84	47.65	1.61	2.65	0	0	5.34	.35	.18	19.41	5.92	.04	12.15
	3	14.74	20.10	0	0	.04	.18	.41	.26	.05	.47	1.46	.05	17.18
	4	5.33	9.41	0	0	0	0	0	0	0	0	0	0	9.41
	Sum		*94.87*	*3.14*	*4.16*	*.09*	*.18*	*12.48*	*.61*	*.23*	*22.72*	*7.38*	*.09*	*43.79*

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[1] Mortality factor abbreviations are defined in footnote 1, table 9.

(con.)

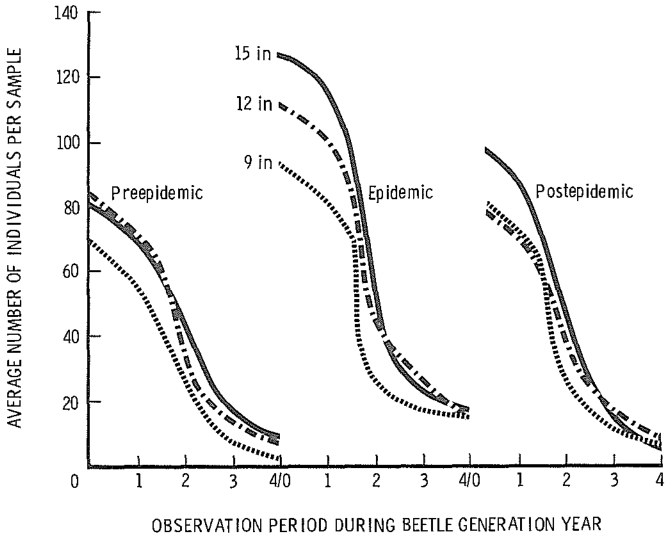

Figure 35.—Mountain pine beetle brood survival by observation, tree diameter class, and stage of infestation.

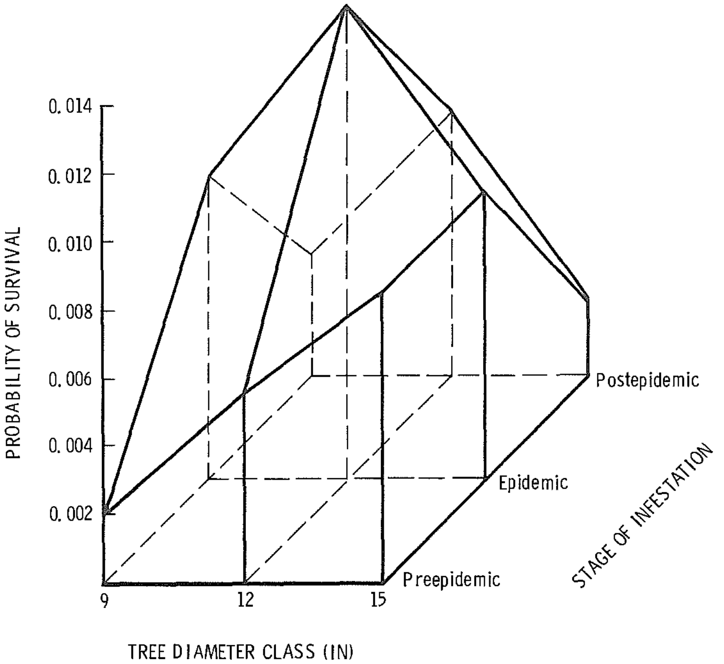

Figure 36.—Probability of any one mountain pine beetle egg surviving to the adult stage by tree diameter class and stage of infestation.

Table 12.—General probability of a mountain pine beetle surviving from egg to adult by lodgepole pine diameter class and stage of infestation

	Tree diameter class		
Stage of infestation	**23 cm**	**30 cm**	**38 cm**
Preepidemic	0.00196	0.00551	0.00850
Epidemic	.00900	.01403	.00850
Postepidemic	.00360	.00776	.00223

The greater survival in the 12-inch (30-cm) over the 15-inch (38-cm) class during the epidemic and postepidemic periods is probably that most of the large diameter trees have been killed, leaving only a few that may be of low quality. Residual trees within the 15-inch (38-cm) class may be slow growing and therefore provide a low amount of food (thin phloem) and moisture (thin sapwood) for beetle survival. These assumptions will be discussed more fully below.

Life Expectations.—Life table studies focus upon life expectation and survival rates. By comparing these, the intensity of risks during the stages of an infestation can be evaluated. The rate of survival (or conversely, mortality) governs life expectation. For the mountain pine beetle, the total life interval from egg to adult is approximately 365 days. The abridged life table for proportions of survival and death, life expectation, and the variances for both are given in table 13. When the cause of beetle death is not specified, the probabilities of survival and death and their variances become general probabilities.

Life expectations for mountain pine beetle populations fluctuate within diameter classes and within and among stages of infestations. However, life expectations generally increase from the smallest to the largest diameter tree class and are greatest during the epidemic stage (table 14 and fig. 37). Life expectations within the 12-inch (30-cm) diameter class appear consistent (table 14). Lack of variation in this class over the three infestation classes suggests that significant population changes that affect the beginning or end of an epidemic are not occurring within the 12-inch (30-cm) class. It is in the 9- and 15-inch (23- and 38-cm) classes where life expectations show considerable change and reflect infestation trend.

Table 13.—The abridged cohort life table and life expectations for mountain pine beetles in three lodgepole pine diameter classes and three stages of infestation

Infestation/tree diameter class	Interval length (days) x_i to x_{i+1}	Number live at start of x_i (1_i)	Number dying during x_i to x_{i+1} (d_i)	Surviving x_i to x_{i+1} (p_i)	Dying x_i to x_{i+1} (q_i)	Variance $(V_{p_i}V_{q_i})$	Fraction of last interval of life (a_i)	Life expectations observed at age x_i		
								(e_i)	(Ve_i)	(SEe_i)
Pre-	30	69.64	14.27	0.795	0.205	0.00234	0.50	158.26	137.58	11.73
epidemic	180	55.37	25.01	.436	.564	.00444	.50	165.18	124.33	11.15
	60	30.36	22.15	.118	.882	.00343	.50	47.10	8.24	2.87
23 cm	30	8.21	4.88	.048	.952	.00557	.50	33.25	6.34	2.52
	60	3.33	3.33	0	1.000	—	—	30.00	—	—
	30	83.68	12.90	.856	.154	.00158	.50	163.01	107.11	10.35
	180	70.78	38.08	.391	.609	.00336	.50	159.99	90.67	9.52
30 cm	60	32.70	17.24	.185	.815	.00461	.50	61.49	19.33	4.40
	30	15.46	8.04	.089	.911	.00524	.50	36.60	7.21	2.69
	60	7.42	7.42	0	1.000	—	—	30.00	—	—
	30	82.56	12.58	.848	.152	.00156	.50	176.40	131.83	11.48
	180	69.98	29.62	.489	.511	.00357	.50	175.42	115.54	10.75
38 cm	60	40.36	23.40	.205	.795	.00404	.50	58.11	15.19	3.90
	30	16.96	8.71	.100	.900	.00531	.50	36.89	7.42	2.72
	60	8.25	8.25	0	1.000	—	—	30.00	—	—
Epidemic	30	93.60	7.82	.916	.084	.00082	.50	169.95	72.21	8.50
	180	85.78	58.40	.293	.707	.00241	.50	146.43	57.61	7.59
	60	27.38	8.03	.207	.793	.00600	.50	86.80	54.80	7.40
23 cm	30	19.35	4.14	.162	.838	.00702	.50	50.37	18.17	4.26
	60	15.21	15.21	0	1.000	—	—	30.00	—	—
	30	113.48	9.83	.913	.087	.00070	.50	181.14	82.90	9.10
	180	103.65	54.17	.436	.564	.00237	.50	166.90	71.68	8.47
30 cm	60	49.48	19.44	.265	.735	.00394	.50	71.09	22.26	4.72
	30	30.04	14.90	.133	.867	.00384	.50	37.68	5.60	2.37
	60	15.14	15.14	0	1.000	—	—	30.00	—	—
	30	128.88	11.65	.848	.152	.00100	.50	173.31	77.71	8.82
	180	117.23	66.05	.489	.511	.00213	.50	159.04	57.41	7.58
38 cm	60	51.18	24.88	.205	.795	.00318	.50	68.15	16.79	4.10
	30	26.30	9.22	.100	.900	.00342	.50	44.22	6.84	2.62
	60	17.08	17.08	0	1.000	—	—	30.00	—	—
Post-	30	80.43	10.47	.870	.130	.00141	.50	159.01	93.76	9.68
epidemic	180	69.96	43.12	.334	.666	.00318	.50	150.56	76.51	8.75
	60	26.84	13.60	.165	.835	.00513	.50	67.85	26.81	5.18
23 cm	30	13.24	17.24	.075	.925	.00524	.50	46.72	11.68	3.42
	60	6.00	6.00	0	1.000	—	—	30.00	—	—
	30	80.15	13.16	.836	.164	.00171	.50	168.08	125.01	11.18
	180	66.99	32.78	.427	.573	.00365	.50	168.14	109.39	10.46
30 cm	60	34.21	17.43	.209	.791	.00483	.50	63.03	21.41	4.63
	30	16.78	8.45	.104	.896	.00555	.50	37.34	7.95	2.82
	60	8.33	8.33	0	1.000	—	—	30.00	—	—
	30	100.20	17.71	.823	.177	.00145	.50	152.18	77.16	8.78
	180	82.49	47.65	.348	.652	.00275	.50	151.63	63.64	7.98
38 cm	60	34.84	20.10	.147	.853	.00360	.50	55.92	12.08	3.47
	30	14.74	9.40	.053	.947	.00341	.50	31.26	3.44	1.85
	60	5.33	5.33	0	1.000	—	—	30.00	—	—

Table 14.—The observed life expectation for mountain pine beetles (e_i) at age x_i in three lodgepole pine diameter classes and three stages of infestation

Stage of infestation	Observation (age x_i)	Tree diameter class		
		23 cm	30 cm	38 cm
Preepidemic	0	158.26	163.01	176.40
	1	165.18	159.99	175.42
	2	47.10	61.49	58.11
	3	33.25	36.60	36.89
	4	30.00	30.00	30.00
Epidemic	0	169.95	181.14	173.31
	1	146.43	166.90	159.04
	2	86.80	71.09	68.14
	3	50.37	37.68	44.22
	4	30.00	30.00	30.00
Postepidemic	0	159.01	168.08	152.18
	1	150.56	168.14	151.63
	2	67.85	63.03	55.92
	3	46.72	37.34	31.26
	4	30.00	30.00	30.00

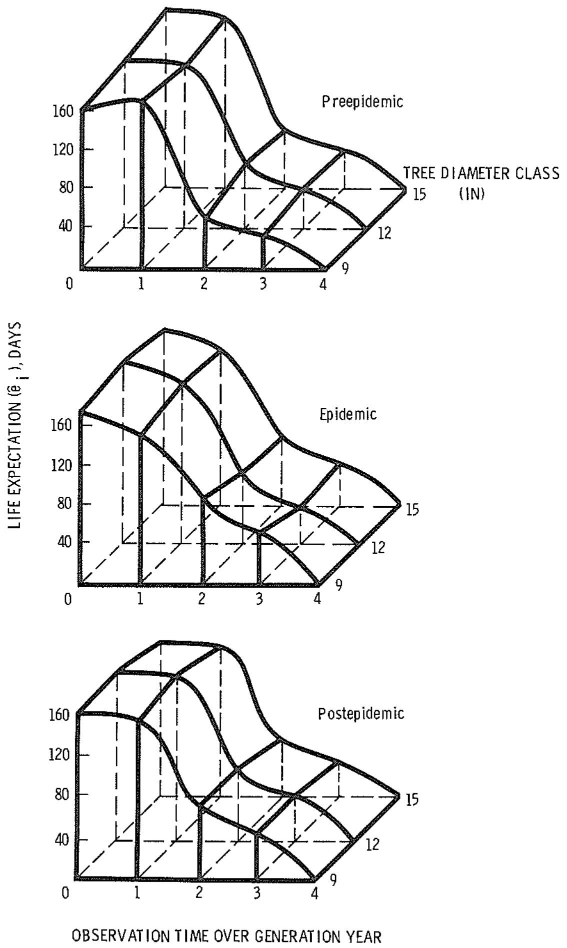

Figure 37.—Life expectations for mountain pine beetles in days at each observed time during the generation year by tree diameter class and stage of infestation.

During the preepidemic period, the greatest beetle life expectations occur in large diameter trees; during epidemic and postepidemic periods, life expectations are greatest within the smallest diameter class. When they do occur, changes in life expectation ($\hat{e}_i$) are probably associated with shifts in the attack and gallery densities of the beetle by diameter over the life of an infestation. During the early years, attack density declines, then begins to increase as the infestation progresses (fig. 38) (Cole and others 1976; Klein and others 1978). During the postepidemic period in particular, minimal numbers of large diameter trees remain, and these are infested at denser rates than those earlier in the infestation, resulting in low brood production.

