SOME ASPECTS OF THE POPULATION DYNAMICS
OF THE MOUNTAIN PINE BEETLE, DENDROCTONUS PONDEROSAE,
IN LODGEPOLE PINE FORESTS OF BRITISH COLUMBIA

by

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We accept this thesis as conforming to the
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Outbreaks of mountain pine beetle (Dendroctonus ponderosae Hopk.) are common in lodgepole pine forests of western North America. Characteristics of both the bark beetle and its host tree were compared using field replicates of epidemic and endemic areas to test for any possible intrinsic differences between populations of trees or insects in these two different states. Laboratory studies were conducted on beetle dispersal characteristics and on effects of attack density and female parent size on beetle reproductive success and offspring size. Results are as follows:

Trees in outbreak areas are older than in endemic regions, and trees of a given size and beetle attack density are more likely to be overcome and to permit successful beetle reproduction in epidemic than in endemic areas. However, tree spatial distributions, average attack densities and proportions of trees unsuccessfully attacked by beetles do not differ consistently between epidemic and endemic areas. A method (in which blue-staining fungi were inoculated into trees) of measuring potential of trees to resist mountain pine beetle was tested and found to be inadequate.
Epidemic and endemic bark beetles did not differ consistently in dispersal, size, or reproductive characteristics. However, early emerging beetles were larger than late emergers and females had a larger coefficient of variation in size than males. Field and laboratory data show that the number of offspring emerging per parent decreases with increasing attack density. Breeding experiments further indicated that, 1) small female parents produce fewer and smaller offspring than large females, 2) small female parents produce female offspring with more strongly bimodal size distributions than large females, and 3) high parental attack densities result in smaller offspring.

Dispersal studies on the insect using chemical extracts of lodgepole pine bark showed that early emerging beetles are more likely to respond positively to tree chemicals than late emergers with the same flight history. Increasing lengths of flight increase female but not male responses to these chemicals.

Evidence from a simulation model is presented to support the hypothesis that the age at which lodgepole pine normally becomes susceptible to mountain pine beetle attack is close to the age at which certain tree fitness measures are maximized.
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I. INTRODUCTION

A. Background

Ecologists have been interested for many years in animal populations that exhibit cycles in numbers. Numerous physical and biotic factors have been related to these population changes but no explanation has been completely convincing. Most of these theories have been related to changes in numbers of predators or parasites, food quality and quantity, or other limiting resources. Since the mid-1960's, increasing research effort has been put into two different topics related to population changes: environmental heterogeneity and within-population variation in characteristics.

Morris (1971) and Morris and Fulton (1970a, 1970b) have shown that population genetic changes are closely related to population density in the fall webworm, Hyphantria cunea. In addition, the consequences of changes in maternal parent types for population trends have been illustrated by Wellington (1957, 1959, 1960, 1964) with the western tent caterpillar, and by Campbell (1962) with the spruce budworm. These workers have shown that certain important characteristics are heritable, either in the strict genetic sense or through maternally transmitted physiological effects. They suggest that in some species it is necessary to consider variation
within populations in order to obtain a better understanding of population trends.

Most terrestrial animals live in spatially and/or temporally heterogeneous environments. However, until recently, most ecologists have either ignored heterogeneity or tried to control for it in the laboratory. Many animal adaptations might be more clearly understood by explicitly taking this heterogeneity into consideration. Some beginning theoretical considerations of the topic have been made by MacArthur (1968), MacArthur and Levins (1964), MacArthur and Pianka (1966), Pimentel et al. (1963, 1965), Levins (1962, 1965, 1968), den Boer (1968), and Levins and MacArthur (1966). All of these authors conclude that the patchiness or "graininess" of the environment in time and/or space can have a profound influence on determination of strategies for survival. Some of these investigators discuss the significance of the dispersal process for utilizing heterogeneous environments.

Dispersal (the act of moving to a new oviposition or feeding site before reproduction) has received mainly descriptive study. It has been very well described for many animals but it has rarely been looked at in terms of its evolutionary context, i.e., the selection pressures that have caused the particular dispersal characteristics of the animal group to evolve as they have. In addition, little is known about how rapidly dispersal characteristics change as a result
of selection pressures. Wellington (1957, 1959, 1960, 1964), Huffaker (1958), Huffaker, Shea, and Herman (1963), Huffaker (1966), and White and Huffaker (1969) have been among the few ecologists to use this evolutionary viewpoint in designing field studies. These works show that dispersal is a key feature in determining how populations will behave through the course of time. In addition, Huffaker's work points out the importance of spatially heterogeneous environments in creating unique situations for the predator-prey system. The works of Wellington, Huffaker, Birch (1971), den Boer (1968, 1971), and Green (1974) suggest that grosser system behaviors such as overall stability of predator-prey systems can be more clearly understood by taking into account dispersal and heterogeneous environments. Kitching (1971), through the use of a simulation model, has also explored the relationships between some characteristics of dispersal, heterogeneity in the environment, and success at colonization. He too has found that the results of dispersal are significantly affected by environmental heterogeneity.

Because of these indications that dispersal processes and environmental heterogeneity are linked, it might be useful to look at dispersal as one adaptation of animals to surviving in changing environments. Atkins (1966a), Southwood (1962), and Brown (1951), among others, have shown that those insect species which occupy temporary habitats are generally better adapted to dispersing to new habitats than those species
inhabiting more persistent environments. For those adaptations whose selective advantages are affected by spatial or temporal patterning in the environment, some within-population variability in those adaptations may be required to insure population persistence. An example of this might be the searching pattern of insect predators. If prey are usually randomly distributed in space, and if predators always search in a random pattern, then the capture rate will decrease if prey should become highly clumped. In such a case, those individual predators with searching patterns that enabled efficient utilization of clumped prey would be at an advantage. Thus, there may be a selective advantage in maintaining some phenotypes which are less efficient under normal conditions of prey distribution in order to insure some flexibility for coping with future changes in selection pressures or limiting resource availability.

The same might be true for dispersal behaviors. Marked variation in dispersal characteristics has been observed within insect populations (e.g. Atkins, 1966b; Rose, 1972; Syed, 1972; Wellington, 1957, 1960) and this variation has been interpreted as being advantageous for utilizing spatially discontinuous and temporally unstable environments (Wellington, 1964).

Some characteristics of insect dispersal that might have evolved as a result of certain environmental patterns are: yearly timing of movement, directionality and speed of
movement, total distance covered, and amount of active control as opposed to passive movement. A familiar and extreme example is the spruce budworm which disperses largely passively by wind. These and similar insects have not had to evolve active dispersal mechanisms because of high reproductive rates and because of the particular spatial and temporal distribution of their host trees and of appropriate weather conditions. These patterns in time and space, though probabilistic in occurrence, are consistent enough to enable spruce budworm populations to persist. At another extreme are insect species that have some active part in determining their long range movements and that rely on attracting pheromones for location of mates and suitable hosts.

B. The Study

In order to investigate the effect of spatially and temporally heterogeneous environments on dispersal strategies, it was necessary to choose a situation where habitat changes which are selectively important for the animal occur with about the same periodicity as the lifespan of the animal. If the frequency of such temporal or spatial habitat changes were much shorter than the lifespan, the animals would respond physiologically and/or behaviorally (for instance, fish acclimation to new salinity). If the frequency were much longer than the lifespan, (e.g. climatic change and insect flight temperature thresholds), adaptations to changes might
be much too slow and gradual to be studied in a reasonable length of time. My experimental animals, bark beetles, live among habitats whose important selective characteristics (tree resistance) change every summer, coinciding with the beetle breeding season. These insects also exhibit drastic changes in numbers. Populations in different localities are at different points in their cycles at any given time and offer useful cases for comparison.

In this study, I compared several characteristics of bark beetles and their host trees which were sampled from two types of areas: endemic (low insect numbers and low tree mortality) and epidemic (high insect numbers and high tree mortality). In particular, for each of the two population states, I investigated the patterning in time and space of suitable tree hosts, beetle reproductive success, beetle dispersal, and several other characters related to dispersal. I wanted to find out whether there were any intrinsic differences between trees or beetles in an endemic area and those in an epidemic area.

In addition, I attempted to answer the following questions: How much variability is there in dispersal characteristics within a population? How closely do offspring resemble parents in these characteristics, and can the degree of resemblance change as the population climbs and drops in numbers? Are observed adaptations which are related to dispersal maintained by selection only when insect numbers are
low, or are these adaptations necessary even in times of epidemics? Finally, is there any significance to the tree age at which insect outbreaks normally occur in host tree stands?
II. THE BARK BEETLES

A. General

The bark beetles (order Coleoptera, family Scolytidae) are insects which provide a wealth of comparative information for answering some of the questions posed in Section I. Furthermore, the associations of these insects with their host trees are fairly well understood and are amenable to observation and experimental manipulation.

Bark beetle life histories can generally be described as follows. Female adults normally attack logs or trees in summer or late spring. They bore galleries underneath the bark and lay eggs periodically along the gallery walls as they dig. The eggs hatch, the larvae extend peripheral galleries some distance, and then they pupate. In many bark beetle species, larvae or pupae are the main overwintering stage and new adults do not emerge from the tree to attack new hosts until the following spring or summer. In some ambrosia beetles, a wood-boring group within the scolytids, adults emerge the summer of parental attack and fly to overwintering sites in the forest litter.

Bark beetles in general attack hosts varying in states of health from trees fallen months previously, either by wind or
man, to standing and apparently healthy trees. Each species concentrates on trees in a particular physiological state of health, which is usually subnormal (Graham, 1963; Rudinsky, 1962), because all trees of a given species are not suitable for beetle reproduction or growth of their symbiotic fungi (Graham, 1967; Rudinsky, 1962). Preference of bark beetles for trees with certain physiological states leads to an interpretation of the role of these insects in forest communities as natural pruners or thinners (Graham, 1963; Smithers, 1962). This is especially true of those species which normally attack trees that are still standing and are competing for light and nutrients, but which are in some way physiologically weakened. When present in a tree stand in low numbers, bark beetles preferentially remove such trees, decreasing the competition among remaining trees.

Successfully attacked trees (ones that succumb and produce beetle offspring) are generally not re-used in subsequent years by the same bark beetle species, so new trees must be sought each year. Also, trees of the preferred state of health are not usually spatially distributed in a uniform manner, so many bark beetles have evolved two types of complex behavioral mechanisms for locating trees. The first mechanism depends upon differences in tree chemicals generally referred to as primary attractants (Francia and Graham, 1966; Graham 1959; Graham and Werner, 1956; Renwick and Vité, 1970). Once suitable trees are found, other individuals in the population
are attracted to these sites by another set of complex adaptations, usually involving pheromones and generally classed as secondary attractants (Renwick and Vité, 1970; many others). Since attacks on single trees usually occur almost simultaneously by many members of a population, owing to secondary attractants, even healthy trees can be killed. Such mass insect attacks appear to be adaptations to overcoming natural defense mechanisms of trees such as oleoresin exudation (Cobb et al., 1968; Reid 1962a, 1963; Vité and Wood, 1961). Later, I will discuss the tradeoffs involved in mass attacks between increasing probability of overcoming a tree's resistance and decreasing success of beetle reproduction.

Bark beetles are associated with symbiotic blue-staining fungi, which are hypothesized to function in helping overcome tree defense mechanisms, thereby insuring successful beetle reproduction (Graham, 1967; Reid et al., 1967; Safranyik et al., 1974a). The insects have special morphological adaptations for carrying fungal spores and mycelia with which to infect newly attacked trees (Farris, 1963; Graham, 1967; Whitney and Farris, 1969).

Bark beetles are especially well-suited for dispersal studies because their dispersal-and-attack phase is usually contained within a short period of the year, the rest of the time being spent inside the trees or in the forest litter. Also, the scolytids exhibit a wide range of dispersal strategies and tactics, probably owing to the various states
of health of trees attacked. It is even possible that the wide range of states of tree deterioration utilized by different scolytids is a character divergence resulting from competition among ancestral members of the group. Also, the difference in dispersal behavior between insects in outbreak conditions might be different from the behavior of insects at a low population level. This last topic seemed to be a more fruitful comparison because of the problems of comparing different species, and it is therefore the main line I have followed throughout the study.

B. The Mountain Pine Beetle

The mountain pine beetle, _Dendroctonus ponderosae_ Hopkins (= _D. monticola_ Hopkins) was chosen for intensive study. This bark beetle is a native of North America and has been a reported pest since the early 1900's (Powell, 1961). It prefers lodgepole pine (_Pinus contorta_ Douglas var. _latifolia_ Engl.) as a host but also infests ponderosa pine (_Pinus ponderosa_ Laws), western white pine (_Pinus monticola_ Dougl.) and Engelmann spruce, (_Picea engelmanni_ Parry), (Powell, 1961; Reid, 1962a, 1962b; Cobb et al., 1968). Despite its small size (3 to 4 mm in length), this insect accounts for large volume losses of lodgepole pine every year. In western Canada alone, 1.3 million cu ft of timber were lost per year from 1950 to 1970, approximately 3% of the average annual cut (Safranyik et al., 1974a).
The life history of the mountain pine beetle is similar to that of most bark beetles. All adults carry symbiotic blue-staining fungi (*Ceratocystis montia* (Rumb.) Hunt and an unidentified *Europhium* species) (Robinson, 1962). Adults and larvae feed on wood as well as on phloem as they dig galleries in the outer sapwood-phloem region of the host tree. Females do the initial searching for host trees and all of the gallery digging. Dispersal and attack on potential hosts occurs in midsummer (July and August) on days when ambient temperature exceeds about 60° F (16° C) (Reid, 1962a; Shepherd, 1966). Beetles emerging from overwintering sites in trees are photopositive (Reid, 1962a; Shepherd, 1966) and they fly to preferentially attack large, relatively healthy trees (Amman, 1969; Cole and Amman, 1969; Reid, 1963; Roe and Amman, 1970). Preference for what appear to be the most vigorous trees seems to be related to moisture content and thickness of the phloem, the region where most gallery construction occurs (Amman, 1969, 1972; Reid, 1962b, 1963, 1969; Roe and Amman, 1970; Safranyik and Vithayasai, 1971). Trees weakened by drought or disease are also attacked, but they are normally avoided (Cobb et al., 1968; Vité and Wood, 1961). Highest concentrations of mountain pine beetle attacks are at the bases of trees, and decrease with increasing height (Reid, 1963; Safranyik and Vithayasai, 1971).

Like other bark beetles attacking standing trees, *D. ponderosae* has to face the defense mechanisms of the trees.
These tree resistance responses, to be described in detail in the section on lodgepole natural defenses, consist mainly of production of resins which can cause mortality of attacking bark beetles. The effectiveness of resistance responses is reduced by mass attacks.

A large beetle population is attracted to a tree through a secondary attractant system described by Pitman and Vité (1969), Pitman et al. (1969), Renwick and Vité (1970), and Vité and Pitman (1968). Once a female begins to dig in a suitable tree, a pheromone (trans-verbenol) is released which, in conjunction with a volatile tree terpene, alpha-pinene, attracts more males and females to the site. The sex ratio of beetles attracted depends on the relative concentrations of the pheromone and the tree terpene. As the female-produced pheromone becomes more predominant, the proportion of males arriving increases. Both males and females will respond to the pheromone only in the presence of alpha-pinene (Renwick and Vité, 1970). Therefore, when resin exudation and copious terpene release stop, there are no more new attacks.

Once galleries are successfully established, mating occurs in them and the male frequently goes to another gallery and mates again (Reid, 1958b). This polygamous behavior results in sex ratios of about one male for every two females in each tree (Reid, 1958b). Between forty and seventy eggs are normally laid by a female in one gallery system, and, depending on sapwood moisture and ambient weather conditions,
she may emerge and attack another tree before the summer is over (Reid, 1958b, 1962b). During each egg laying period, flight muscles degenerate, as in other scolytids (Reid, 1958a). This may be due to rechannelling of energy to the reproductive system. Toward the end of egg laying, flight muscles regenerate to enable adults to emerge and reattack new trees. 

Adult galleries are as long as 18 inches and are more or less vertically oriented. Larvae dig their galleries horizontally, as much as 6 inches away from the parent gallery (Fig. 1). Larvae go through four instars and constitute the main overwintering stage (underneath the bark), although pupae occasionally go into the winter (Reid, 1962a, 1962b). This is a critical stage for selection in this beetle because the earlier in the summer a brood is established, the larger is the proportion of offspring reaching pupal and teneral adult stages during the winter. These are the least cold resistant stages, so greater beetle mortality occurs in broods established early in long, warm summers (Reid, 1963). This phenomenon has important implications for the theory that many mountain pine beetle outbreaks occur during or immediately following several years of drought (Smithers, 1962; others). Warm, dry summers reduce the effectiveness of tree resistance and enhance brood development (Reid, 1963). Also, when there is an unusually warm and dry spring and summer, the probability of each female's successfully starting two broods
FIGURE 1

A typical mountain pine beetle gallery system with the adult, or egg, gallery vertically oriented and the larval galleries extending horizontally away from the parental gallery.
increases because of unusually early emergence. However, winter survival of the first brood may be very low if summer temperatures are high for a long period and if the winter is as cold as normal. Therefore, depending on the fecundity of each female in her second gallery, there may actually be a decrease in *D. ponderosae* populations after very long, warm summers.

Another important factor for brood survival is initial attack density. Reid (1963) and Cole (1962) have found that adult gallery length, egg production per female, and larval survival per adult become reduced with increasing attack density owing to intraspecific competition. This effect of attack density is similar to the finding of McMullen and Atkins (1961) for the Douglas-fir beetle.
III. THE HOST TREE SPECIES, LODGEPOLE PINE

A. Systematics And Distribution

The preferred host species of mountain pine beetle is lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engl.), a native North American conifer. This variety of lodgepole pine inhabits interior and mountain regions of British Columbia, Alberta and some of the western United States. There is great variation in the characteristics of lodgepole pine throughout its range (Critchfield, 1957; Smithers, 1956, 1962; Roche, 1962); the interior form differs remarkably from both the coastal (or "shore") and Sierra Nevada forms. Since the mountain pine beetle is normally associated only with the interior form, all further discussions of lodgepole pine will pertain only to this interior variety. In particular, I will discuss characteristics of lodgepole found in the Okanagan Valley area and the Rocky Mountain region of B.C. and Alberta.

B. Life History

Interior lodgepole usually inhabits regions that have warm, dry summers and high fire hazards due to lightning storms (Armit, 1966). As might be expected for trees evolving in such areas, lodgepole is well adapted to regenerating
successfully after fires (Armit, 1966; Smithers, 1962). It produces serotinous, or closed, cones which remain on the tree and retain seeds until high temperatures (113-122° F or 45-50° C) and low humidity are achieved (Bates, 1930). These conditions normally are met only during a forest fire, although some serotinous cones do open from heating by the sun (Crossley, 1956b; Tackle, 1954). Viable seeds have been found in cones as much as 75 years old (Mason, 1915). Most seeds released from serotinous cones germinate in the spring following the summer in which the fire occurs (Boe, 1956). Clements (1910) has also noted other benefits of fire: seed-eating rodents such as squirrels and chipmunks are temporarily eliminated, the overstory is opened up to give more sunlight to the shade-intolerant saplings, other competing ground-cover species are destroyed, and ground litter accumulations are burned and removed, leaving a more suitable bed for seed germination and growth.

Lodgepole pine is relatively shade-intolerant, that is, young trees do not grow well when underneath an overstory of other trees, even of its own species (Clements, 1910; Powells, 1965). However, in open areas, young lodgepole have higher growth rates and can outcompete other tree species such as aspen, white spruce or hemlock (Horton, 1956; others). As a result of fire-released seeds, shade intolerance, and fast sapling growth, lodgepole tends to produce pure, even-aged stands appearing remarkably uniform over wide areas (Smithers,
1962). Later, I will discuss the implications of this even-age phenomenon for mountain pine beetle populations.

Lodgepole pine is also noted for its tendency to produce densely stocked stands which result in smaller trees (Smithers, 1962). Under normal stocking densities (about 250-500 trees per acre), 90-year-old trees have an average d.b.h. (diameter at breast height) of 10.5 inches, and 65-year-old trees average 8.5 inches (Smithers, 1962). For overstocked stands, Trappe and Harris (1958) found a 65-year-old stand with 10,000 trees per acre and an average diameter of 2 inches, and Smithers (1962) found a 90-year-old stand with 3010 trees/acre and an average d.b.h. of 3.2 in. Other stands have been seen to range to an extreme of 500,000 trees per acre (Smithers, 1962). Such overstocked stands tend to stagnate, or stop their growth, at an early age, and lodgepole is the most likely to stagnate of any North American tree (Fowells, 1965). Seed production by lodgepole is very sensitive to crowding so this characteristic of overstocking is important when considering the reproductive potential of stands of different ages killed by mountain pine beetle. The evolutionary significance of this topic will be considered along with a detailed description of lodgepole reproduction in Section X.

C. Natural Enemies

Mountain pine beetle is the major pest species of
lodgepole pine but other insects also attack this tree, only rarely inducing mortality. Some of the more common species are the lodgepole needle miner (*Coleotechnites starki*), jack-pine budworm (*Choristoneura pinus*), lodgepole sawfly (*Neodiprion burkei*), terminal weevil (*Pissodes terminalis*), and pine loopers (*Cariophila* spp.) (Armit, 1966; Powells, 1965). Dwarf mistletoe (*Arceuthobium americanum*) prefers vigorous hosts (Powells, 1965) and redheart stain (several fungi of the genera *Stereum* and *Fomes*) is most common in older trees (Armit, 1966).

Mountain pine beetles normally kill host trees through destruction of phloem and outer sapwood (Reid, 1962a). Adult and larval galleries sever cells in these regions, reducing moisture transport within the tree. Although this girdling action is probably the most significant cause of tree death, the bark beetle's symbiotic blue-staining fungi are known to be pathogenic to lodgepole, even in the absence of mountain pine beetle (Reid et al., 1967 and many references therein).

D. Natural Defenses

1. Types of resistance

Lodgepole has two levels of defense mechanisms against the mountain pine beetle and its associated blue-staining fungi. The first mechanism involves a fast-acting but passive
system which is present even without beetle attack while the second is a delayed but actively produced response to wounding. The passive mechanism is known as primary resinosis (Berryman, 1972; Reid et al., 1967). When a bark beetle cuts through the bark, vertical and horizontal resin ducts are severed. The pitch which flows out of these canals by force of gravity pours over the insect and, if copious enough, can either kill or expel it. This initial resin flow begins almost immediately after a duct is cut.

The success of primary resinosis is affected by several resin characteristics: 1) exudation pressure, 2) rate and quantity of flow, 3) chemical composition, and 4) rate of crystallization (Reid, 1963). Resin produced in response to an attack often flows out the beetle's entrance hole and hardens into a plug which stands out at right angles to the bark and can readily be seen at a distance. The presence of such a pitch tube does not necessarily indicate that the attacking bark beetle was killed or expelled, although beetles can sometimes be found embedded in them.