General probability of survival.—The general probability of survival from egg to adult follows the configuration of life expectations (table 15; fig. 39). During the preepidemic period, the general probability of survival increases over diameter class within each brood developmental period. These probabilities shift slightly in favor of the 12-inch (30-cm) diameter class during the epidemic and increase strongly for it during the postepidemic stage. The greater survival in 15-inch (38-cm) trees in the preepidemic stage suggests these trees provide the impetus for an epidemic.

Within diameter class, over stage of infestation, the probability of survival generally peaks, as expected, during the epidemic. Survival is greater during the postepidemic than during the preepidemic in the 9-inch (23-cm) class, only slightly greater in the 12-inch (30-cm), but less in the 15-inch (38-cm) (fig. 40). The lower survival in large trees during the postepidemic is probably due to the large increase in attack and gallery densities in the 15-inch (38-cm) d.b.h. class.

Table 15.—General probabiilties of mountain pine beetles surviving the growth interval, x_i to x_{i+1}, in three lodgepole pine diameter classes and three stages of infestation

Stage of infestation	Interval (x_i to x_{i+1})		Tree diameter class		
			23 cm	30 cm	38 cm
		Days			
Preepidemic	0.	30	0.795	0.856	0.848
	1.	180	.436	.391	.489
	2.	60	.118	.185	.205
	3.	30	.048	.089	.100
	4.	60	0	0	0
Epidemic	0.	30	.916	.913	.848
	1.	180	.293	.436	.489
	2.	60	.207	.265	.205
	3.	30	.162	.133	.100
	4.	60	0	0	0
Postepidemic	0.	30	.870	.836	.823
	1.	180	.334	.427	.348
	2.	60	.165	.209	.147
	3.	30	.075	.104	.053
	4.	60	0	0	0

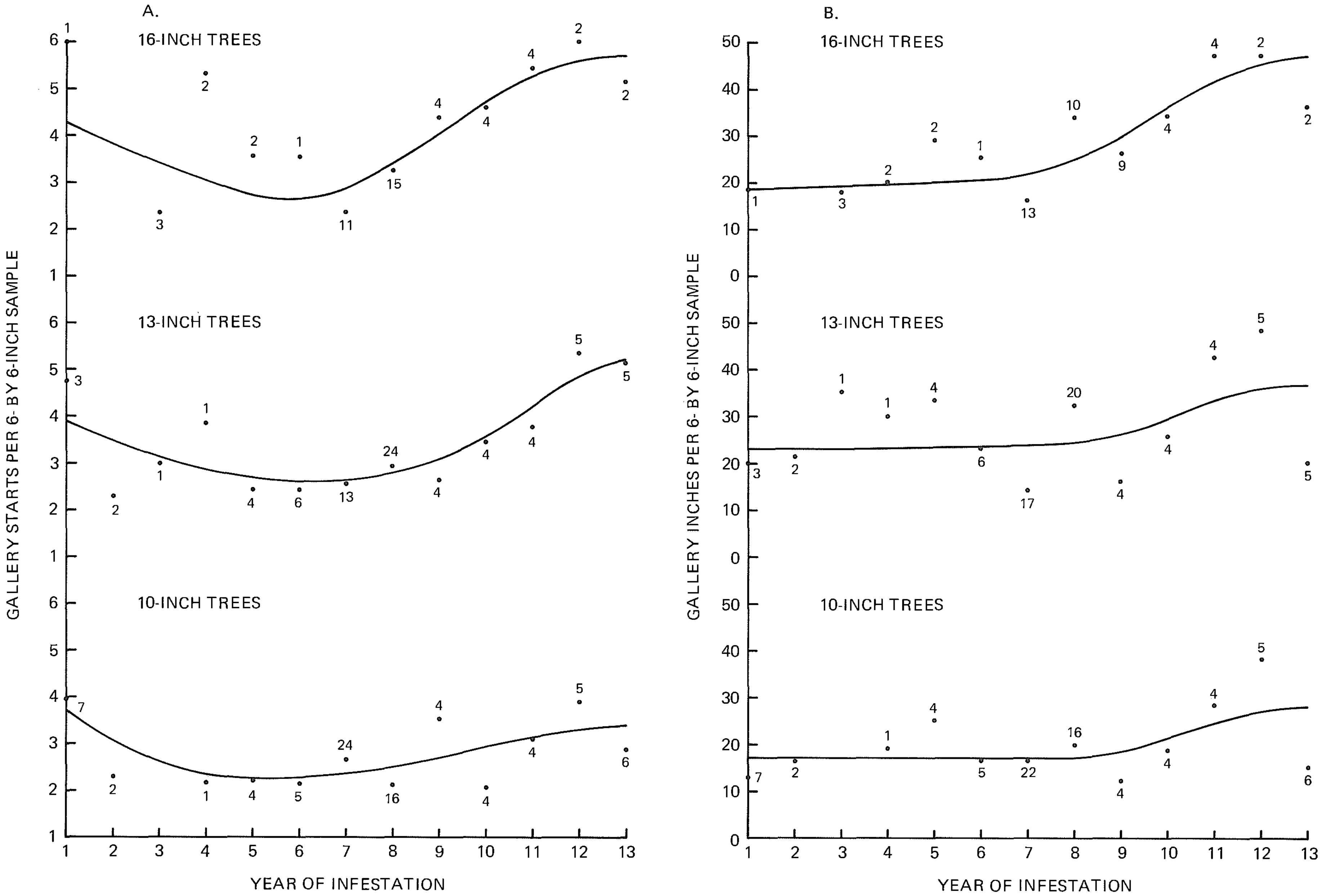

Figure 38.—Mountain pine beetle egg gallery starts and egg gallery inches by diameter for 13 years. A. Egg gallery starts; B. egg gallery inches. Number at each data point indicates number of trees sampled (Cole and others 1976).

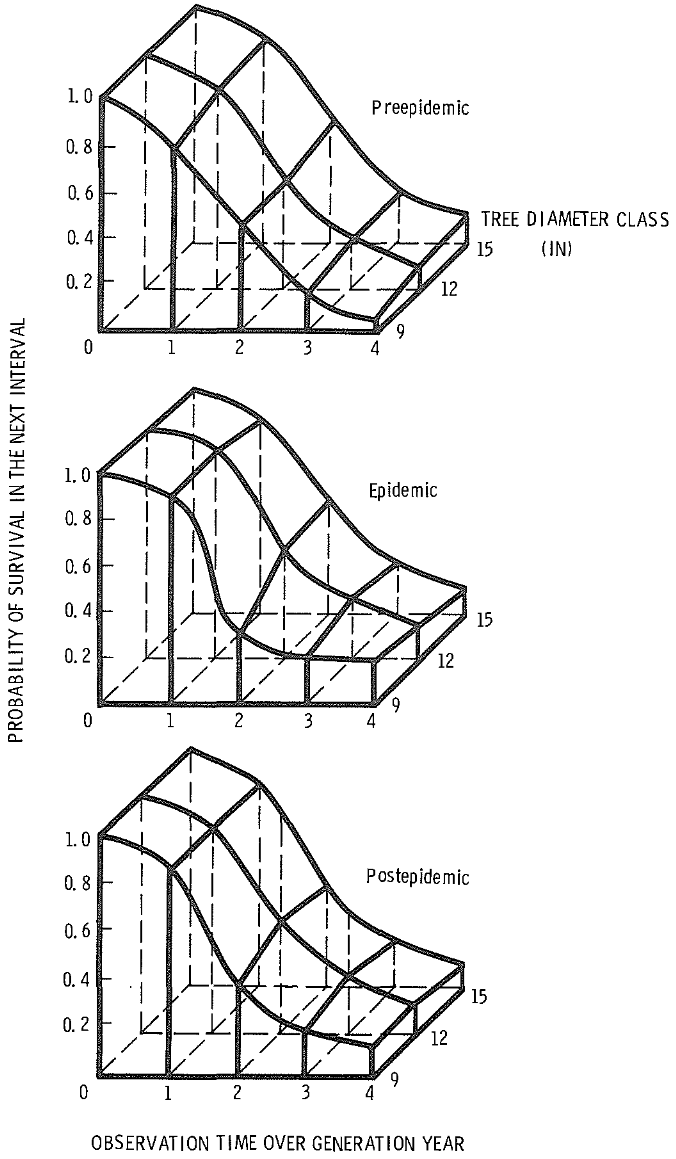

Figure 39.—Probability of mountain pine beetle survival to the next interval by tree diameter class and stage of infestation.

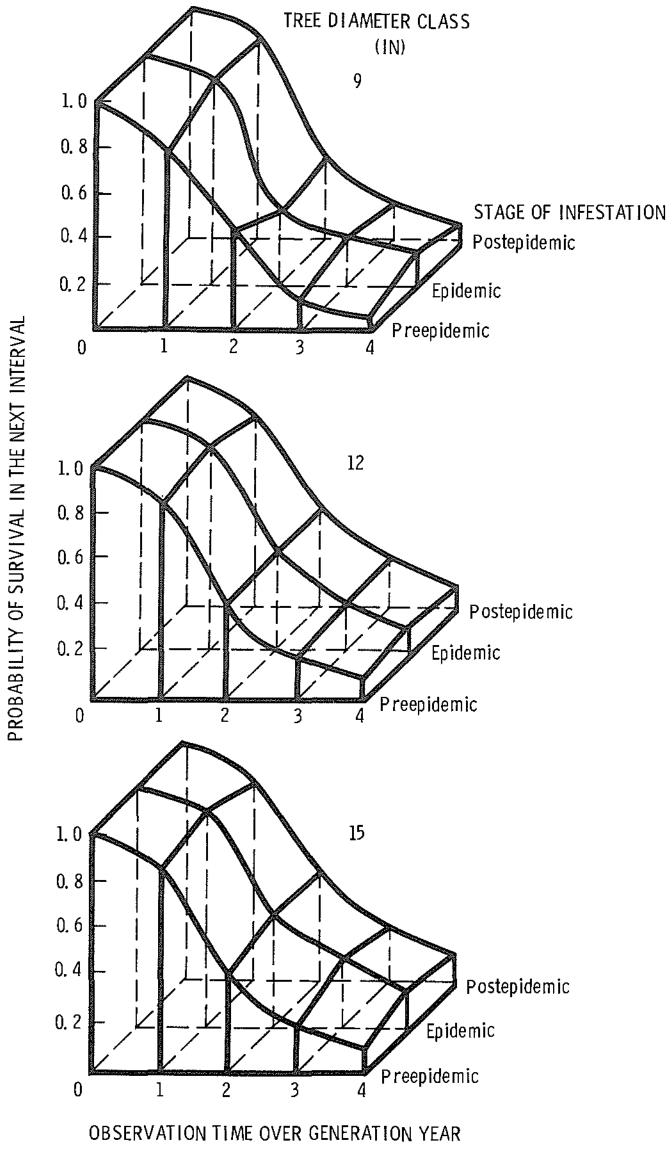

Figure 40.—Probability of mountain pine beetle survival to the next interval by stage of infestation and tree diameter class.

Crude probability of death.—General mortality is the total mortality at a particular time. The component probabilities of death (crude probabilities) to specific mortality factors are additive to the sum of the general mortality. The greatest cause of mortality is listed as "unknown," which accounted for approximately 50 percent of mortality during any beetle generation, within any diameter class of trees, and during any infestation stage (fig. 41). If the causes were known, unknown mortality probably would be proportionally distributed among the other causes according to their respective occurrence. However, in interpreting the following analyses, mortality will be evaluated as originally recorded.

The crude probabilities of death due to specific mortality factors are shown in table 16 and figure 42. The general probability of death is the rear profile in each case. Smoothed curves have been drawn through mortality estimates for discrete points in time to facilitate visual appraisal of mortality trends over time. Mortality read from these graphs, however, is only pertinent at that particular time.