If the bark beetle survives the initial onslaught of resin, the tree responds further with a delayed system known as secondary resinosis (Reid et al., 1967) or hypersensitive reaction (Berryman, 1972). As the female bark beetle moves along (at about 1.3 to 2 cm per day; Reid, 1962b) digging its gallery and laying eggs, the tree cells surrounding the gallery begin to change physiologically. Bark and sapwood
parenchyma cells become swollen with resin (not their normal function) and many of these cells burst and release their resin into the adult insect's gallery (Reid et al., 1967). This resin is toxic to both mountain pine beetle eggs (Reid and Gates, 1970) and to the symbiotic fungi (Shrimpton and Whitney, 1968; Reid et al., 1967). If the secondary resinosis response is too weak, the bark beetle continues gallery construction and the pathogenic fungi continue to spread in the phloem of the tree.

Successful primary resinosis either kills the mountain pine beetle or causes the live female to back out of the gallery and seek another tree. In either case, the pathogenic blue-staining fungi are contained (Reid et al., 1967). However, when a tree expels an adult female, there is a finite probability that the insect will go to a nearby tree, successfully reproduce, and thereby provide new insects to attack the original expelling tree the following year. It would therefore be better for trees to kill all adult bark beetles as they enter the bark. However, there is a disadvantage in having a very strong and rapid primary resinosis response because a bark beetle may have a greater chance of escaping unharmed. It will have dug a shorter gallery and will have a lower probability of being trapped by resin. A more delayed tree response would seem more propitious.

This is where secondary resinosis might become important.
This reaction is delayed until several days after gallery digging is begun (Reid et al., 1967). Adult beetles do not flee the gallery even if this secondary tree response is successful in killing eggs and larvae. The bark beetles behave as though reproduction were proceeding normally, which is similar to the effect of the sterile male technique of controlling screw-worm fly (Bushland et al., 1955). Strong secondary resinosis, when combined with weak primary resinosis, thus appears to be the most profitable tree resistance mechanism because adults are trapped and do not reproduce. One must remember, however, that the primary system is largely a passive one and is not easily controllable, whereas an active channelling of energy is required to produce the secondary response. Also, by relying on the delayed response, there may be too great a risk in letting the bark beetle and its associated pathogenic blue-staining fungi get a foothold; unpredictable events which affect tree physiology rapidly, such as weather, may frequently prevent trees in this tenuous state of balance from containing the invading species. Rational arguments can therefore be made for the predominance of either tree resistance mechanism in nature, and relevant data will be presented later.

Both primary and secondary resinosis can be initiated by inoculating blue-staining fungi in the absence of bark beetles (Reid and Shrimpton, 1971; Reid et al., 1967). This
phenomenon has led to the development of a system for rating the potential of lodgepole pine to resist mountain pine beetle (Reid et al., 1967; Shrimpton and Reid, 1973). I attempted to use and evaluate this rating system and the topic will be considered more fully in the section entitled "Fungal Rating System".

2. Factors affecting resistance mechanisms

Several factors influence the effectiveness of tree resistance mechanisms. Physiological state of the tree at the time of attack is the major determinant of this effectiveness. Tree health is in turn affected by 1) calendar and "physiological" age (Morris, 1948), 2) local site factors such as soil type, slope, and density of surrounding and competing trees, 3) recent moisture availability, 4) lightning and fire history, and 5) historical presence of defoliators or fungi in nearby areas. Reid and Shrimpton (1971) note that resistance also changes through the summer and in their study areas, bark beetles have normally been observed to attack just after the peak in resistance in July.

The behaviors of *D. ponderosae* and its associated fungi tend to decrease the effectiveness of both levels of tree resistance. Primary resinosis may be affected by the shape of the parental beetle gallery. The bark beetle begins gallery formation by cutting a J-shaped hook at its base (Fig. 1). Berryman (1972) and Reid et al. (1967) have suggested that the
purpose of this hook is to drain the vertical and horizontal resin ducts which are severed, causing an initial flush of resin but reducing the amount of resin to be faced later by the adult. Blue-staining fungi carried by bark beetles grow in sapwood (outer xylem) cells, rendering them non-functional as water conductors (Reid et al., 1967 and references therein). In addition, phloem cells can no longer distribute vital products throughout a tree once they are severed by adult and larval beetle galleries. All of these effects become critical to the tree when large numbers of bark beetles attack. Reduced numbers of functional phloem and sapwood cells result in lowered ability to produce the actively generated secondary resinosis, believed by some to be the more important of the two tree resistance mechanisms (Reid et al., 1967). Also, adult beetle survival is enhanced by increasing attack density because the more cuts there are in resin canals, the smaller is the amount of resin spilling into each gallery.

These obvious benefits to bark beetles of ensuring large numbers of attacking insects on individual trees have led some investigators to conclude that aggregation behavior is essential to kill relatively healthy trees. However, before concluding that this is the primary advantage of aggregation, we must look at other bark beetle species. For instance, the ambrosia beetle *Trypodendron lineatum* also attacks *en masse* through pheromone action but it is known to prefer fallen
trees that have been on the ground for three to seven months (Kinghorn and Chapman, 1957). These trees have no viable resistance mechanisms, so aggregating behavior cannot function for *T. lineatum* in reducing the effectiveness of host resistance.

The literature offers no reasonable explanations for mass attacks in *T. lineatum* or other bark beetles with similar life histories. There are several rather speculative possibilities, however. *T. lineatum* will occasionally attack standing trees, but usually only those trees which are already extremely unhealthy due to some other cause (K. Graham, pers. comm.). It could be that some of these alternative hosts are vigorous enough that there could be strong selection in such cases for maintaining an aggregating pheromone system to help overcome the host's resistance. Such an explanation depends on the frequency of these situations and the proportion of the beetle populations which are affected, both of which are unknown. Another possible explanation for aggregating pheromones in bark beetles that normally attack fallen trees is that these beetles may still maintain a behavioral system, derived from their ancestors, which was not lost because it was never selected against (Atkins, 1966a). Yet another possibility is that the probability of each insect's being preyed upon or parasitized may decrease with increasing numbers of other bark beetles present (e.g. Tinbergen, 1960). However, this explanation depends on
the rapidity of the numerical response of the predators and parasites and on the shapes of their functional response curves. Another equally speculative idea dealing with efficiency of host utilization involves kin selection (Hamilton, 1964a, 1964b, 1972). This idea depends upon future data on the attractive distance of pheromones in the field, the amount of "flocking" during adult dispersal, and the degree of genetic relatedness of individuals that attack the same tree.

The selective importance of tree resins on bark beetle behavior can be discerned by comparing the adult galleries constructed by different species of bark beetles. Berryman (1972) has pointed out that most species of bark beetles which attack healthy, resinous species of trees, such as those among the Pinus or Picea genera, normally dig vertical adult galleries in order to sever as few vertical resin ducts as possible. In contrast, those bark beetle species which attack trees such as firs that do not have well-developed resin duct systems usually bore horizontal galleries. It could be implied from these observations that horizontal adult galleries are the optimal situations for bark beetles because more tree transport cells are severed than when vertical galleries are dug. There are thus fewer beetles required in order to kill each tree by girdling action. The only reason we find species digging vertical galleries is because of the constraints imposed by the well-developed resin duct systems
in some tree species. In these tree species, there is strong selection against beetles that dig horizontal galleries owing to the degree of tolerance to resin that would be required by the bark beetles.

It also is of interest to know whether this orientation of adult galleries is constant throughout a beetle species or whether, as Berryman (1972) suggests, it is a behaviorally plastic characteristic, shifting with different resin flow conditions encountered. This idea can be tested by looking at bark beetle species which attack several different tree species with different resin characteristics. Within a beetle species, one would predict that if gallery orientation were a variable characteristic, and if horizontal galleries were the evolutionary optimum, adult galleries would tend to be more horizontal in tree species with less developed resin systems than in trees of equal vigor with better resin systems. If gallery orientation were a fixed characteristic of the beetle species, it should be the same regardless of host tree species. Mountain pine beetle does not offer evidence here because all of its host species are quite resinous. However, evidence may be available for other bark beetle species.

E. Variability In Host Attractiveness

Because conditions of the trees and the bark beetles at the time of encounter are variable, not all trees are equally attractive to dispersing bark beetles that are looking for a
new host. Internal factors inducing variability in beetle response to trees will be discussed in the section on dispersal data; here, only agents affecting tree attractiveness are considered.

There is presently a controversy surrounding the concept of primary attractants (those tree chemicals thought to aid bark beetles in choosing hosts). Some bark beetle investigators, most notably those in D.L. Wood's group at Berkeley, claim that dispersing bark beetles initially attack trees randomly in space. Other researchers believe that bark beetles are able, before attack, to detect which trees are going to be most suitable for reproduction. It appears that the cause of the discrepancy is the different species with which the researchers work.

First, we must consider whether there are differences between species of trees which can potentially be detected by insects and second we must decide whether bark beetles are able to discriminate between these differences. Data relevant to these questions fall into two categories: 1) within tree species, and 2) between tree species. Some bark beetles such as Douglas-fir beetle, mountain pine beetle, and western pine beetle are relatively host-specific in that they are found only in a few coniferous species (Rudinsky, 1962). The existence of host specificity indicates that at least some bark beetles are able to recognize something unique about their hosts, presumably tree chemicals.
The evidence concerning differences between trees within species is not so straightforward. Potential visual cues such as size and location must be separated from olfactory ones. Trees of any given species that appear to be the same size may differ in chemical constituents. Roe and Amman (1970) present evidence that the mountain pine beetle preferentially attacks and kills ponderosa pine trees which have the thickest phloem, even when trees used for comparison are all the same diameter and in the same locality. Moeck (1970b) found that *T. lineatum* is attracted by ethanol and Graham (1968) noted that this species responds differentially to the various ethanol concentrations produced by cut hemlock logs of different physiological ages. Less vigorous or more senescent trees may produce more ethanol (Graham, 1968). On the other hand, *D. brevicomis*, the western pine beetle, appears to attack ponderosa pine trees at random (Wood, 1973) and brood success is highly variable between trees with equal attack density (Vité and Wood, 1961).

Let us consider now the specific case of mountain pine beetle and its host trees. Numerous forest entomologists feel that tree age is a very crude predictor of likelihood of attack by *D. ponderosae* (e.g., Safranyik et al., 1974b). Only recently have investigations begun to reveal the proximal factors associated with tree age which are used by mountain pine beetle in deciding which trees to attack.
Tree aging induces quantitative but not qualitative changes in chemical compositions of lodgepole and some other pines (Syed, 1972). Syed has shown that there is more limonene and less 3-carene in mature ponderosa pine trees than in younger trees. Similarly, Syed (pers. comm.) has found that mature lodgepole pines have more limonene and alpha-pinene than young trees, and that young lodgepole have more 3-carene than older trees. Factors such as prolonged competition and drought which affect tree physiological age may also cause these chemical changes which are normally associated with calendar aging.

Syed (1972) showed that mountain pine beetle responded positively to total bark extracts containing these and other chemicals. He also found a positive response to ethanol in various concentrations. *D. ponderosae* are known to respond to the female aggregating pheromone only in the presence of host tree chemicals (Pitman and Vité, 1969), particularly alpha-pinene (Pitman, 1969; Renwick and Vité, 1970).

In conclusion, the evidence for mountain pine beetle is that there is some use of tree chemicals in host selection, though other bark beetles such as the western pine beetle do indeed appear to attack trees randomly. If there were no detectable differences between trees attacked by the western pine beetle, or if there were no advantage in discriminating between tree types, then random attack would be biologically effective, especially when combined with the observed fact
that this beetle has one of the highest reproductive rates of any bark beetle and can have up to 3 or 4 broods per summer (Miller and Keen, 1960; Stark and Dahlsten, 1970). On the other hand, *D. ponderosae* chooses its host trees more carefully and has the reproductive behavior common among this type of bark beetle: only one or two broods per year and a relatively small number of eggs per brood.

Bark beetle ecologists use some terms which need to be clearly defined. The probability that an individual tree will be attacked by one or more bark beetles is generally termed the tree's attractiveness. The probability that a tree in a given vigor class will die after being attacked by a given number of beetles is termed its susceptibility or resistance ability. This resistance ability is also inversely related to beetle reproductive success. In addition, larger numbers of bark beetles attacking a single tree of given vigor class will increase the probability of death.
IV. STUDY AREAS

To answer the questions posed in Section I concerning differences between epidemic and endemic beetles and trees, it was necessary to find two replicate study sites in each of these two types of areas. If only one area representing each type were used, then any differences found could have been attributed to differences in geographical location rather than population state. The terms epidemic and endemic are somewhat arbitrary but I define them as follows. Endemic areas are those in which only a few dozen trees are killed every year by mountain pine beetle within an area of, say, several square miles. Epidemic areas, on the other hand, generally have several hundred acres of trees killed per annum.

Data on tree characteristics were collected from May through September 1973 in four study sites shown in Fig. 2 and described in Table 1. These areas contain mostly lodgepole pine, although the two endemic areas have some large aspen and white spruce. The mountain pine beetle outbreak at Elk Creek (henceforth called Elk), near Canal Flats, B.C., has destroyed a high percentage of trees over large acreage since about 1967. To date, more than 200,000 acres of lodgepole pine have been destroyed. Parson, B.C., approximately 75 air miles to the northwest in the Columbia Valley, supports a small D. ponderosae population. Tree losses numbered about 35 over a square mile in 1972. There has not been a large mountain
FIGURE 2

A map of southern British Columbia showing the location of the four 1973 study areas (black squares).
TABLE 1

Characteristics of the four study areas.

<table>
<thead>
<tr>
<th>Population type</th>
<th>Location</th>
<th>Epidemic</th>
<th>Endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Elk</td>
<td>Terrace</td>
</tr>
<tr>
<td>Location</td>
<td></td>
<td>3900</td>
<td>3550</td>
</tr>
<tr>
<td>Elevation (ft.)</td>
<td></td>
<td>97.7</td>
<td>90.6</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>15</td>
<td>9</td>
</tr>
<tr>
<td>tree age (years)</td>
<td></td>
<td>10.2</td>
<td>5.0</td>
</tr>
<tr>
<td>Number trees</td>
<td></td>
<td>220</td>
<td>261</td>
</tr>
<tr>
<td>age-sampled</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.D. tree age</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number trees/acre</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
pine beetle population in the vicinity of Parson for at least 10 years. Terrace Creek was the other epidemic area studied and is located 10 miles northwest of Kelowna, B.C. Beetles in this area have begun to do considerable damage only during the past 3-4 years and dead trees cover several hundred acres. The other endemic area, Lean-to Creek (henceforth called Lean), is located only 1.25 miles to the northeast of the farthest extent of the Terrace Creek dead trees. Owing to the proximity of these two areas, beetles from Lean might possibly have come from Terrace Creek. However, Lean has definitely supported a very low beetle population from 1969 to 1972 (C. Cottrell, pers. comm.). In 1973 the number of trees killed from the previous year's attack rose to about 30 per acre from 15 in a two acre patch, giving signs that the population may be increasing in numbers. Because of these indications that Lean may be in transition to an outbreak state, some of my conclusions concerning differences between epidemic and endemic area trees and beetles are not as firm as they might otherwise be.

Throughout the rest of this paper, my data on endemic areas will refer specifically to Lean and Parson and epidemic will refer to Elk and Terrace Creek.
V. FIELD EVALUATIONS OF TREES

A. Age

The ability of lodgepole to resist attacks by mountain pine beetle is thought to decrease with age after a tree reaches about 50 years (Shrimpton, 1973). Increase in probability of succumbing after a given number of attacks is also associated with increased attractiveness to beetles, as discussed in the section on host attractiveness. Safranyik et al. (1974a) note that most D. ponderosae outbreaks occur in stands 80-90 years old and only a few occur in younger stands.

Tree ages were measured in the study areas with a standard 3 mm increment borer and rings were counted in the field without the aid of a hand lens. Results are shown in Table 1. Trees in the two epidemic areas are older (95 vs. 70) than those in endemic areas (t=8.50, 41 d.f., P<.001). This substantiates the findings of other workers discussed above.

B. Determination Of Tree Status

In the past, bark beetle ecologists have concentrated on trying to predict individual tree mortality by looking at tree resistance ability prior to attack (e.g. Vité, 1961; Reid
et al., 1967). I too used such a method (to be discussed in the section entitled "Fungal Rating System"), but I was also interested in trying to predict beetle mortality and reproductive success. Thus, for testing the other ideas concerning trees, a system was required for determining the success of bark beetles attacking individual trees. This success measure needed to be defined in terms of bark beetle reproduction rather than tree mortality for two reasons. First, although successful beetle reproduction and tree mortality are normally correlated, some *D. ponderosae* females do succeed in reproducing even though the host tree is not killed. Second, it is difficult to tell in the spring (when data were collected) whether a tree is going to die from bark beetle attacks made the previous summer.

The following system was devised for determining the status of individual lodgepole trees. At most, three randomly chosen beetle galleries located at breast height were investigated by peeling off the bark with a chisel. If any live larvae or pupae were found, the tree was classed "successfully attacked". If no live larvae or pupae were revealed after three adult gallery systems were exposed, the tree was classified "unsuccessfully attacked". The reason for lack of bark beetle reproduction was determined by looking at lengths of adult galleries and presence of resins. Resistance due to primary resinosis was diagnosed if, a) the adult gallery did not extend past the entry hole, b) adults in the
gallery were dead and covered in resin, or c) the adult
gallery was present but it was at least half-filled with
pitch. Secondary resinosis (the delayed response) was
considered responsible if adult galleries were present and a)
no larval galleries were found, or b) larval galleries were
present but larvae were dead or not visible. Trees which
showed signs of extensive woodpecker feeding were not
analyzed.

On the basis of these criteria of success of bark beetle
reproduction, attacked lodgepole trees fell into one of three
categories: 1) successful, 2) unsuccessful due to primary
resinosis, or 3) unsuccessful due to secondary resinosis.
This all-or-none measure of mountain pine beetle reproduction
was not as precise as a more quantitative figure, but
qualitative data from many different trees were deemed more
appropriate for answering my comparative types of questions
than detailed quantitative data from just a few trees.

Data on beetle success were gathered either in May and
early June, 1973 (before new attacks) or in late September
(two months after new attacks). Numerous standing trees were
sampled in addition to those which were cut and brought back
to Vancouver.

C. Spatial Distribution

Successful location of hosts by bark beetles depends upon
distance over which appropriate host chemicals are sensed, density of hosts per unit area, and spatial distribution of hosts relative to dispersal ability of the searching species. Numbers of trees per acre were estimated from counts taken in two 100 ft by 100 ft plots in each study site. Data at the bottom of Table 1 show that the density of trees is not necessarily higher in epidemic or endemic areas. I hypothesized, however, that susceptible trees in epidemic areas might be more uniformly distributed in space than trees in endemic plots. Dispersing bark beetles might then suffer greater mortality in endemic areas because susceptible trees are clumped, clumps are randomly distributed in space and they are more difficult to find.

To test this hypothesis, spatial distributions of successfully attacked trees (defined in terms of beetle reproduction as described above) were measured by the "Point-to-plant distance ratio" test of Holgate (1965). This test uses distances to plants from a series of randomly chosen points. These points in my study sites, determined from random number tables, all fell within 600 ft of one another. Data in Table 2 show that for the 20 trees sampled in each area, there was no significant deviation from a random distribution. On the basis of these data, I cannot conclude that suitable trees in endemic areas are more clumped than in epidemic areas. However, the hypothesis could be more rigorously tested if data from a wider spatial scale were
TABLE 2

Spatial distributions of successfully attacked lodgepole pine trees using Holgate's test. If coefficient of aggregation, A, equals 0.5, distribution is random; if less than 0.5, distribution tends toward uniform, and if greater than 0.5, clumping is indicated. Data are based on samples of 20 trees from each area.

<table>
<thead>
<tr>
<th>Population type</th>
<th>Epidemic</th>
<th>Endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Elk</td>
<td>Terrace</td>
</tr>
<tr>
<td>A</td>
<td>--</td>
<td>0.482</td>
</tr>
<tr>
<td>Z statistic</td>
<td>--</td>
<td>0.286</td>
</tr>
<tr>
<td>Probability that distribution is random</td>
<td>--</td>
<td>&gt;0.1</td>
</tr>
</tbody>
</table>
available. This scale should be defined in relation to dispersal capabilities of bark beetles. Erroneous conclusions may be drawn if arbitrary spatial scales are utilized, such as the one I used. For example, if one chose a scale about the same size as the area covered by an extant outbreak, successfully attacked trees would be much more evenly distributed in epidemic sites than in endemic areas when measured with that same scale. If we determine that dispersing mountain pine beetles normally cover several miles, then a scale of this magnitude is needed to test adequately for heterogeneity in hosts with respect to the capabilities of beetles finding them. Since the mountain pine beetle, being in part passively dispersed, can travel at least a mile at a time (see data in dispersal section), the measurements of spatial distribution made across only a few hundred feet in this study are obviously inadequate for meaningfully testing the hypothesis. It is possible that large-scale aerial photographs of old beetle-killed areas can be more useful for testing this idea.

D. Attack Densities

As discussed above, trees with high attack densities should be more likely to host successfully reproducing bark beetles than trees with lower attack densities. Ideally, this hypothesis should be tested with trees in the same state of health prior to bark beetle attack. This was not possible, so
data were collected from trees independent of their previous physiological health.

Attack densities were measured with a square-gridded wire-and-string overlay, 1 ft by 1 ft, which was laid tightly over the tree trunk. All entrance holes (distinguished from exit holes by the presence of pitch tubes) inside this square were counted. Three consecutive samples were taken per tree starting at the base and working upward on the side of the tree having the most attacks. Reproductive success of beetles was determined with the gallery inspection method described in Section V-B. Data were collected in each study area by looking at trees in two separate 100 ft by 100 ft plots and on a 1000 ft straight-line transect.

Table 3 shows results comparing average attack densities on successfully attacked trees with those on unsuccessful ones. When all four sample areas were lumped, successfully attacked trees did have significantly higher attack densities than unsuccessfully attacked ones, indicating that attack by a large number of beetles can result in a greater probability of overcoming a tree's resistance attempts or that more beetles are attracted to weaker trees. However, when data are broken down by study area (bottom of Table 3) we find slightly different results: although trees which produced beetle offspring tended to have higher attack densities, on average, than unsuccessfully attacked trees, there was no statistical significance in the differences. This was due to the
TABLE 3

Comparison of average attack densities (from 3 samples per tree), by area, and by tree type defined in terms of bark beetle reproductive success. Under tree type, S=successful beetle reproduction, US=unsuccessful (see text).

All areas lumped:

<table>
<thead>
<tr>
<th></th>
<th>Successful</th>
<th>Unsuccessful</th>
</tr>
</thead>
<tbody>
<tr>
<td>Average attack density</td>
<td>8.95</td>
<td>7.36</td>
</tr>
<tr>
<td>Standard error</td>
<td>0.47</td>
<td>0.34</td>
</tr>
<tr>
<td>N</td>
<td>140</td>
<td>75</td>
</tr>
<tr>
<td>t-statistic</td>
<td>2.75</td>
<td>&lt;.01</td>
</tr>
</tbody>
</table>

Broken down by area:

<table>
<thead>
<tr>
<th>Population type</th>
<th>Epidemic</th>
<th>Endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Elk</td>
<td>Terrace</td>
</tr>
<tr>
<td>Tree type</td>
<td>S</td>
<td>US</td>
</tr>
<tr>
<td>Average attack density</td>
<td>12.1</td>
<td>10.3</td>
</tr>
<tr>
<td>Variance</td>
<td>13.2</td>
<td>9.0</td>
</tr>
<tr>
<td>No. trees sampled</td>
<td>17</td>
<td>9</td>
</tr>
<tr>
<td>t-statistic</td>
<td>1.35</td>
<td>1.70</td>
</tr>
<tr>
<td>P</td>
<td>&gt;0.1</td>
<td>&gt;0.09</td>
</tr>
</tbody>
</table>
relatively large variances, possibly associated with sampling from trees with a wide variety of tree vigors prior to attack. Epidemic areas did not tend to have different attack densities than endemic areas within either the successfully- or unsuccessfully-hit tree categories (t-tests, \( P > .2 \) and \( P > .5 \), respectively).