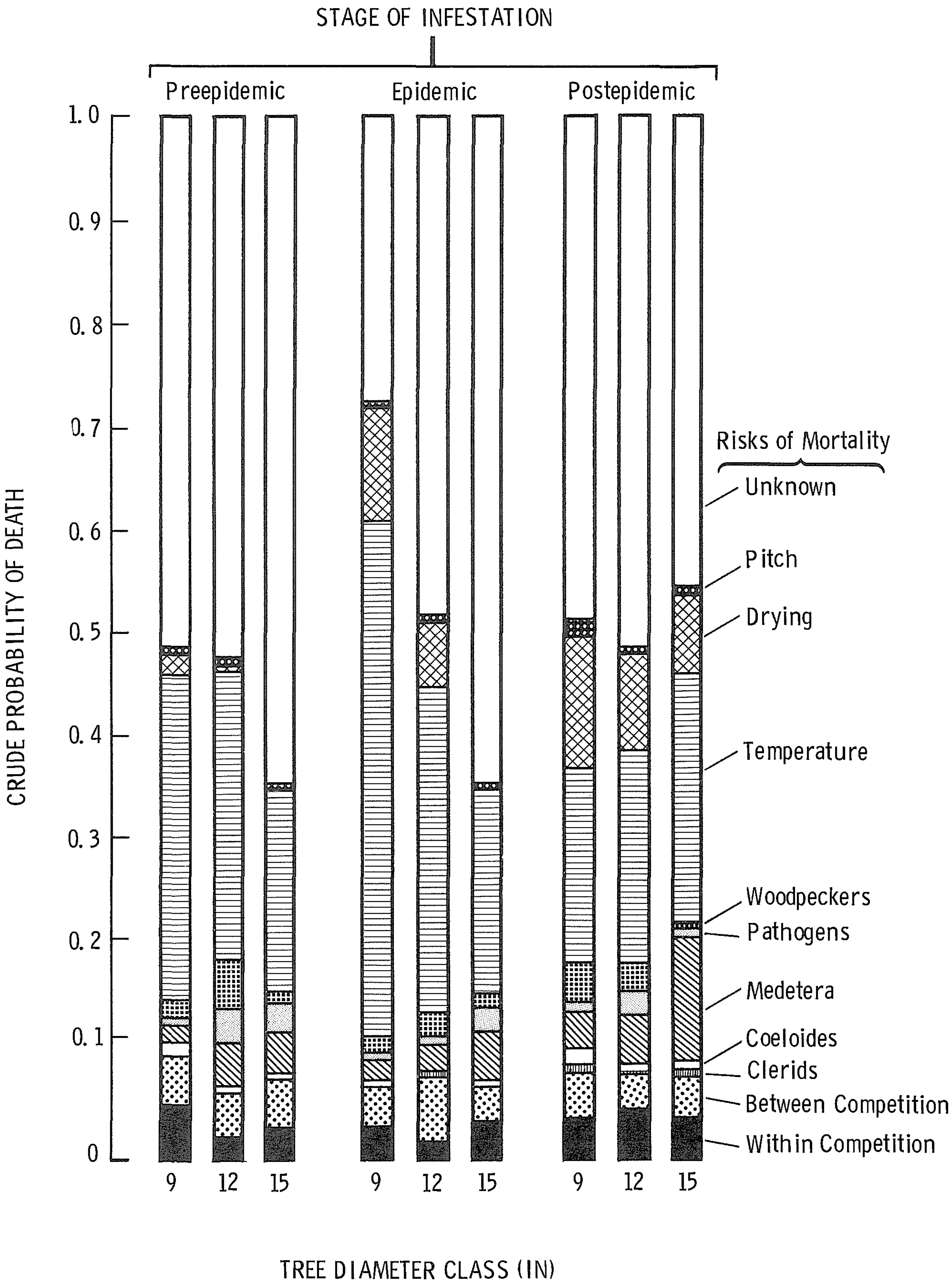

Figure 41.—Crude probability of mountain pine beetle death by specific mortality factors in three lodgepole pine diameter classes.

Table 16.—Crude probability of mountain pine beetle death due to a specific mortality factor[1] in the presence of all other mortality factors by lodgepole pine diameter class and stage of beetle infestation

Stage of infestation	Observations	General probability		Crude probabilities										
		Survival	Death	WC	BC	CL	CD	MD	PA	WP	T	D	PI	UNK
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
Pre-	1	.795	.205	.077	.076	0	0	.018	0	0	.018	0	0	.811
epidemic	2	.436	.564	.049	.050	.001	0	.028	0	.023	.551	.040	0	.258
23 cm	3	.118	.882	.032	.050	.001	.016	.012	.018	.028	.319	.014	.005	.506
	4	.048	.952	0	0	0	0	0	0	0	0	0	0	1.000
Crude probability per generation				.046	.052	.001	.005	.018	.006	.018	.318	.020	.002	.514
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.856	.154	.026	.045	0	.002	.086	.065	0	.002	0	0	.774
30 cm	2	.391	.609	.013	.053	0	0	.035	.007	.061	.403	.009	.004	.415
	3	.185	.815	.032	.026	.002	.021	.050	.058	.091	.356	.004	0	.360
	4	.089	.911	0	0	0	0	0	0	0	0	0	0	1.000
Crude probability per generation				.018	.039	.001	.005	.044	.028	.051	.282	.006	.002	.525
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.848	.152	.033	.040	.002	0	.091	.137	0	.019	0	0	.678
38 cm	2	.489	.511	.044	.003	0	0	.064	0	.008	.333	.002	0	.546
	3	.205	.795	.013	.105	.001	.006	.018	0	.013	.209	.003	0	.633
	4	.100	.900	0	0	0	0	0	0	0	0	0	0	1.000
Crude probability per generation				.027	.041	.001	.002	.047	.023	.007	.202	.002	0	.649
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
Epidemic	1	.916	.084	.096	.093	0	0	.061	0	.013	.132	0	.026	.579
	2	.293	.707	.022	.040	0	0	.007	.001	.020	.634	.147	0	.129
23 cm	3	.207	.793	.019	.044	.004	.037	.016	.022	.025	.021	.083	.004	.725
	4	.162	.838	0	0	0	0	0	0	0	0	0	0	1.000
Crude probability per generation				.028	.044	.001	.004	.013	.003	.018	.448	.118	.003	.281
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.913	.087	.166	.214	0	0	.168	0	.023	.129	0	.015	.285
30 cm	2	.436	.564	0	.060	0	0	.008	.013	.025	.550	.124	0	.220
	3	.265	.735	0	0	.005	.024	.008	.003	.035	.005	.048	0	.872
	4	.133	.867	0	0	0	0	0	0	0	0	0	0	1.000
Crude probability per generation				.017	.055	.001	.005	.023	.008	.023	.317	.078	.001	.472
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.848	.152	.033	.040	.002	0	.091	.137	0	.019	0	0	.678
38 cm	2	.489	.511	.044	.003	0	0	.064	0	.008	.333	.002	0	.546
	3	.205	.795	.013	.105	.001	.006	.018	0	.013	.209	.003	0	.633
	4	.100	.900	0	0	0	0	0	0	0	0	0	0	1.000
Crude probability per generation				.027	.041	.001	.002	.047	.023	.007	.202	.002	0	.649
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
Post-	1	.870	.130	.188	.282	.014	.003	.176	.019	.003	.202	.011	.031	.071
epidemic	2	.334	.666	.005	.020	.001	.001	.020	.003	.038	.287	.111	.010	.505
	3	.165	.835	0	0	.006	.079	.004	.006	.046	.034	.319	.001	.505
23 cm	4	.075	.925	0	0	0	.003	0	.003	0	0	.010	0	.984
Crude probability per generation				.029	.051	.004	.015	.037	.006	.031	.201	.125	.011	.490
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.836	.164	.190	.117	.002	.006	.160	.008	.014	.236	0	0	.267
30 cm	2	.427	.573	.012	.021	.001	.005	.051	.009	.022	.371	.092	.003	.413
	3	.209	.791	0	0	.012	.020	.004	.045	.037	.024	.202	0	.656
	4	.104	.896	0	0	0	0	0	0	0	0	.004	0	.996
Crude probability per generation				.040	.031	.004	.008	.054	.016	.021	.218	.091	.002	.515
	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.823	.177	.086	.085	.003	0	.038	0	0	.160	0	0	.286
38 cm	2	.348	.652	.034	.056	0	0	.112	.007	.004	.407	.124	.001	.255
	3	.147	.853	0	0	.002	.009	.020	.013	.002	.023	.073	.003	.855
	4	.053	.947	0	0	0	0	0	0	0	0	0	0	1.000
Crude probability per generation				.033	.044	.001	.002	.132	.006	.002	.240	.078	.001	.461

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[1] Mortality factor abbreviations are defined in footnote 1, table 9.

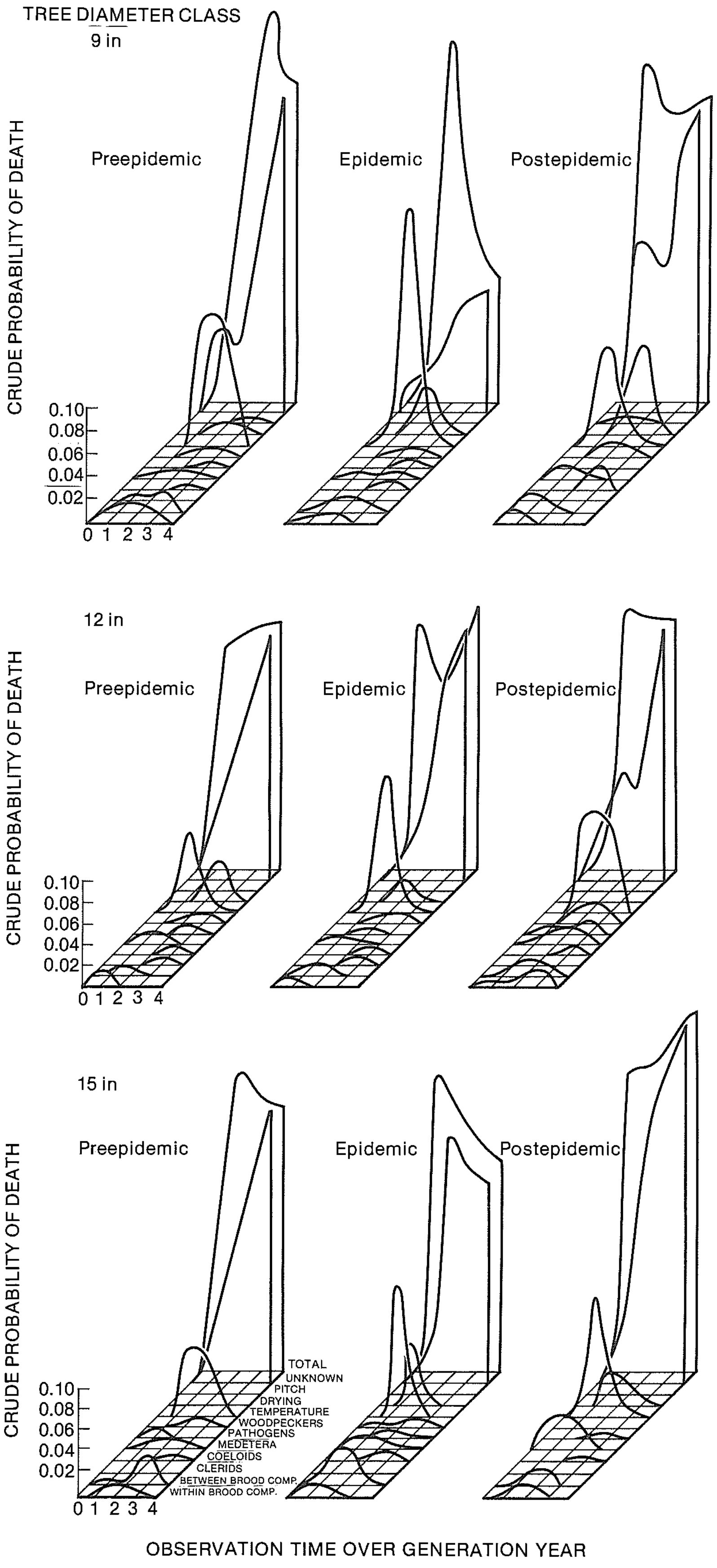

Figure 42.—Graphic display of crude probability of mountain pine beetle death from specific mortality factors by tree diameter class, stage of infestation, and observation.

These data support previous studies (Cole 1974, 1975) showing that winter temperatures followed by drying of phloem in the early summer are the two major causes of mountain pine beetle brood mortality. These factors decrease as diameter increases. Losses to temperature were highest during the epidemic except in the 15-inch (38-cm) class where they were slightly higher in the postepidemic. Losses to drying showed a steady increase with stage of infestation, probably reflecting increases in egg gallery density.

Specific mortality factors.—Within competition (WC) decreased with increased diameter during the preepidemic stage of infestation, but was higher in the 12-inch (30-cm) than the other two diameter classes during the epidemic stage. Within competition, although higher in the postepidemic than in earlier infestation stages, tended to decrease with increased tree diameter (fig. 43). Between competition (BC) followed somewhat the same pattern as within competition (fig. 44). Combining the effects of these two forms of competition, or crowding, an increase generally occurs from preepidemic to postepidemic stages (fig. 45). This increase is large in the 9-inch (23-cm) class. The 12-inch (30-cm) class also shows a large increase in both epidemic and postepidemic phases, with losses to competition slightly higher during the epidemic phase. These increases are probably related to the increased egg gallery densities as infestations progress (Cole and others 1976). Very little increase in mortality to competition occurs in the 15-inch (38-cm) class, probably because the thick phloem that usually occurs in large trees generally provides adequate space and food for the larvae.