The important question concerning the effect of higher attack densities on the probability of overcoming tree resistance is how rapidly that probability increases per unit increase in numbers of beetles attacking. In other words, is the "effective" resistance (intrinsic resistance minus decrease due to beetles attacking) a rapidly or slowly decreasing function of attack density (see Fig. 3)? The answer to this question is significant for the understanding of outbreaks because present theories predict that epidemic beetles overcome normally unassailable trees and spread faster by sheer weight of numbers.

Figure 4 shows the frequency distribution, by reproductive success categories, of the average attack densities summarized in Table 3. Three conclusions can be drawn from these data. 1) The only two areas showing differences in frequency distributions between successfully and unsuccessfully attacked trees are Parson and Terrace Creek \( (X^2, \ P < .03) \). There is no consistent pattern based on population type (epidemic or endemic areas). 2) Only when attack densities fall below about 3 per sq ft is there a large
FIGURE 3

A hypothetical relationship between the probability of trees in various vigor classes dying and attack density of mountain pine beetle. Steepness of the slopes are critical to the concept of epidemic centres (see text).
PROBABILITY OF TREE SUCCUMBING OR PRODUCING BARK BEETLES

ATTACK DENSITY

TREE VIGOR CLASS:

POOR

GOOD
FIGURE 4

Distribution of attack densities on trees by class of beetle reproductive success (see text). Attack densities are the average of 3 samples per tree. SUCC=successful and UNSUCC=unsuccessful. Elk and Terr are the epidemic areas and Pars and Lean are the endemics. Chi-square values were found using frequency data. N is the number of trees sampled.
probability of tree resistance overcoming beetles. 3) There does not appear to be any difference in this minimum density for success between epidemic and endemic areas.

E. Predicting Tree Status

Since attack densities are not sufficient to predict tree status, I attempted to use tree age measures, in conjunction with attack density, to discriminate between populations of trees with different beetle productivity. Tree age and beetle success were determined as before and tree circumference was measured at 50 inches height. If tree age were a good predictor of tree resistance ability, one would expect that for a given attack density, successfully reproducing beetles would be on older (and presumably weaker) trees. Figure 5 shows that this is not the case, at least for the 29 trees sampled. Unsuccessfully attacked trees seem to be distributed randomly with respect to age, regardless of attack density.

Tree size may be a more useful basis for discriminating between tree status types (based on beetle reproduction) for two reasons. One, diameter or circumference reflects phloem thickness, which has been related to success of beetle reproduction by Amman (1972). Two, size at any given age reflects the degree of competition that a tree has been faced with in the past or that it is still encountering. It is therefore a measure of physiological age as determined by the number of years since initial release from competition.
FIGURE 5

The use of tree age and mountain pine beetle attack density for predicting beetle reproductive success on trees. Data come from all study areas. As before, SUCC = successfully attacked trees and UNSUCC = unsuccessfully attacked trees. Sample size is 29.
ALL AREAS 1973

+ = SUCC., ▲ = UNSUCC.

NO. ATTACKS PER SQ. FT.

TRE AGE (YEARS)
(Morris, 1948). This may be a better indicator of tree health at any point in time than calendar age. When tree size is used as the basis for a discriminant function analysis along with attack density, the data plot as indicated in Fig. 6. These two independent variables do not provide a good separation of the two tree types. However, as before, beetles attacking with a density of less than about 3 per sq ft do not reproduce successfully, independent of host tree size. This suggests, for the sizes of trees sampled, that this minimum attack density is required to overcome tree resistance.

When these same data are disaggregated into epidemic and endemic types (Fig. 7), another interesting point appears. The size distributions of trees sampled in both area types were the same ($X^2, P>.1$) but trees with successfully reproducing beetles were, within a given attack density class, smaller sized in epidemic than in endemic areas. This is seen by comparing the position on the circumference axis of the "cloud" of +'s (successfully attacked trees) in the top and bottom graphs of Fig. 7. These data indicate that trees with equal size and equal mountain pine beetle attack densities are more likely to be overcome by the beetles in epidemic areas than in endemic ones. Therefore, higher beetle attack densities and/or larger trees are not the causes of bark beetles building up so rapidly in outbreak regions; there must be something else intrinsically different about trees or beetles between epidemic and endemic areas.
FIGURE 6

The use of tree circumference and mountain pine beetle attack density for predicting beetle reproductive success on trees. Data come from all study areas. SUCC = successfully attacked trees and UNSUCC = unsuccessfully attacked trees. Sample size is 142 trees.
ALL AREAS 1973

+ = SUCC., ▽ = UNSUCC.

NO. ATTACKS PER SQ. FT.

TREE CIRCUMFERENCE (IN.)
FIGURE 7

Same data as Figure 6 except that data are broken down into epidemic and endemic areas. SUCC = successfully attacked trees and UNSUCC = unsuccessfully attacked trees. Sample size for epidemic areas is 74 trees and for endemic is 78.
F. Proportion Successfully Attacked

If the prevailing dogma is correct that at any one time there are more susceptible trees per unit area in epidemic than endemic areas, then one would predict that a smaller proportion of bark beetles in epidemic areas would be resisted by their host trees. This would be true if beetles attacked trees randomly or if their system for discriminating between host attractants were less than perfect. If this beetle discriminating system were absolutely precise, there should be no unsuccessfully attacked trees in either epidemic or endemic areas because beetles should have found only susceptible trees. These predictions assume that, 1) the pheromone system used by initial attackers is very efficient at attracting the remaining population to attacked trees and 2) there is no change in the efficiency of discriminating systems or pheromone systems with beetle population density.

Data sampled from two 100 ft by 100 ft plots and a 1000 ft straight-line transect in each of the four study areas are summarized in Table 4. First, note that when all study areas are lumped, more than one third of the trees successfully resist the attacking beetles. Therefore, the beetle mechanisms for determining which trees are the best to attack are anything but precise; beetles misclassified about 36% of the 555 trees sampled.

When these data are broken down by study area (bottom of
TABLE 4

Status of attacked trees defined in terms of production of beetles. Numbers of attacked trees are in each category, proportions of trees in each area are in parentheses. US#1 = primary resinosis, US#2 = secondary resinosis.

<table>
<thead>
<tr>
<th></th>
<th>Succ.</th>
<th>Unsucc. #1</th>
<th>Unsucc. #2</th>
<th>N</th>
<th>% Unsucc.</th>
</tr>
</thead>
<tbody>
<tr>
<td>All areas lumped</td>
<td>358 (.64)</td>
<td>99 (.18)</td>
<td>98 (.18)</td>
<td>555</td>
<td>35.5</td>
</tr>
</tbody>
</table>

Broken down by study area:

<table>
<thead>
<tr>
<th></th>
<th>Succ.</th>
<th>Unsucc. #1</th>
<th>Unsucc. #2</th>
<th>N</th>
<th>% Unsucc.</th>
<th>% beetles on US trees</th>
</tr>
</thead>
<tbody>
<tr>
<td>Elk (Epidemic)</td>
<td>168 (.65)</td>
<td>37 (.14)</td>
<td>53 (.21)</td>
<td>258</td>
<td>34.9</td>
<td>31</td>
</tr>
<tr>
<td>Terrace (Epidemic)</td>
<td>80 (.71)</td>
<td>17 (.15)</td>
<td>16 (.14)</td>
<td>113</td>
<td>29.2</td>
<td>20</td>
</tr>
<tr>
<td>Lean (Endemic)</td>
<td>84 (.68)</td>
<td>24 (.20)</td>
<td>15 (.12)</td>
<td>123</td>
<td>31.7</td>
<td>28</td>
</tr>
<tr>
<td>Parson (Endemic)</td>
<td>26 (.43)</td>
<td>21 (.34)</td>
<td>14 (.23)</td>
<td>61</td>
<td>57.4</td>
<td>47</td>
</tr>
</tbody>
</table>
Table 4) two points are raised. First, there are no more resistant trees in endemic than epidemic areas, unless Lean is considered more epidemic than endemic because of its apparent state of transition. Perhaps most of the susceptible trees in epidemic areas have already been removed from the stand and insects are attacking successfully only because of their large populations. Second, the proportion of female beetles (determined from my 3 samples per tree) that attacked trees on which they could not successfully reproduce ranged from .20 to .47. Such large proportions indicate that there should be strong selection for a better discriminating system.

However, there may be a hidden advantage in this apparent inefficiency: those individuals that attack what are under normal conditions unsuitable hosts, may reproduce quite well should those hosts suddenly become more susceptible (for example, due to rapidly changing weather conditions). This possible advantage rests on two assumptions; 1) resistant trees are healthier than non-resistant ones (see introduction) and 2) healthier trees provide a better medium for beetle reproduction if they should quickly become unable to resist adequately. This second assumption is substantiated by Safranyik and Jahren (1970), who show that larger insects emerge from larger and thicker barked trees, and by Reid (1963) who shows that larger females produce more offspring. It is also presumed that this change in tree physiology would occur more rapidly than would be detectable by so-called
primary attractants. The magnitude of the selective advantage of attacking normally unsuitable hosts is dependent on the frequency of rapid deterioration in tree conditions. The unpredictable nature of causal agents in such changes may require some built-in flexibility in the bark beetle population for coping with changing conditions.

Another hypothesis that can be tested with these data concerns the relative advantage of secondary resinosis over primary resinosis. Previously, the relative advantages to trees of each of these resistance mechanisms were discussed. Data in Table 4 indicate that primary resinosis is not any more common than secondary resinosis as the cause of failure of beetle reproduction (t-test, paired by area, P>.1). There are three possible reasons why weak primary and strong secondary reactions do not predominate. First, as mentioned previously, the primary resinosis system may be difficult to regulate because of its passive mode of action. Second, tree resin systems probably function in general wound healing (Berryman, 1972) and as a barrier to infection (Whitney and Denyer, 1969). There are many other sources of tree wounds besides bark beetles; for example, other falling trees and woodpeckers. Because of the presence of these other selection pressures, one would not expect resin reactions to have evolved in such a way as to optimize only the interactions with bark beetles. Third, if primary resinosis is sufficient to resist the beetles and their fungi, no secondary response
is needed. Note that the two endemic areas are the only ones with a preponderance of primary responses, although these differences are not significant with a t-test (P > .1).

G. Fungal Rating System

Many workers have attempted in the past to find measures of potential of individual trees to resist bark beetles. These indices have ranged from primary resin exudation pressure (Vité and Wood, 1961) and chemical composition (Smith, 1963) to determination of crown class (Keen, 1943). Most workers have concentrated on some aspect of primary resinosis. Recently, a method was developed and used by Reid et al., (1967) and Shrimpton and Reid (1973). This technique derives from the observation that lodgepole pine reacts in the same way to the beetles' symbiotic blue-staining fungi alone as it does to the mountain pine beetle in the presence of fungi (Reid and Shrimpton, 1971; Reid et al., 1967). Thus, unattacked trees can be inoculated with fungi and, through observation of the resistance responses, an estimate of susceptibility to mountain pine beetle can be obtained.