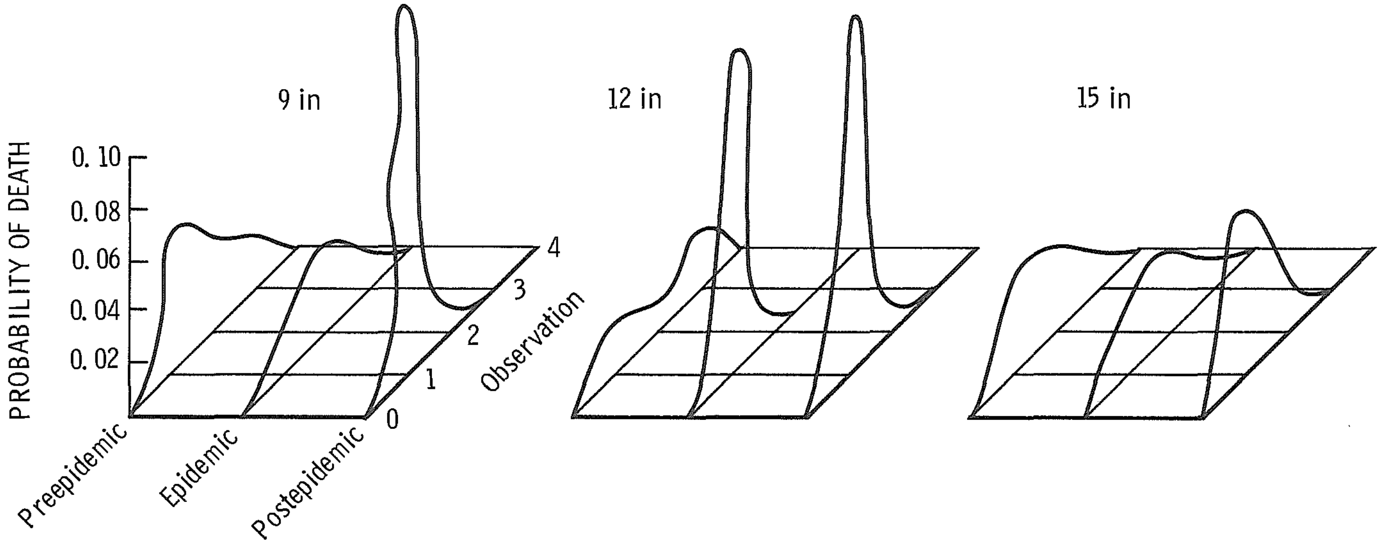

Figure 43.—Crude probability of mountain pine beetle death due to within competition by tree diameter class and stage of infestation.

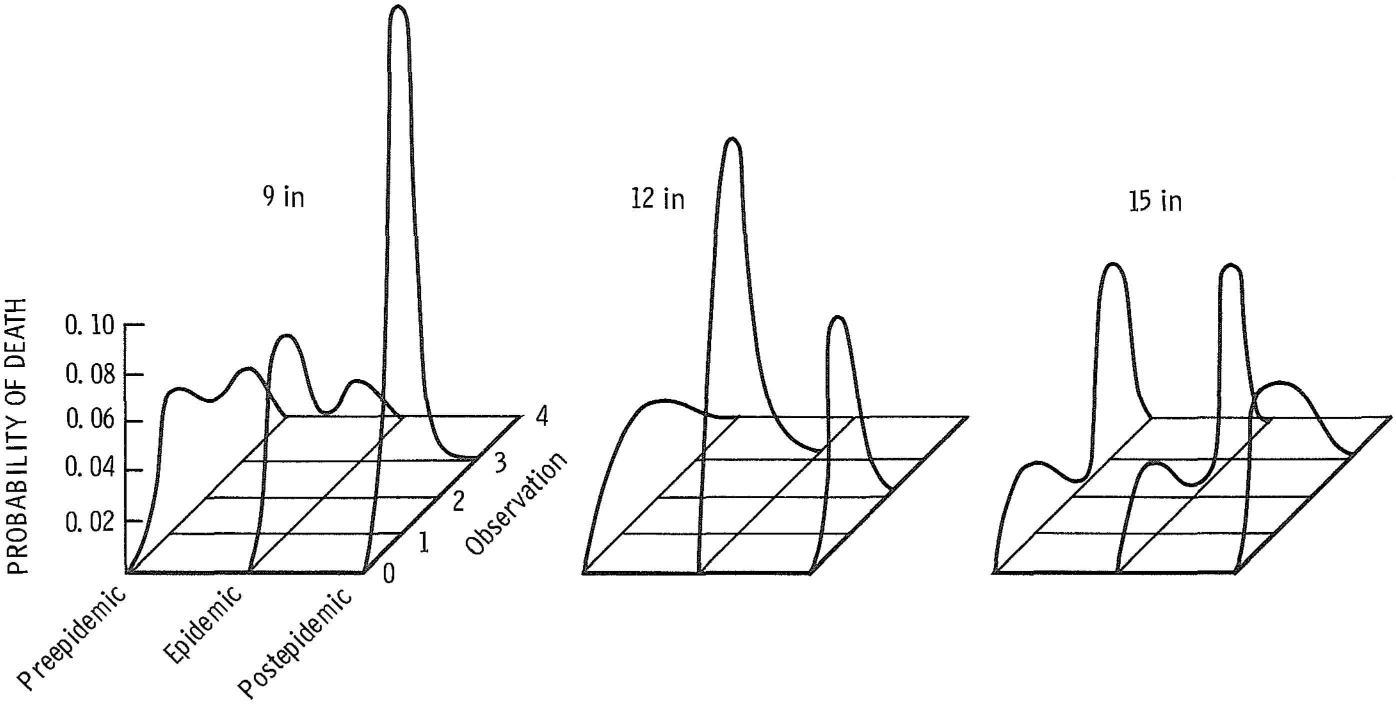

Figure 44.—Crude probability of mountain pine beetle death due to between competition by tree diameter class and stage of infestation.

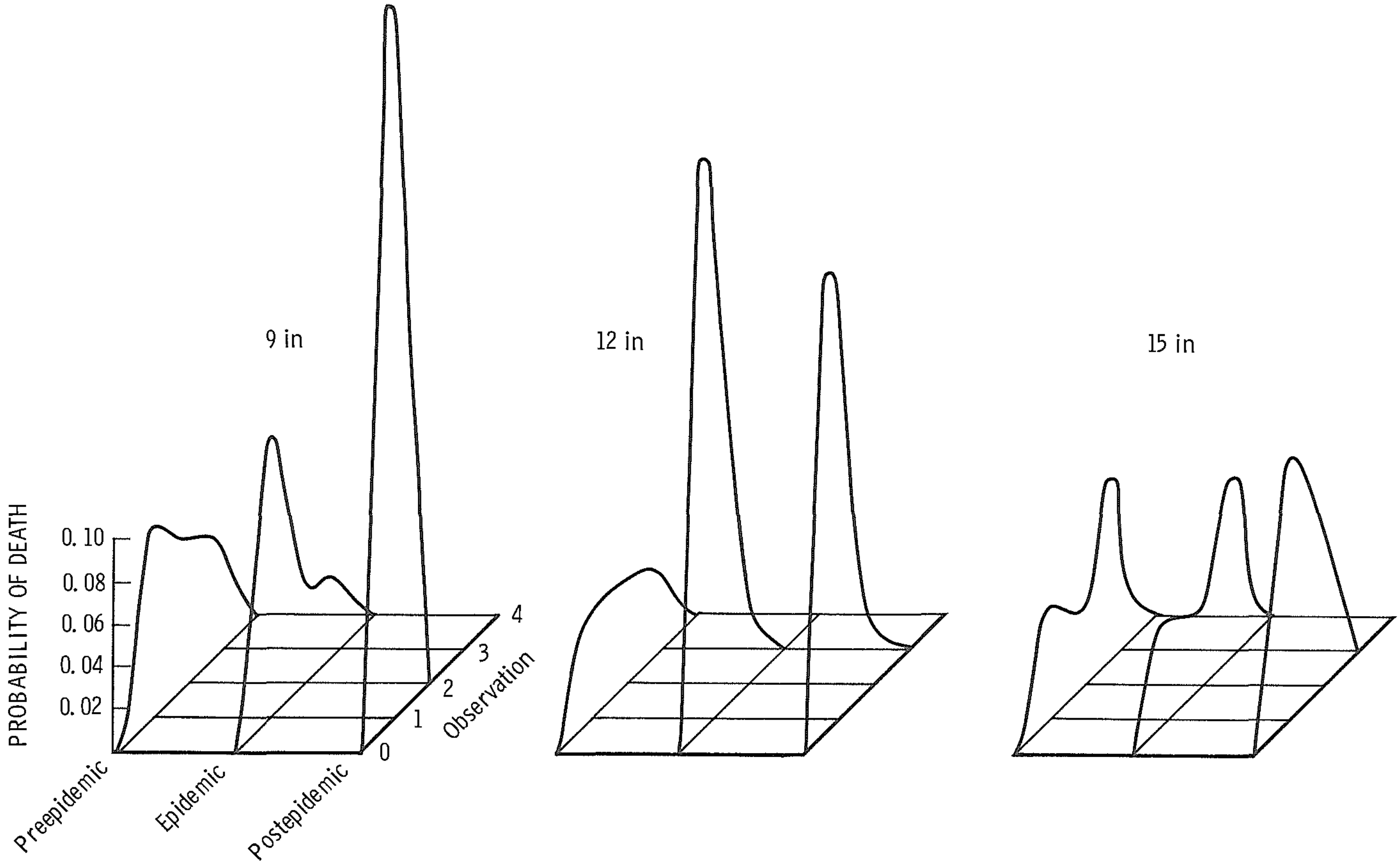

Figure 45.—Combined crude probability of mountain pine beetle death from within and between competition by tree diameter class and stage of infestation.

Medetera aldrichii showed a density-dependent response over time (fig. 46). *Medetera* not only increased by stage of infestation but also showed preference for the greater beetle populations by diameter class. Because of this response and its magnitude, *Medetera* appears to be the most important of the insect predators and parasites of mountain pine beetles. *Medetera* probably is a significant factor in altering expected beetle production from large diameter trees during the postepidemic period.

The probability of a mountain pine beetle being killed by clerids (*Thanasimus undatulus* and *Enoclerus sphegeus*) was extremely small and appears not to significantly reduce mountain pine beetle populations in lodgepole pine (fig. 47).

Probability of death by *Coeloides dendroctoni* also showed a density dependent response from preepidemic to postepidemic infestations in the 9-inch (23-cm) diameter trees (fig. 48). The increased parasitism by *Coeloides* in small diameter trees is probably due to the thin bark. Thick bark restricts parasitism by *Coeloides*, because *Coeloides*'s ovipositor is too short to reach the larvae under the bark.

Death due to woodpeckers showed a low density dependent response in the 9-inch (23-cm) trees and an inverse density dependent response in the 12-inch (30-cm). Probability of death increased over stage of infestation in the 9-inch (23-cm) trees and decreased in the 12-inch (30-cm). Woodpecker predation remained low with slight decrease in the 15-inch (38-cm) trees (fig. 49). The continual low amount of predation in the 15-inch (38-cm) trees was probably related to bark thickness, with greater effort required to remove larvae from thick than from thin bark. The greatest woodpecker predation occurred during the preepidemic stage and in the 12-inch (30-cm) class. During the preepidemic, few infested trees exist, and the woodpecker population is concentrated on these few trees. However, as the beetle population becomes epidemic, the woodpecker population, which does not increase proportionally to the beetle population, consumes proportionally less of the beetle population. The beetle population may still be too high in the postepidemic stage for woodpeckers to consume proportionally as many as in the preepidemic; however, an increase is evident in the 9-inch (23-cm) tree class.

Freezing temperatures were the greatest single cause of mountain pine beetle mortality (fig. 50). The evident peaks of probability of death during the epidemic stage of infestation were probably due to somewhat lower temperatures during that stage rather than to beetle population level. However, probability of death due to temperature was inversely related to increasing diameter in the preepidemic and epidemic stages, and directly related to increasing diameter in the postepidemic stage.

Probability of death due to desiccation caused by phloem drying increased over stage of infestation within each diameter class. Death due to drying, however, decreased with increased tree diameter (fig. 51). The increase in beetle losses to desiccation over the infestation is probably related to increased attack and egg gallery densities (Cole and others 1976), which open up the bark to more rapid drying. The inverse relation of probability of death to drying and tree diameter probably is at least partially related to quantity of moisture as indicated by sapwood thickness, which is positively related to diameter (Amman 1978).

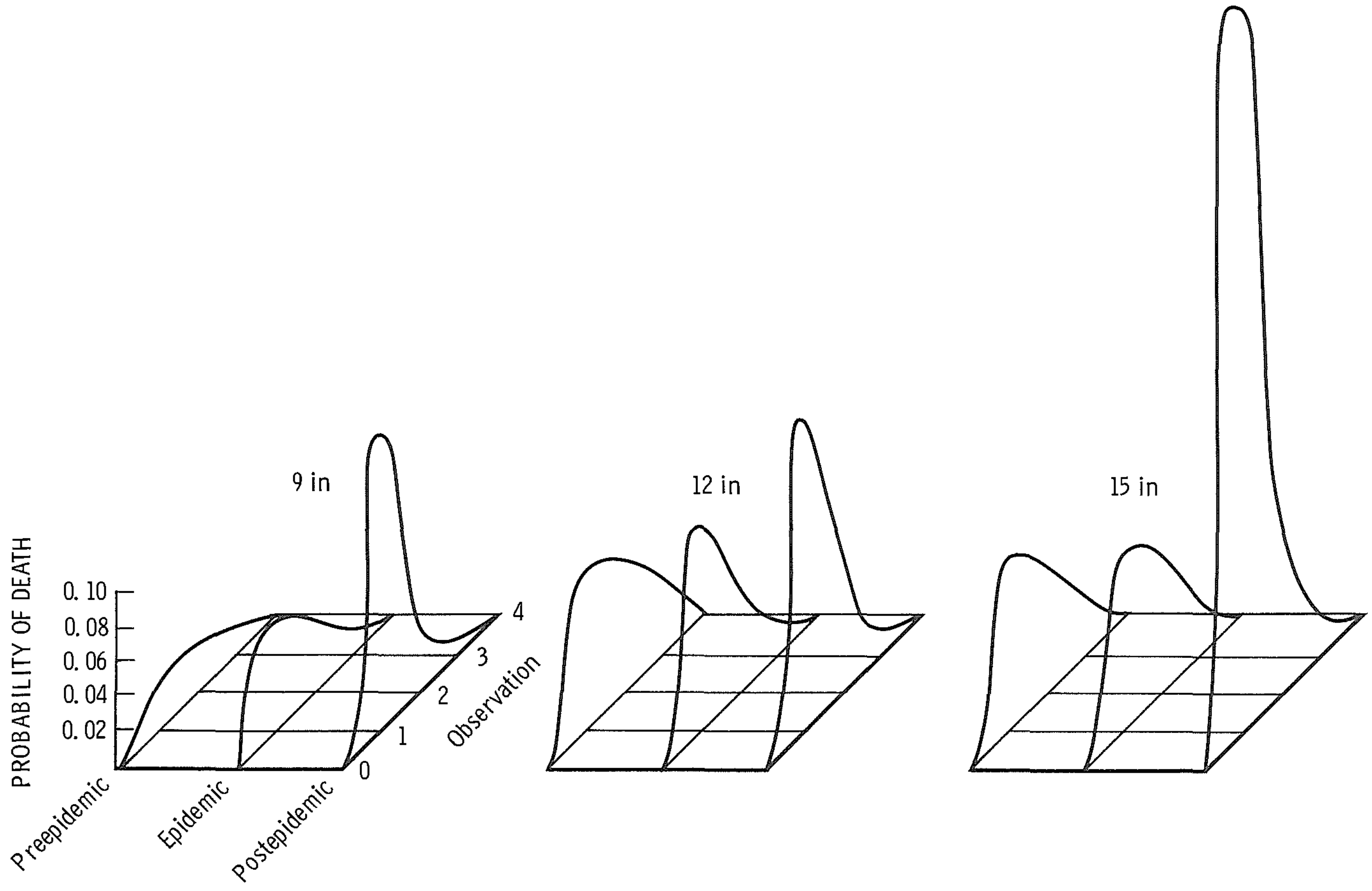

Figure 46.—Crude probability of mountain pine beetle death from *Medetera aldrichii* by tree diameter class and stage of infestation.

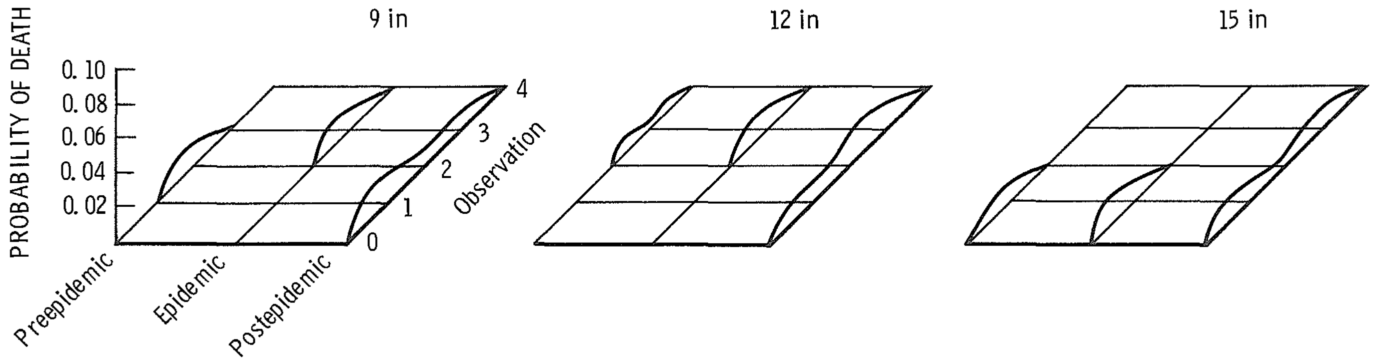

Figure 47.—Crude probability of mountain pine beetle death from clerids by tree diameter class and stage of infestation.

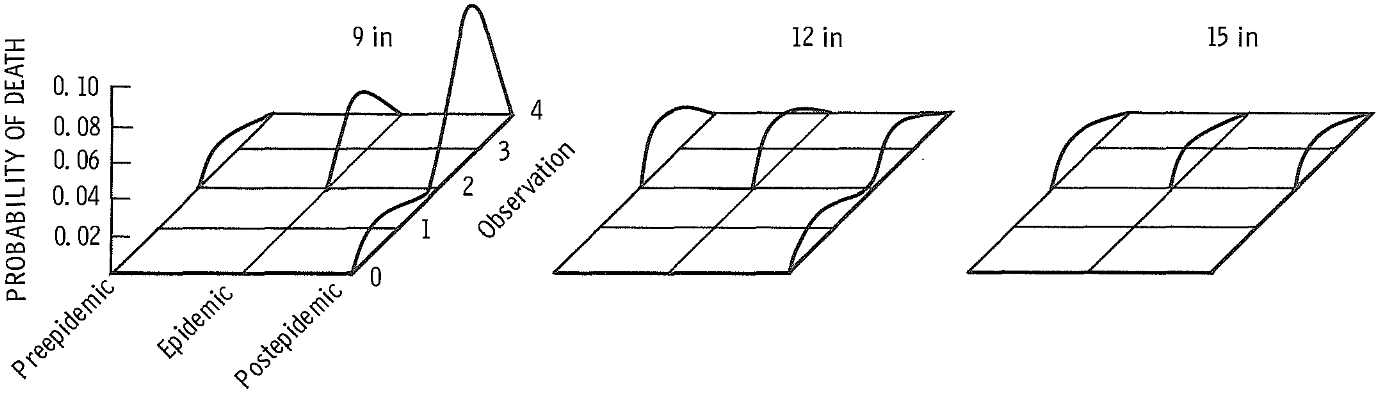

Figure 48.—Crude probability of mountain pine beetle death from *Coeloides dendroctoni* by tree diameter class and stage of infestation.

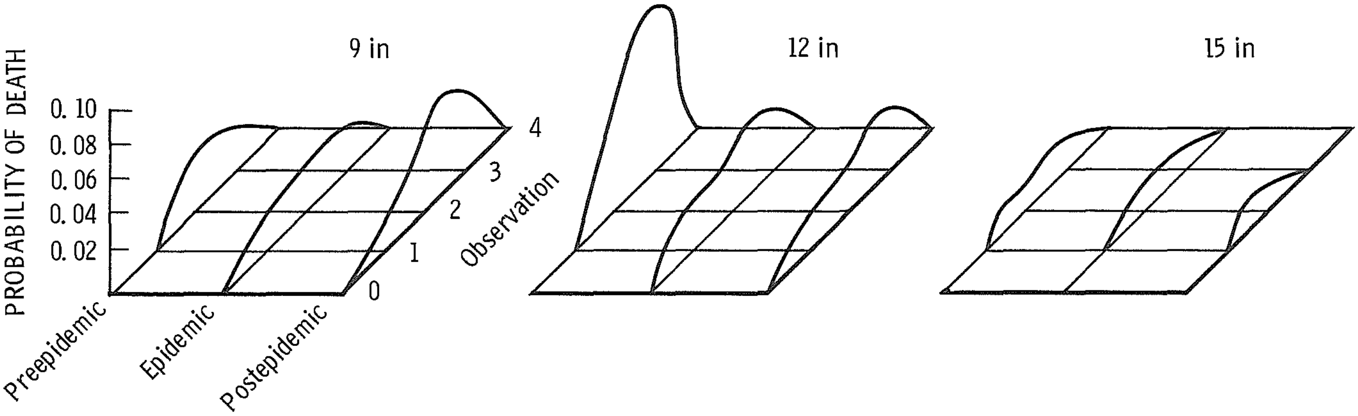

Figure 49.—Crude probability of mountain pine beetle death from woodpeckers by tree diameter class and stage of infestation.

Survival from egg to adult was highest in the 12-inch (30-cm) diameter tree class. However, survival was only 1.4 percent, and that occurred during the epidemic stage. Survival in the 9- and 15-inch (23- and 38-cm) classes was less than 1 percent. These survival rates suggest, first, that approximately 0.5 percent difference in survival separates increasing from static or decreasing populations. However, percentages do not reflect population numbers. Second, the mountain pine beetle is synchronized so closely with stand development and growth that the increased food supply, as a contributor to population explosion, probably far outweighs the concurrent influence of population reduction by biological and physical factors of mortality.

A special case.—The Logan Canyon plot on the Wasatch-Cache National Forest in northeastern Utah illustrates some discussion points. The mountain pine beetle has been at a "high endemic" level in this area for 9 years, based on rate of tree mortality and beetle survival rates. If certain risks of mortality were to be density dependent or independent, or if a steady mountain pine beetle population was to provide an opportunity for these factors to increase, they should have done so in the Logan Canyon infestation.

In the Logan Canyon infestation, the probability of any one egg reaching the adult stage was 0.00358 for populations within the 9-inch (23-cm) diameter class, 0.00639 for the 12-inch (30-cm), and 0.00560 for the 15-inch (38-cm). These survival probabilities are between those presented for preepidemic and epidemic populations in other study areas (table 12), with the exception of the 15-inch (38-cm) class where survival was lower than the preepidemic stage in other study areas. Percent beetle survival for each tree class was 10.4 for the 9-inch (23-cm) trees, 10.5 for the 12-inch (30-cm), and 9.9 for the 15-inch (38-cm) (table 17). These survival rates fit between the preepidemic and epidemic survival rates observed for beetles in the other study areas (table 16). Therefore, an infestation designation of high endemic (between preepidemic and epidemic) appears appropriate. Percent survival for mountain pine

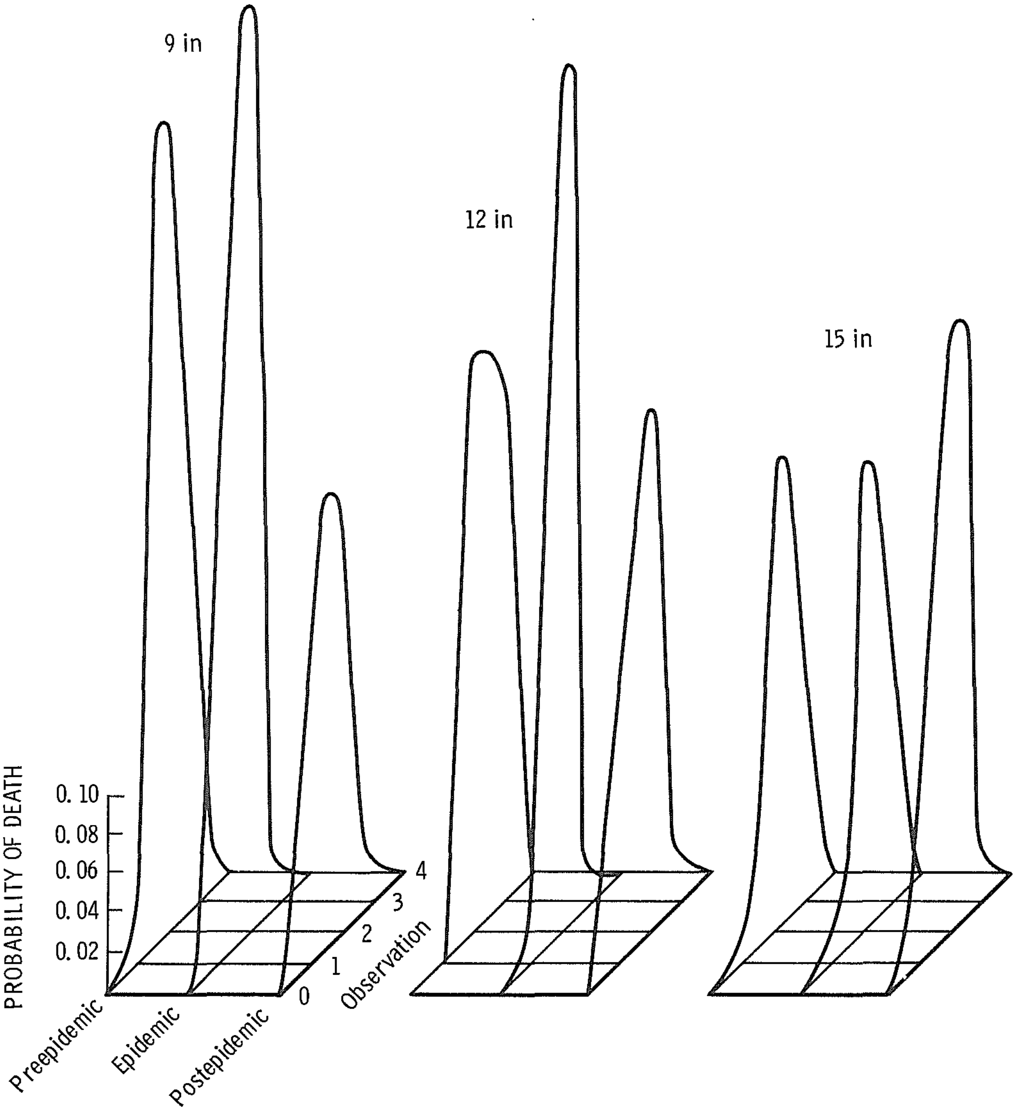

Figure 50.—Crude probability of mountain pine beetle death from winter temperatures by tree diameter class and stage of infestation.