I attempted to use this fungal assay method to test the hypothesis that there are more susceptible trees in epidemic than endemic areas. I closely followed the technique of Reid et al., (1967). Cultures of the blue-staining fungi isolated from mountain pine beetles sampled in the Canadian Rockies were obtained from Dr. H.S. Whitney, Canadian Forest Service
Research Lab, Victoria, B.C. Fungi were grown on sterilized wood chips (popsicle sticks cut 1.5 x 4 x 21 mm) which were soaked in 2% malt extract broth. Once the fungi were established, wood chips were inoculated into unattacked trees through an incision made in the bark on the N-E side of the tree with a sterilized chisel. Control chips (all the same treatments but without addition of fungi) were also inoculated into trees on the N-E side to control for effects of aseptic wounds and response to plain wood chips. Test trees were numbered with spray paint and, approximately three weeks after inoculation, the same trees were checked and their responses recorded.

Another aim of this fungal assay experiment was to determine how good this rating system was for predicting beetle productivity success. Shrimpton and Reid (1973) have evidence that the method is fairly good at predicting which lodgepole pine trees will be killed. In order to provide a rigorous test for this method, I carefully chose plots of trees to be inoculated that were in the vicinity of current mountain pine beetle activity in each of the four original study areas. These test trees were usually within 300 to 800 ft of the nearest trees with live mountain pine beetle larvae.

The temporal layout of the experiment was as follows. Test trees were inoculated in late June and responses were read and ratings were assigned in mid-July. This was before mountain pine beetle dispersal flight in the areas of study.
In late September these same trees were inspected to see which ones had been attacked by *D. ponderosae* and beetle reproductive success was ascertained. Table 5 summarizes the dates of these various steps.

For rating the response to fungal inoculation, the bark surrounding the wood chip was peeled off and trees were closely inspected. Rated trees fell into one of three categories: susceptible, resistant or intermediate, based upon criteria set out in Reid et al. (1967) and communicated by D.M. Shrimpton (pers. comm.). Those trees which showed external resin flow, discolored phloem and resin-soaked wood in the vicinity of the wood chip were classed resistant. Trees not having any of these characteristics except for external resin flow were called susceptible. The intermediate category was assumed if some but not all of the other characteristics were present.

Results of the July fungal rating experiment are shown in Table 6. Fungal ratings predicted that in all four areas, regardless of population state, most of the trees would be resistant to mountain pine beetle. There were no indications that a greater proportion of the trees in epidemic areas were susceptible than in endemic areas.

The real test for this method of analysis came when trees were inspected in late September, about two months after new attacks were initiated. This late date insured that trees had
TABLE 5


<table>
<thead>
<tr>
<th>Population type</th>
<th>Epidemic</th>
<th>Endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Elk</td>
<td>Terrace</td>
</tr>
<tr>
<td>Date of fungal inoculation</td>
<td>24 June</td>
<td>27 June</td>
</tr>
<tr>
<td>No. of trees inoculated</td>
<td>123</td>
<td>114</td>
</tr>
<tr>
<td>Date fungal readings taken</td>
<td>20 July</td>
<td>23 July</td>
</tr>
<tr>
<td>Approximate week of beetle flight</td>
<td>25 July</td>
<td>30 July</td>
</tr>
<tr>
<td>Date beetle Success measured</td>
<td>25 Sept.</td>
<td>27 Sept.</td>
</tr>
</tbody>
</table>
TABLE 6

Resistance ratings of lodgepole pine trees in July 1973 based on response to inoculation with blue-staining fungi.

<table>
<thead>
<tr>
<th>Population type</th>
<th>Epidemi</th>
<th>Endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Elk</td>
<td>Terrace</td>
</tr>
<tr>
<td>Number of trees</td>
<td>123</td>
<td>114</td>
</tr>
<tr>
<td>Proportion:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Resistant</td>
<td>.70</td>
<td>.55</td>
</tr>
<tr>
<td>Intermediate</td>
<td>.28</td>
<td>.38</td>
</tr>
<tr>
<td>Susceptible</td>
<td>.02</td>
<td>.07</td>
</tr>
</tbody>
</table>
had plenty of time to respond to the bark beetles and their blue-staining fungi. Since inoculated trees were numbered in June, the same trees were inspected in September. Bark beetle galleries were evaluated with the same method as described under "Determination of Tree Status". Galleries were exposed by peeling back the bark and success of tree resistance was determined.

This test showed that the resistance ratings given to trees by the fungal assay method appear to be completely independent of their actual ability to resist beetle attacks. Most trees that were attacked produced bark beetle offspring, whereas the fungal rating method predicted most of the trees would be resistant. Data presented in Table 7 show the number of trees in each study plot, cross-classified by fungal and beetle rating categories. The Elk trees rated potentially resistant in July illustrate the lack of relation between these categories. Of these 85 trees, 46 were attacked and produced bark beetles, 22 were attacked but did not, and 17 were not attacked. Chi-square tests of independence were done on the cross-classification tables for each area separately. These tests showed the beetle bioassay and fungal ratings were independent (probabilities in Table 7).

There are several possible reasons why my conclusions about this assay method differ from those of Shrimpton and Reid (1973). 1) My sample size for beetle-hit trees (168) was substantially larger than theirs (44). 2) My blue-staining
TABLE 7

Results of beetle bioassay of fungal ratings of tree potential to resist. 1973 data.
Trees are cross-classified by fungal rating and beetle rating.

| Area   | July fungal rating | September beetle bioassay ratings | Row sums | Sample size | No. of trees hit | $\chi^2$ | P |
|--------|--------------------|-----------------------------------|----------|-------------|------------------|---------|
|        |                    | S       | US1     | US2      | Not hit |         |         |         |
| ELK    | Susceptible        | 0       | 0       | 0       | 2        | 123    | 95      | 8.25  | .25 |
|        | Intermediate       | 19      | 1       | 7       | 9        | 36     | 85      |        |     |
|        | Resistant          | 46      | 8       | 14      | 17       |        |         |        |     |
| TERRACE| Susceptible        | 1       | 0       | 1       | 6        | 8      |         |        |     |
|        | Intermediate       | 9       | 0       | 3       | 30       | 42     | 23      | 7.95  | .25 |
|        | Resistant          | 5       | 2       | 2       | 55       |        | 64      |        |     |
| PARSON | Susceptible        | 1       | 0       | 0       | 1        | 2      |         |        |     |
|        | Intermediate       | 1       | 3       | 2       | 19       | 25     | 28      | 5.39  | .5  |
|        | Resistant          | 12      | 5       | 4       | 68       |        | 89      |        |     |
| LEAN   | Susceptible        | 0       | 0       | 0       | 5        | 5      |         |        |     |
|        | Intermediate       | 3       | 4       | 0       | 25       | 32     | 131     | 5.37  | .5  |
|        | Resistant          | 9       | 4       | 2       | 79       |        | 94      |        |     |

1 July fungal rating classes:
- Susc. = Likely to be overcome if attacked
- Inter. = Intermediate resistance
- Resis. = Not likely to be overcome if attacked

2 September beetle bioassay rating classes:
- S = Successfully produced broods
- US1 = Unsuccessful broods due to primary resinosis
- US2 = Unsuccessful broods due to secondary resinosis
- Not hit = No bark beetles attacked these trees
fungi may not have been of normal viability, though this is doubtful. 3) The unusually cool and wet weather in my study areas in the summer of 1973 may have slowed the growth of the blue-staining fungi or maintained high tree vigor for longer than normal. D.M. Shrimpton (pers. comm.) does not feel that these cool temperatures were a problem because the fungi actually prefer cooler temperatures than they experience in normal, hot summers. 4) My study trees were in different geographical locations from those of Shrimpton and Reid (1973) and may have had slightly different characteristics.

H. Summary

Average age and probability of succumbing to attacks were the only tree characteristics which were found to be consistently different between epidemic and endemic areas. Trees in outbreak areas were older than those in endemic regions, and within a given size and beetle attack density class, trees were more likely to be overcome and to successfully produce beetles in epidemic areas than endemic ones. This latter finding suggests either that epidemic trees have different resistance potentials from endemic trees or that epidemic beetles are more "potent" attackers than endemics. However, there were no consistent patterns between areas with respect to the spatial distribution of successfully attacked trees, average attack densities, or proportions of trees which successfully resisted mountain pine beetle. The
method of assaying tree resistance potential by using blue-staining fungi was found to be inaccurate when compared with subsequent beetle bioassays of the same trees. The rest of my work was concentrated on looking for differences in bark beetles occupying the different study areas.
VI. SAMPLES OF FIELD BEETLES

To study intrinsic differences in mountain pine beetle populations between epidemic and endemic areas, it was necessary to sample beetles from trees that were as similar as possible. This sampling was done in May of 1972 and 1973 when most insects were in third or fourth instar or pupae. Bark was removed from several attacked trees to determine whether numerous live larvae and pupae were present. If so, the tree was cut down and two 30-inch-long sections were removed from the base. Sample trees were selected to be highly productive in order to obtain a good yield of beetles in the lab. After logs were cut, both ends were sealed with latex paint to retain moisture. Logs were then placed in finely screened cages to await emergence of adult beetles. All four logs (five for Parson) for each area were stored together in the same cage. These cages were in a room with 24 hour fluorescent lighting, relative humidity of 60-70%, and temperatures ranging from 68 to 79°F (20-26°C). Adults were collected the day of emergence with an aspirator and were stored in jars with a lichen, Alectoria spp., for future size measurement or for use later in the day in dispersal or breeding experiments.

Beetle sizes were measured for two main reasons. Reid (1963) has shown that a female's size is a determinant of the
quantity of eggs produced. There are also indications that fat content, which is weakly related to body size, affects dispersal behavior (Atkins, 1966b, 1967, 1973a).

Dead insects were measured with an ocular micrometer on either 20 or 40 power. Insects were measured in random order with respect to sex, sampling location and emergence date. Both pronotum width and elytra length were measured. Three measurements were made on the first several hundred insects to obtain an estimate of error variance. Within-animal variance amounted to 0.001 mm for pronotum width (an insignificant amount compared with the average width of 1.5 to 2.5 mm) and hence it is ignored in all subsequent analyses. Females are larger than males, so all statistical analyses of size data are performed with sexes separated.

The first step was to compare insect sizes between study areas. Adult beetles emerged in the temporal patterns shown in Fig. 8. Some of the major deviations from a normal distribution are accounted for by the presence of holes in the lean cage discovered on July 2, 6, 16 and 17. Insect sizes varied with emergence date as shown in Figs. 9 and 10. Females predominated among the offspring with the sex ratio changing from 4:1 at the start of emergence to approximately 1:1 at the end. Pronotum width was highly correlated with elytra length ($r=.94$, $N=1350$, $P<.001$), so it will be the only size measure discussed. Beetle size was regressed against emergence date, number of beetles of both sexes emerging the
Emergence patterns of adult mountain pine beetles from logs sampled from trees in the field and stored in the laboratory. The two areas on the left are the epidemics and the two on the right are the endemics. N=total number of insects emerging from logs, by area.
FIGURE 9

Sizes of female mountain pine beetles in relation to emergence date. Vertical bars represent ± one standard error in size for beetles measured on that date. Data are from logs sampled in the four 1973 study areas. N = the number of emerging insects that were sized with a microscope.
FIGURE 10

Sizes of male mountain pine beetles in relation to emergence date. Vertical bars represent ± one standard error in size for beetles measured on that date. Data are from logs sampled in the four 1973 study areas. N = the number of emerging insects that were sized with a microscope.
same day in that cage, and cumulative number of beetles emerging to that date in the cage. Results in Table 8 show data for the only significant (P<.05) regression, which is size on emergence date (as measured in numbers of days from start of emergence in each cage). This regression establishes that in all areas but Terrace Creek, early emerging male and female beetles are in general larger than beetles of the same sex coming out later. These first-emerging beetles may have arisen from eggs laid the earliest in galleries, or from first attacking females. It is not possible to know which is the case because the period over which any tree is attacked by new females is not precisely known. My own observations in the field indicate that last attacks on any one tree occur 4-7 days after first attacks.