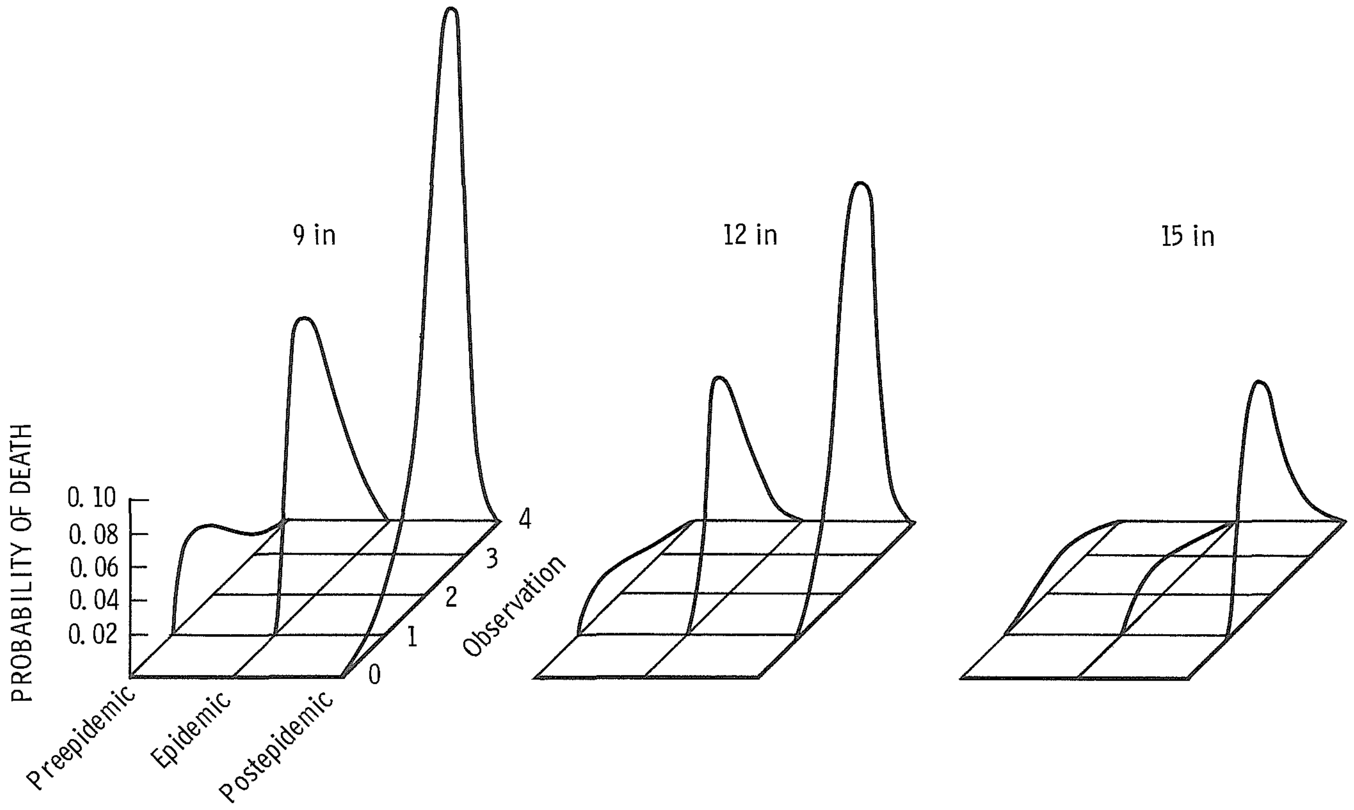

Figure 51.—Crude probability of mountain pine beetle death due to desiccation by tree diameter class and stage of infestation.

Table 17.—Crude probability of mountain pine beetle death due to a specific mortality factor[1] in the presence of all other mortality factors by lodgepole pine diameter class, Logan Canyon Plot, Wasatch-Cache National Forest

Tree diameter class	Observations	General probability		Crude probabilities										
		Survival	Death	WC	BC	CL	CD	MD	PA	WP	T	D	PI	UNK
23 cm	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.829	.171	.276	.251	.006	0	.103	.025	.011	.109	.002	.037	.180
	2	.315	.685	.006	.020	0	.001	.041	.001	.076	.387	.089	.001	.380
	3	.132	.868	.003	0	.003	.044	.010	.004	.001	.009	.189	.002	.735
	4	.104	.896	0	0	0	.117	0	0	.006	.008	.059	0	.310
Crude probability per generation				.057	.059	.002	.013	.045	.006	.056	.244	.092	.007	.419
30 cm	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.832	.168	.187	.131	0	0	.133	.037	.008	.187	.010	.031	.276
	2	.457	.543	.023	.055	0	.001	.078	.005	.077	.372	.056	.004	.330
	3	.160	.840	.004	.012	.007	.023	.012	.007	.039	.030	.108	.007	.751
	4	.105	.895	0	0	.004	.054	.004	0	0	0	.065	0	.873
Crude probability per generation				.046	.052	.002	.011	.062	.011	.047	.201	.065	.010	.493
38 cm	0	1.000	0	0	0	0	0	0	0	0	0	0	0	0
	1	.778	.222	.205	.308	0	0	.317	.009	0	.086	0	.011	.064
	2	.356	.644	.006	.033	0		.050	.001	.007	.307	.029	.012	.554
	3	.204	.796	.066	0	.006	.058	.036	.010	.038	.070	.149	0	.567
	4	.099	.901	0	0	0	.001	.019	0	0	0	.009	0	.972
Crude probability per generation				.065	.091	.001	.010	.110	.004	.010	.176	.040	.009	.484

[1] Mortality factor abbreviations are defined in footnote 1, table 9.

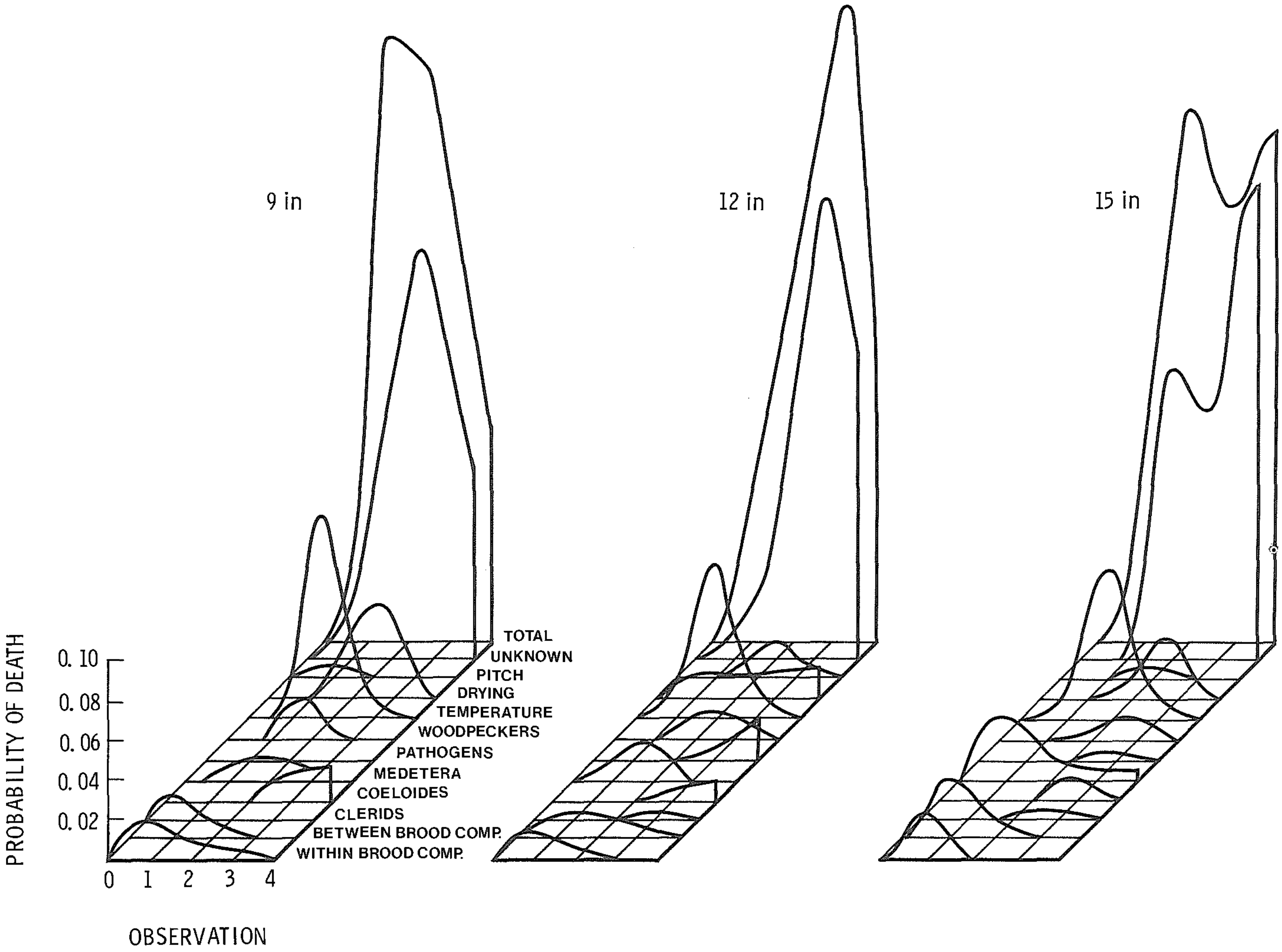

Figure 52.—Crude probability of mountain pine beetle death from specific factors in three diameter classes, Logan Canyon plot, Wasatch-Cache National Forest, Utah.

beetle populations in ponderosa pine in relation to population trend were: decreasing ≤ 1; static about 3; and increasing about 10 (Knight 1959). The higher rate of survival needed to maintain the static situation in lodgepole than in ponderosa pine suggests that large losses of beetles occur during the flight period.

The crude probabilities for each mortality factor show trends similar to those presented for the other study plots, but the magnitudes differ somewhat (table 17; fig. 52). Crude probabilities of survival show that within competition is greatest within the 9-inch (23-cm) class, while between competition is greatest within the 15-inch (38-cm). Combined, the greatest effect on population reduction from these two mortality factors is in the smallest and largest diameter classes (fig. 53).

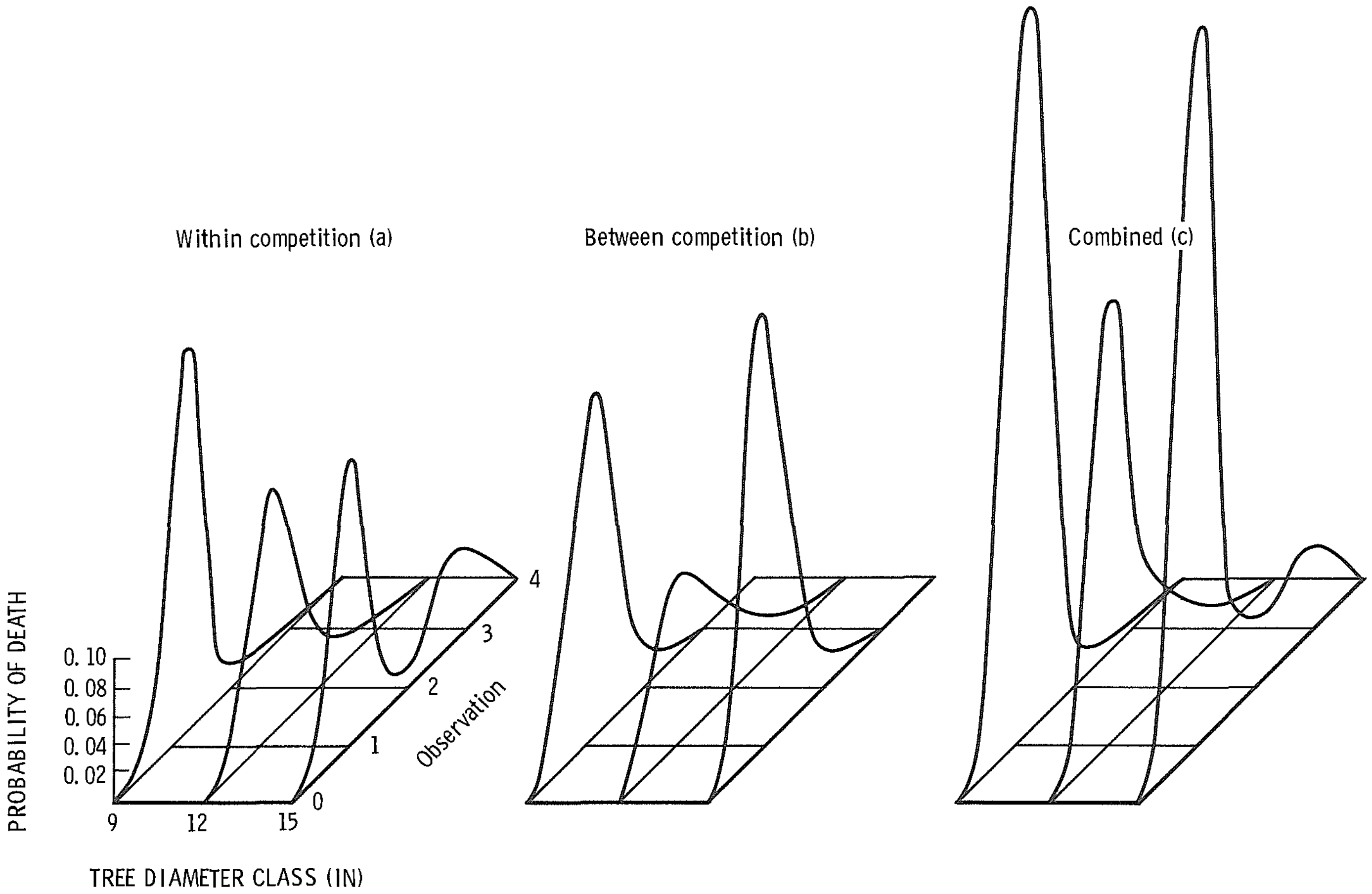

Figure 53.—Crude probability of mountain pine beetle death from within (a); between (b); and combined within-between competition (c), Logan Canyon plot, Wasatch-Cache National Forest, Utah.

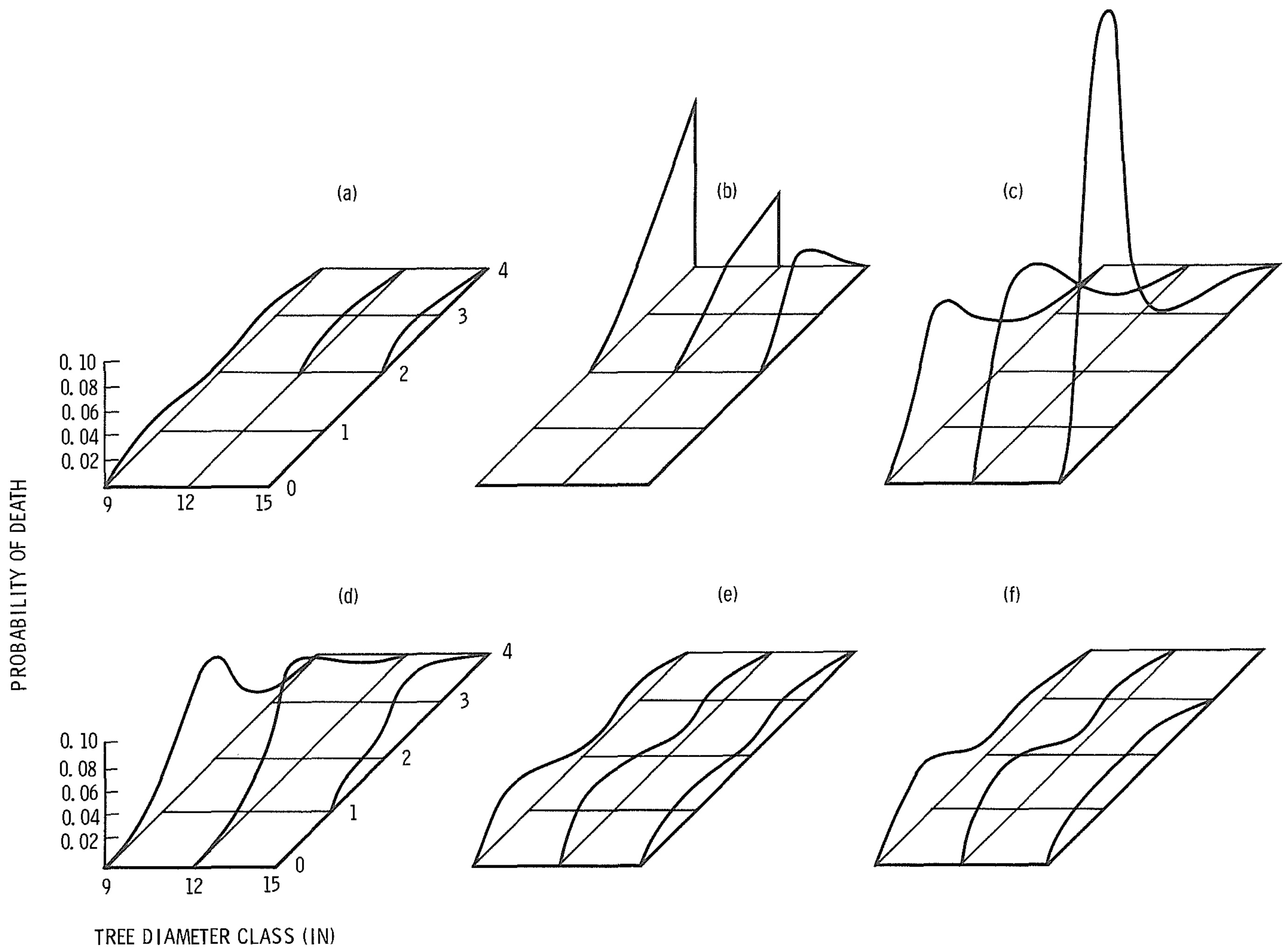

Figure 54.—Crude probability of mountain pine beetle death from clerids (a), *Coeloides* (b), *Medetera* (c), woodpeckers (d), pathogens (e), and pitch (f), Logan Canyon plot, Wasatch-Cache National Forest, Utah.

Probability of death from parasites, predators, pathogens, and pitch is approximately the same as in the other data sets. That is, clerids caused minor losses; *Coeloides* activity was greatest in the smallest diameter class and least in the largest diameter; *Medetera* showed some density dependence, with the greatest probability of predation occurring in the largest diameter class and least in the smallest; probability of death due to woodpeckers was greatest in the 9- and 12-inch (23- and 30-cm) classes; and losses to pathogens and pitch were greatest within the 9- and 12-inch (23- and 30-cm) classes during the fall (fig. 54). The 9- and 12-inch classes are more likely to sustain light attacks than the 15-inch (38-cm), resulting in resinosis and losses to pitch. Temperature and drying presented the greatest influence. Both followed the typical pattern by diameter class, having the greatest impact on beetles in small trees and least in large trees (fig. 55).

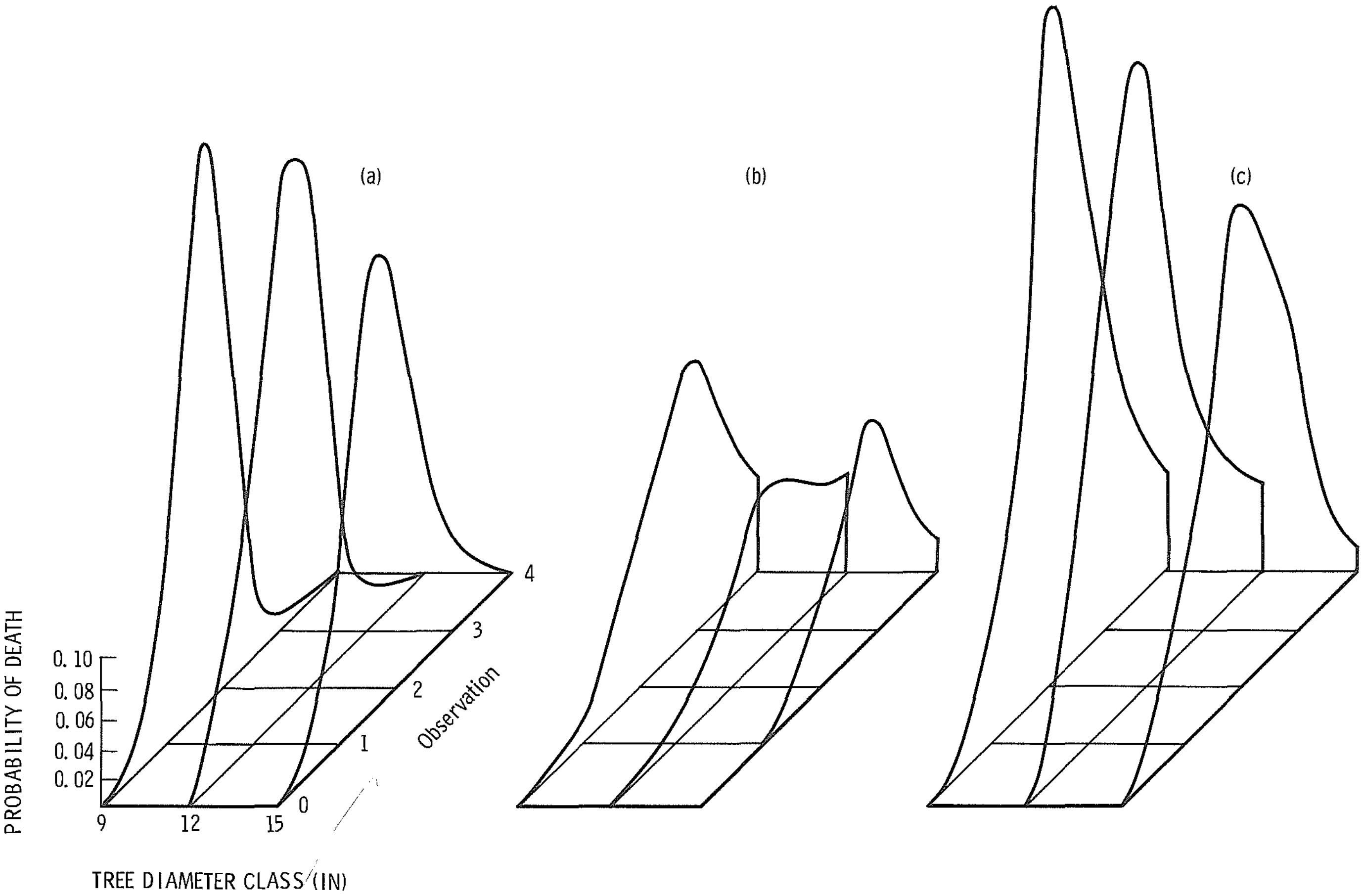

Figure 55.—Crude probability of mountain pine beetle death from winter temperatures (a), drying of phloem (b), and combined temperature-drying (c), Logan Canyon plot, Wasatch-Cache National Forest, Utah.

Probabilities of death due to individual factors in all plots suggest that none of the risks acting in the presence of other risks offers much, if any, regulatory influence upon a mountain pine beetle population. These observations further strengthen the hypothesis that mountain pine beetle populations are food-regulated (Cole and Amman 1969), and therefore are strongly dependent upon tree and stand conditions. The 15-inch (38-cm) trees appear to supply the impetus for starting epidemics, but because of their few numbers, these trees are eliminated early from the stand (Cole and Amman 1969; Klein and others 1978). Once the epidemic is well under way, brood survival in the 12-inch (30-cm) trees is sufficient to maintain the beetle population for several years into the postepidemic stage, when a large proportion of the infested trees are in the 9-inch (23-cm) class. However, the 9-inch (23-cm) trees at this infestation stage do not provide, on the average, adequate habitat for the beetle because of thin phloem and excessive drying. This results in greatly reduced survival. In addition, many beetles emigrate to other stands of trees (Klein and others 1978).