Analysis of variance showed no trend for endemic beetles to be larger than epidemics (P>.1). Comparisons of regressions of size on emergence date also showed no trend with respect to population type (ANOVA, P>.1).

The coefficient of variation of size (standard deviation/mean) was calculated for each group of beetles by emergence date and by sex. Since the exact distribution of the coefficient of variation is unknown (N. Gilbert, pers. comm.), I used non-parametric tests to analyze the data. A Wilcoxon matched-pairs, signed-rank test on these coefficients for corresponding emergence dates showed that females had significantly higher variability than males (N=31,
TABLE 8

Correlation and regression data for beetle size as a function of emergence date. Standard errors are in parentheses.

<table>
<thead>
<tr>
<th>Population type</th>
<th>Epidemic</th>
<th>Endemic</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Elk</td>
<td>Terrace</td>
</tr>
<tr>
<td>Males:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>N</td>
<td>226</td>
<td>56</td>
</tr>
<tr>
<td>r</td>
<td>.298</td>
<td>.018</td>
</tr>
<tr>
<td>p</td>
<td>&lt;.01</td>
<td>&gt;.1</td>
</tr>
<tr>
<td>r²</td>
<td>.089</td>
<td>.0003</td>
</tr>
<tr>
<td>Intercept</td>
<td>1.99 (.024)</td>
<td>1.88 (.06)</td>
</tr>
<tr>
<td>Slope</td>
<td>-.009 (.002)</td>
<td>-.0005 (.004)</td>
</tr>
<tr>
<td>p</td>
<td>&lt;.001</td>
<td>&gt;.1</td>
</tr>
<tr>
<td>Females:</td>
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<td></td>
</tr>
<tr>
<td>N</td>
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</tr>
<tr>
<td>r</td>
<td>.131</td>
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<td>p</td>
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<td>&gt;.1</td>
</tr>
<tr>
<td>r²</td>
<td>.017</td>
<td>.0002</td>
</tr>
<tr>
<td>Intercept</td>
<td>2.03 (.021)</td>
<td>2.01 (.03)</td>
</tr>
<tr>
<td>Slope</td>
<td>-.003 (.001)</td>
<td>-.0004 (.002)</td>
</tr>
<tr>
<td>p</td>
<td>&lt;.01</td>
<td>&gt;.5</td>
</tr>
</tbody>
</table>
P<.005). The ecological significance of greater variability in the female population is not clear. There could be selection for size variability in females, or the phenomenon could simply be due to selection against variability in males but not females. The possible advantages of this female size variation might lie in maintaining variability in dispersal patterns by pioneer females (to be discussed later), or ability to utilize trees with phloem of different thicknesses. Friedman's two-way analysis of variance showed that the coefficients of variation were not affected in either males or females by emergence date, place, or population type from which beetles were sampled (all P>.1).
Introduction

Intraspecific competition is an important determinant of reproductive success in several bark beetle species, including mountain pine beetle (Miller and Keen, 1960; Knight, 1961; McMullen and Atkins, 1961; Cole, 1962; Reid, 1963; and Berryman and Pienaar, 1973). Competition is directly related to attack density (McMullen and Atkins, 1961; Cole, 1962; Schmitz and Rudinsky, 1968). These workers found that as attack density on a tree increases, adult gallery length decreases along with the number of eggs per unit gallery length. Larval survival also drops off, probably due to limitations on the quality and quantity of food eaten.

An interesting tradeoff is brought out here. It is advantageous to attract numerous other bark beetles to the same tree in order to increase the probability of overcoming the tree's resistance mechanisms; this is the function of the pheromone systems. However, too many other bark beetles attacking the same tree results in decreased reproductive success. This is why some bark beetles that use pheromone attracting systems also have mechanisms which involve either other pheromones or tree chemicals to turn off tree attractiveness after a given number of attacks (Renwick and
Because of its effect on crowding and subsequent reproductive success, the precision of this switching-off mechanism may be critical in determining how low a bark beetle population can be maintained in endemic stands and how rapidly populations can build up in epidemic areas.

Attack densities might also affect offspring size in bark beetles through depletion of larval food supply at high densities. Such crowding effects are a general phenomenon for lepidopteran species (reviewed in Gruys, 1970) but are not well-studied in other groups.

Female parent characteristics, including size, are also thought to play a role in various reproductive measures including quantity (Engelmann, 1970; McGehey, 1971; Reid, 1963; Tantawy, 1961) and quality (Wellington, 1957, 1960, 1965) of eggs produced. Physiological rather than genetic mechanisms are responsible for some of these effects.

Finally, insect size has been shown to be a heritable characteristic in *Drosophila* (Reeve and Robertson, 1953; Tantawy, 1961); offspring of large maternal parents are larger than offspring of small females.

Methods

In this study of *D. ponderosae*, experiments were designed to look at the effects of both attack density and parental female size on reproductive success and offspring size. I
also wanted to see whether there were intrinsic differences between reproductive success or size heritability (either genetically or physiologically mediated) in beetles from the different sampling locations and population types. The mountain pine beetle can be bred in the laboratory in cut sections of lodgepole pine and offspring will begin to emerge approximately 7-8 weeks later. The experimental design is shown in Fig. 11. Tests on parental female size effects were made only with beetles emerging from the population sampled at Lean Creek. Sized females were sorted into large and small types (exact size distributions are given in Table 9). Females from each size group were then bred at both high (18 pairs/sq ft) and low (2 pairs/sq ft) densities on different logs. There were two replicate logs for each experimental group. Similar experiments were done with beetles emerging from logs sampled from each of the other three areas, but instead of using large and small parental females, intermediate sized ones were used (Table 9).

Logs for breeding experiments were cut on 5 July 1973 from healthy, unattacked lodgepole pine in the Smith Creek valley, southeast of Princeton, B.C. Twenty 30-inch-long sections averaging 8.5 inches in diameter were removed from a total of five different trees. After two days of drying to prevent molding, log ends were painted with latex paint to retain the remaining moisture.

Parental insects were collected on the evening of 9 July
FIGURE 11

The experimental design for 1973 breeding experiments. These experiments were designed to test the effects of attack density and parent female size on reproductive success and offspring size. Log numbers given at bottom are the replicate log numbers which are referred to in the text. A total of 200 parent females were used in this experiment.

High attack density = 18 pairs/sq ft
Low attack density = 2 pairs/sq ft
For each of the 3 other study areas

Area
LEAN

Emerging Population

Large
Small

high attack density
N=2

low attack density
N=2

high attack density
N=2

low attack density
N=2

Average

high attack density
N=2

low attack density
N=2

high attack density
N=2

low attack density
N=2

Log #'s: 1,7 2,8 3,5 4,6

9,11,13 10,12,15 14,17,18 16,19,20
TABLE 9

Size distributions of female parents used in breeding experiments. Pronotum widths are in mm.

Average sized females:

<table>
<thead>
<tr>
<th>Attack Density = 2/sq ft</th>
<th>Attack Density = 18/sq ft</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>Size</td>
</tr>
<tr>
<td>2</td>
<td>1.93</td>
</tr>
<tr>
<td>3</td>
<td>2.13</td>
</tr>
<tr>
<td>4</td>
<td>1.87</td>
</tr>
</tbody>
</table>

Large sized females:

<table>
<thead>
<tr>
<th>Attack Density = 2/sq ft</th>
<th>Attack Density = 18/sq ft</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>Size</td>
</tr>
<tr>
<td>2</td>
<td>2.13</td>
</tr>
<tr>
<td>(Log # 1)</td>
<td>3</td>
</tr>
<tr>
<td>13</td>
<td>2.13</td>
</tr>
<tr>
<td>(Log # 7)</td>
<td>3</td>
</tr>
<tr>
<td>12</td>
<td>2.13</td>
</tr>
<tr>
<td>3</td>
<td>2.00</td>
</tr>
</tbody>
</table>

Small sized females:

<table>
<thead>
<tr>
<th>Attack Density = 2/sq ft</th>
<th>Attack Density = 18/sq ft</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number</td>
<td>Size</td>
</tr>
<tr>
<td>2</td>
<td>1.73</td>
</tr>
<tr>
<td>3</td>
<td>1.73</td>
</tr>
<tr>
<td>1</td>
<td>1.60</td>
</tr>
</tbody>
</table>
(middle of the emergence period) and sized immediately with a binocular dissecting microscope equipped with an ocular micrometer. Sexes were separated by holding insects loosely between the fingers and listening for male stridulation, a method used for another scolytid by Chapman (1955). Iterative sampling experiments with several small groups of beetles and subsequent microscopic examination for the male stridulating mechanism (Lyon, 1958) confirmed that this auditory method was a reliable way of sexing mountain pine beetle.

Actual breedings were begun 10 July after insects had been stored overnight in jars with some lichen, Alectoria spp., to prevent beetles from walking over one another and losing their antennae and legs. Atkins' (1973b) technique was used for starting breedings. A 6 mm hole was drilled in the host log through the outer bark and to the depth of the phloem. A sized female was then put into the hole and it was plugged with an empty half of a #1 gelatin capsule. Twenty-four hours later, each hole was checked for signs of boring dust and if any was present, the capsule was removed, a randomly sized male from the corresponding geographic location was added, and the capsule was replaced.

Some females did not immediately start digging galleries, either because the wood was not suitable in their particular location, or for some physiological reason. Those which had not dug any gallery after one day were replaced by a female of the same size, emergence date and sampling location. Of the
200 females started on 10 July, 31 did not start digging that day. The replacement procedure was followed and 9 females still had not taken by the 12th. However, all females had males added to their galleries by the 14th save one, which finally took on the 15th (on Log 10).

Only one square foot was used on each log for laying out the entrance holes. The spatial arrangement of attack holes was as shown in Fig. 12. The extreme values of 2 and 18 entrances per square foot were chosen because they were at the extremes of observed field attack density distributions (Fig. 4), and they were thought to be most likely to produce differences in offspring size or reproductive success.

After initiation of gallery construction and addition of males, all logs were put inside 30-inch-tall plastic barrels with screened tops and with a glass Mason jar mounted in a hole cut in the barrel side. These barrels were stored in a room with 24 hour fluorescent lighting from above, 60-70% relative humidity and a constant temperature of 70° F (21° C). When a barrel top was loosely covered with black plastic, photopositive emergent beetles moved into the jar, since this was the only source of light. Emergent insects were collected daily from these jars, counted, sexed, and stored in the same way as beetles from field populations.
Spatial arrangement of attack holes which were drilled for females used in the breeding experiments. All of these holes were used for the attack density of 18/sq ft and the two circled holes were used for the attack density of 2/sq ft. The relative positions of some adult galleries are also shown.
Results

A. Attack Density Effect On Reproductive Success

The effects of attack density on reproductive success are shown in Table 10. When all twenty experimental logs are considered, there are significant differences in various reproductive measures between attack density treatments. The number of beetles emerging per female parent was significantly higher at low attack density than at high attack density (44 vs. 12). More total offspring emerged per log at high attack densities, but it was only 2.46 times as many as at the low attack densities, not 9 times as many as expected if there were no attack density effect.

When experimental logs with large and small female parents are removed from this analysis leaving only logs with average sized parents (bottom half Table 10), the same results are obtained except that the number of beetles emerging per entrance is not significantly different between density treatments. The same trend is present as before, but between-log variance is too great for the differences to be significant.

These attack density effects agree with the findings of Cole (1962) and Reid (1963) in showing that more crowded conditions result in fewer offspring per parent. However, my
TABLE 10

Attack density effects on reproductive success of mountain pine beetle. N gives the number of replicate logs in the treatment class. Means are given and standard errors are in parentheses.