A SUMMARY OF HOST INFLUENCE

This section on biology and ecology of the mountain pine beetle demonstrates a number of beetle population characteristics associated with lodgepole pine size and associated characteristics. Small trees, on the average, have thin phloem of low quality and usually dry excessively during beetle development. Consequently, such trees generally produce low ratios of brood adults to parent adults. Beetles from small trees are small, appear to have slightly different genotype have sex ratios strongly skewed toward females, and show slow brood development. On the other hand, trees of large size usually have thick phloem of high quality and remain moist throughout beetle development. As a result, these trees generally produce high ratios of brood adults to parent adults. Beetles from large trees are large, have a genotype somewhat different from that of brood adults in small trees, have more even sex ratios, and are faster developing than beetles in small trees of thin phloem.

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APPENDIX

Regression Statistics for Figures

Figure 7.—Beetles (number/ft^2) as a function of emergence holes (number/ft^2).

$\hat{Y} = 0.308\ (X^{1.4})$; $r = 0.85$

Figure 9.—Female beetles emerging (percent) as a function of emergence day (number).

$$\begin{array}{lll} & & \text{Limits}\rightarrow \\ 1974: & \hat{Y} = 59.3 - 0.375\,(7 - X)^{1.65} & 0 \le X \le 7 \\ & \hat{Y} = 59.3 - 0.439\,(X - 7)^{1.4} & 7 < X \le 18 \end{array} \left.\begin{array}{l} \\ \\ \\ \end{array}\right\} r^2 = 0.042;\ P > 0.10$$

$$\begin{array}{lll} 1975: & \hat{Y} = 68.4 - 0.480\,(7 - X)^{1.65} & 0 \le X \le 7 \\ & \hat{Y} = 68.4 - 0.669\,(X - 7)^{1.4} & 7 < X \le 18 \end{array} \left.\begin{array}{l} \\ \\ \end{array}\right\} r^2 = 0.518;\ P < 0.005$$

Figure 11.—Beetle length (mm) as a function of emergence day (number).

$$\begin{array}{lll} \text{Females} & 1974{:}\hat{Y} = (X)-0.0371 + 5.3821; & r^2 = 0.59;\ P < 0.005 \\ & 1975{:}\hat{Y} = (X)-0.0162 + 5.0790; & r^2 = 0.20;\ P < 0.100 \\ \text{Males} & 1974{:}\hat{Y} = (X)-0.0448 + 4.9255; & r^2 = 0.54;\ P < 0.005 \\ & 1975{:}\hat{Y} = (X)-0.0193 + 4.6755; & r^2 = 0.46;\ P < 0.005 \end{array}$$

Figure 13.—Female length (mm) as a function of egg gallery density (meters/ft^2).

$$\left.\begin{array}{ll} \text{Thin phloem} & \hat{Y} = 4.769 - 0.0146X^3 \\ & S_{y.x} = 0.21 \\ \text{Thick phloem} & \hat{Y} = 5.006 - 0.0146X^3 \\ & S_{y.x} = 0.19 \end{array}\right\} r^2 = 0.30;\ P < 0.005$$

Limits: $0.4 \le X \le 3$

Figure 14.—Female length (mm) as a function of tree diameter (cm) at breast height.

Logan Canyon: $\hat{Y} = 4.357 + 0.049X$; $S_{y.x} = 0.328$; $r^2 = 0.18$; $P < 0.005$

Stillwater: $\hat{Y} = 4.74 + 0.03X$; $S_{y.x} = 0.37$; $r^2 = 0.03$; $P < 0.05$

Figure 19.—Eggs (number) as a function of inch of egg gallery (number).

$$\hat{Y} = 7.65 - \left[A\left(1/2 + 1/2\left[\frac{4.25 - X}{\lvert 4.25 - X \rvert}\right]\right) + B\left(1/2 + 1/2\left[\frac{X - 4.25}{\lvert X - 4.25 \rvert}\right]\right)\right]$$

$$A = 7.35\,\lvert 4.25 - X \rvert\,\frac{2.09}{(3.25)^{2.09}}$$

$$B = 4.50\,\lvert X - 4.25 \rvert\,\frac{1.215}{(9.75)^{1.215}}$$

$1 \le X \le 14$ and $X \neq 4.25$

$S_{y.x} = 2.71$; $r^2 = 0.34$; $P < 0.005$

Figure 21.—Eggs (number) as a function of female length (mm).

A. The average number of eggs laid per inch of gallery.
$\hat{Y} = 2.52 + 0.54X$; $S_{y.x} = 0.91$; $r^2 = 0.09$; $P < 0.05$

B. The average number of eggs laid per day.
$\hat{Y} = -\ 0.261 + 1.06X$; $S_{y.x} = 1.17$; $r^2 = 0.20$; $P < 0.005$

Figure 22.—Eggs (number) as a function of phloem thickness (inch).

A. The average number of eggs laid per inch of gallery.
$\hat{Y} = 4.54 + 9.91X$; $S_{y.x} = 1.3$; $r^2 = 0.16$; $P<0.01$

B. The average number of eggs laid per day.
$\hat{Y} = 3.02 + 9.65X$; $S_{y.x}$ 1.39; $r^2 = 0.14$; $P<0.025$

Figure 23.—Egg gallery (inches) and eggs (number) as functions of temperature (°C).

A. The average number of eggs laid per inch of gallery.
$\hat{Y} = 5.32 - 0.0547(20-X)^{1.48}$; $S_{y.x}$ 1.16; $r^2 = 0.35$; $P<0.005$

B. The average number of eggs laid per day.
$\hat{Y} = 0.146 + 0.06\,(0.75 + 0.01293(X-7)^{2.25})$; $S_{y.x} = 0.91$; $r^2 = 0.70$; $P<0.005$

C. The average length of gallery constructed per day.
$\hat{Y} = 0.014 + 0.986\,(0.274 + 0.00023(X-7)^{3.105})$; $S_{y.x}$ 0.11; $r^2 = 0.81$; $P<0.005$

Figure 27.—Beetles (number) as a function of phloem thickness (inches).

Males and Females: $\hat{Y} = -\ 23.91 + 947.74X$; $r^2 = 0.69$; $S_{y.x} = 27.1$
Females: $\hat{Y} = -\ 13.01 + 587.86X$; $r^2 = 0.65$; $S_{y.x} = 18.5$
Males: $\hat{Y} = -\ 12.74 + 382.52X$; $r^2 = 0.62$; $S_{y.x} = 12.8$

Figure 29.—Beetles (number/ft^2) as a function of egg gallery density (meters/ft^2).

$$\left.\begin{array}{ll} \text{Thin phloem} & \hat{Y} = 111.247 - 7.965(3 - X)^{2.4} \\ & S_{y.x} = 34.5 \\ \text{Thick phloem} & \hat{Y} = 67.262 - 4.816(3 - X)^{2.4} \\ & S_{y.x} = 25.3 \end{array}\right\} r^2 = 0.38;\ P<0.005$$

Limits: $0 \leq x \leq 3$

Figure 30.—Beetles (number/ft of egg gallery) as a function of egg gallery density (meters/ft^2).

Thin phloem $\hat{Y} = 6.157 + 0.3597(3 - X)^{3.5}$
$S_{y.x} = 8.4$
Medium phloem $\hat{Y} = 10.0492 + 0.5870(3 - X)^{3.5}$
$S_{y.x} = 6.6$
Thick phloem $\hat{Y} = 12.755 + 0.745(3 - X)^{3.5}$
$S_{y.x} = 8.6$
Limits $0.4 \leq x \leq 3$

Figure 32.—Lodgepole pine sapwood thickness (inches) as a function of tree diameter at breast height (inches).

$\hat{Y} = -\ 0.471 + 0.2X$

$S_{y.x} = 0.49$; $r^2 = 0.61$; $P<0.005$

Amman, Gene D.; Cole, Walter E. Mountain pine beetle dynamics in lodgepole pine forests. Part II: Population dynamics. Gen. Tech. Rep. INT-145. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1983. 59 p.

This is the second of a three-part series of General Technical Reports concerning the mountain pine beetle in lodgepole pine forests. Part I (Cole and Amman 1980. GTR INT-89, 56 p.) addresses how the beetle "moves through" a lodgepole pine stand, with emphasis on relationships between the beetle and its environmental factors. Hazard rating systems and management alternatives to reduce losses are presented. Part II deals with the taxonomy, biology, and ecology of the beetle. Part III will present methods of sampling mountain pine beetles and modeling efforts.

Part II represents much original research by the authors but is also a review of published literature, primarily on epidemic beetle populations in lodgepole pine forests. Lodgepole pine tree characteristics such as size and phloem thickness have a strong influence on beetle survival, size, sex ratio, and genotype. Of the many mortality factors acting upon the beetle population alone or in combination with other mortality factors, none regulate the population before severe damage occurs to stands of lodgepole pine. These findings offer additional support that the mountain pine beetle is food regulated.

KEYWORDS: Scolytidae, *Dendroctonus ponderosae, Pinus contorta,* population dynamics

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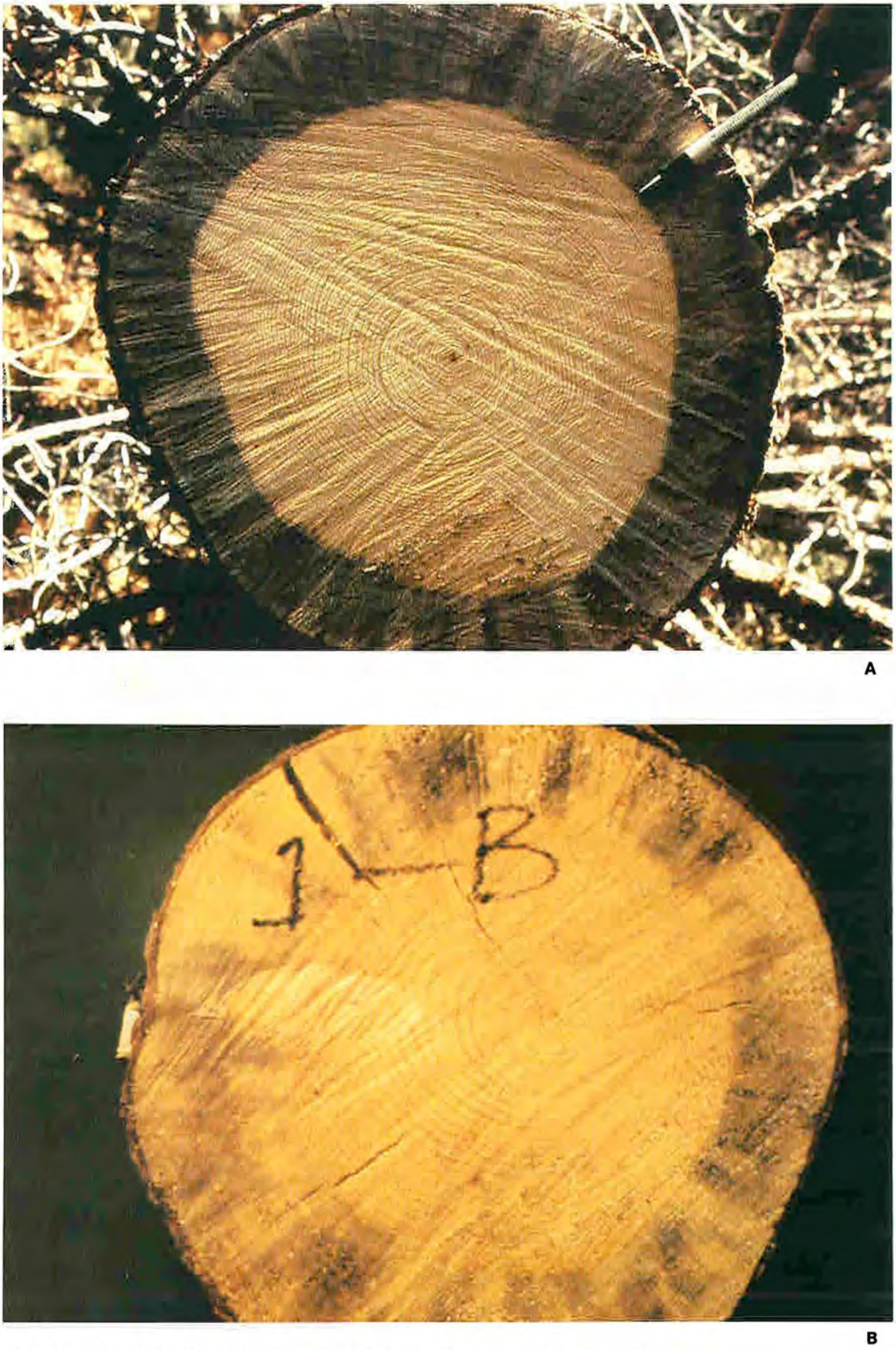

Figure 33.—Blue-staining fungi, carried into the bark by beetles, discolor the sapwood.
A. Well-developed blue stain fungi usually are uniformly distributed throughout the sapwood.
B. Poorly developed blue stain fungi usually are unevenly distributed in the sapwood. (See p. 00.)

The Intermountain Station, headquartered in Ogden, Utah, is one of eight regional experiment stations charged with providing scientific knowledge to help resource managers meet human needs and protect forest and range ecosystems.

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