Data from all 20 logs:

<table>
<thead>
<tr>
<th>Parental attack density</th>
<th>Number exit holes per entrance</th>
<th>Number beetles emerging per entrance</th>
<th>Total number offspring emerging</th>
</tr>
</thead>
<tbody>
<tr>
<td>High N=10</td>
<td>10.09 (0.86)</td>
<td>12.17 (1.4)</td>
<td>220.8 (24.4)</td>
</tr>
<tr>
<td>Low N=10</td>
<td>50.65 (10.8)</td>
<td>44.15 (12.5)</td>
<td>89.6 (24.8)</td>
</tr>
<tr>
<td>T-statistic</td>
<td>3.76</td>
<td>2.53</td>
<td>3.78</td>
</tr>
<tr>
<td>P</td>
<td>&lt;.01</td>
<td>=.02</td>
<td>&lt;.01</td>
</tr>
</tbody>
</table>

Data for logs #9-20 only (no large or small female parents):

<table>
<thead>
<tr>
<th>Parental attack density</th>
<th>Number exit holes per entrance</th>
<th>Number beetles emerging per entrance</th>
<th>Total number offspring emerging</th>
</tr>
</thead>
<tbody>
<tr>
<td>High N=6</td>
<td>10.96 (1.07)</td>
<td>13.23 (1.7)</td>
<td>238.2 (31.3)</td>
</tr>
<tr>
<td>Low N=6</td>
<td>56.92 (16.1)</td>
<td>48.92 (19.9)</td>
<td>100.0 (39.1)</td>
</tr>
<tr>
<td>T-statistic</td>
<td>2.85</td>
<td>1.78</td>
<td>2.76</td>
</tr>
<tr>
<td>P</td>
<td>&lt;.02</td>
<td>&gt;.1</td>
<td>&lt;.02</td>
</tr>
</tbody>
</table>
offspring per parent ratios are much larger than Cole's (at an attack density of 18/sq ft he got 0.3 and I got 6.08), probably because Cole used only one-foot-long logs for breeding substrates. I used logs two and one half feet long and this reduced the crowding of galleries; Reid (1962b) has noted that adult females in the laboratory will turn around and start digging downward upon reaching the end of the log. Therefore, Cole was probably working with much higher effective densities than indicated by his number of entrances per sq ft. T-tests within attack density treatments showed that there was no effect on reproductive success of location or population type from which parents were sampled (P>.1).

Number of exit holes per entrance is a useful measure for field determination of emergent beetle populations (r=.89, P<.01). However, a correction function is needed because, as Reid (1963) and my own data in Fig. 13 have shown, several beetles tend to come from each emergence hole under high attack density conditions. Also, at low densities, there occasionally are fewer emergent beetles than exit holes (Figure 13). This is probably attributable to the observed behavior of some beetles cutting emergence holes and then not using them (Reid, 1963).

Other data which are relevant here but which come from trees sampled in the field in 1972 and 1973, rather than breeding experiments, are illustrated in Fig. 14. Trees sampled in different study areas as sources of beetle
FIGURE 13

The relation between numbers of beetles emerging per sq ft and numbers of exit holes counted per sq ft in the same log. A 1:1 ratio is indicated by the dashed line; points falling above this line indicate that there were more beetles emerging than the number of exit holes. Each point represents one log in the 1973 breeding experiments.
1973 BREEDING EXPERIMENTS
LOGS CLASSED BY ATTACK DENSITY
\(\triangle\) = HIGH DENSITY, + = LOW DENSITY

# BEETLES EMERGING/SQ. FT.

# EXIT HOLES/SQ. FT.
FIGURE 14

Data from logs sampled in the field showing the relation between attack density and resulting numbers of emergence holes per attack. Data are split into those trees sampled in 1972 and those in 1973.
DATA FOR 1972 ONLY

\[ R = -0.618 \]
\[ P < 0.01 \]

DATA FOR 1973 ONLY

\[ R = -0.763 \]
\[ P < 0.01 \]
populations show the effect of increasing attack density on the number of emergence holes per entrance. Both regressions and correlations are significant with $P < .01$ (Table 11). These field data are consistent with the results of my breeding experiments in showing that higher attack densities result in fewer offspring per adult. No differences were found between epidemic and endemic samples in the numbers of emergence holes per attack ($t$-test, $P > .1$).

B. Attack Density Effect On Offspring Size

A two-level nested analysis of variance on the data from all 20 logs showed that attack density had a significant effect on offspring size ($P < .001$) but the between-log effect, though always smaller, was also significant ($P < .001$). This was true for both males and females (Table 12). In other words, the effect of differences between logs on offspring size is about the same as the effect of attack density. Looking at the size distributions (Figs. 15 and 16), the attack density effects are present (higher attack densities producing smaller offspring) and statistically significant for females only ($X^2$, $P < .03$). Fig. 15 illustrates offspring sizes for all 20 experimental logs while Fig. 16 shows only offspring from logs 9-20 (average sized parent females).

C. Parental Female Size Effect On Reproductive Success

Table 13 shows that large females tend to produce more
TABLE 11

The effect of attack density on reproductive success as measured by number of emergence holes per attack. Data come from trees which were sampled in 1972 and 1973 as sources of beetle populations for laboratory studies. Regressions are illustrated in Figure 14. Standard errors are in parentheses.

1972 data:

N = 21

Correlation:
\[ r = 0.618 \quad P < .01 \quad \text{that} \quad r = 0.0 \]
\[ r^2 = 0.38 \]

Regression:
\[ \text{Y-intercept} \quad a = 14.95(2.05) \]
\[ \text{Slope} \quad b = -1.449(0.38) \quad P < .005 \quad \text{that} \quad b = 0.0 \]

1973 data:

N = 17

Correlation:
\[ r = 0.763 \quad P < .01 \quad \text{that} \quad r = 0.0 \]
\[ r^2 = 0.58 \]

Regression:
\[ \text{Y-intercept} \quad a = 13.12(1.54) \]
\[ \text{Slope} \quad b = -0.827(0.16) \quad P < .001 \quad \text{that} \quad b = 0.0 \]
Results of a two-level nested analysis of variance on data from all 20 experimental breeding logs. The dependent variable is beetle pronotum width and the independent variables are attack density and replicate log number.

### Males:

<table>
<thead>
<tr>
<th>Term</th>
<th>D.F.</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attack Density</td>
<td>1</td>
<td>0.01729</td>
<td>13.17</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Log number</td>
<td>18</td>
<td>0.00987</td>
<td>7.51</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Remainder</td>
<td>494</td>
<td>0.00131</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Comparison of Attack Density mean square with Log # mean square:

\[ F = 1.753, \text{ } P > .2 \]

### Females:

<table>
<thead>
<tr>
<th>Term</th>
<th>D.F.</th>
<th>Mean Square</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attack Density</td>
<td>1</td>
<td>0.020</td>
<td>12.92</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Log number</td>
<td>18</td>
<td>0.00929</td>
<td>5.98</td>
<td>&lt;.001</td>
</tr>
<tr>
<td>Remainder</td>
<td>817</td>
<td>0.00155</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Comparison of Attack Density mean square with Log # mean square:

\[ F = 2.16, \text{ } P > .1 \]
Size distributions of offspring classed by sex and attack density at which parents were bred. Chi-square values were found using frequency data. Data in this figure differ from those in Figure 16 in that offspring from all 20 breeding logs are illustrated, including those from logs with large and small female parents.

Sample sizes are as follows:

- Females from high attack density = 582
- Females from low attack density = 255
- Males from high attack density = 317
- Males from low attack density = 197
SIZES OF OFFSPRING BY DENSITY TYPE
HIGH——, LOW——
N=837 FEMALES

$X^2=31.3$
P < .005

SIZES OF OFFSPRING BY DENSITY TYPE
HIGH——, LOW——
N=514 MALES

$X^2=25.6$
P < .03
FIGURE 16

Size distributions of offspring classed by sex and attack density at which parents were bred. Chi-square values were found using frequency data. Data in this figure differ from those in Figure 15 in that only offspring from the 12 logs with average sized parent females are used.

Sample sizes are as follows:

Females from high attack density = 362
Females from low attack density = 163
Males from high attack density = 214
Males from low attack density = 134
SIZES OF OFFSPRING BY DENSITY TYPE
HIGH—— — LOW——
N=525 FEMALES

X²=26.05
P =0.026

SIZES OF OFFSPRING BY DENSITY TYPE
HIGH—— — LOW——
N=348 MALES

X²=20.9
P =0.11
TABLE 13

Effects of female parent size on reproductive success. N gives the number of replicate logs in the treatment class. Means are given and standard errors are in parentheses.

Both attack densities lumped:

<table>
<thead>
<tr>
<th>Parental female size</th>
<th>Number exit holes per entrance</th>
<th>Number beetles emerging per entrance</th>
<th>Total number offspring emerging</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large N=4</td>
<td>33.4 (16.2)</td>
<td>32.2 (14.1)</td>
<td>171.3 (52.4)</td>
</tr>
<tr>
<td>Small N=4</td>
<td>16.6 (6.2)</td>
<td>15.4 (5.8)</td>
<td>97.5 (32.4)</td>
</tr>
<tr>
<td>T-statistic P</td>
<td>0.97</td>
<td>1.10</td>
<td>1.20</td>
</tr>
<tr>
<td></td>
<td>&gt;0.2</td>
<td>&gt;0.2</td>
<td>&gt;0.2</td>
</tr>
</tbody>
</table>
offspring than small ones. However, the differences cannot be shown statistically because of the between-log variance. This is still true even when these data are broken down by attack density classes (Table 14). Reid (1962b) found that larger female mountain pine beetles laid more eggs per day than smaller females. Unfortunately, his data do not extend through to emerging adults. The presence of larger nutritional stores for egg production is probably the reason why larger females produce more offspring.

D. Parental Female Size Effects On Offspring Size

My experiments showed that there was a significant relation between offspring size and parental female size, but only for female offspring of parents bred at high attack density ($X^2$, $P<.01$). Large females tended to produce larger female offspring than small females. Other comparisons of offspring distributions were not significant ($X^2$, $P>.1$). Also, offspring-on-parent regressions, a standard method of measuring heritability (Falconer, 1960), did not reveal significant relationships except perhaps for female offspring (Table 15). Lack of a significant regression is not surprising in view of the experimental design: two non-overlapping distributions of sizes of female parents had to be used (Table 9) and for any one experimental log it was impossible to know which offspring came from which females within the distributions.
Table 14

Table 13 broken down by attack densities. Effect of female parent size on reproductive success. Means are given and standard errors are in parentheses.

**High attack density only:**

<table>
<thead>
<tr>
<th>Parental female size</th>
<th>Number exit holes per entrance</th>
<th>Number beetles emerging per entrance</th>
<th>Total number offspring emerging</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large N=2</td>
<td>10.8 (1.3)</td>
<td>13.1 (4.2)</td>
<td>240.0 (72.0)</td>
</tr>
<tr>
<td>Small N=2</td>
<td>6.74 (0.15)</td>
<td>8.1 (1.0)</td>
<td>149.5 (22.5)</td>
</tr>
<tr>
<td>T-statistic</td>
<td>3.01</td>
<td>1.15</td>
<td>1.20</td>
</tr>
<tr>
<td>P</td>
<td>&gt;.2</td>
<td>&gt;.4</td>
<td>&gt;.2</td>
</tr>
</tbody>
</table>

**Low attack density only:**

<table>
<thead>
<tr>
<th>Parental female size</th>
<th>Number exit holes per entrance</th>
<th>Number beetles emerging per entrance</th>
<th>Total number offspring emerging</th>
</tr>
</thead>
<tbody>
<tr>
<td>Large N=2</td>
<td>56.0 (23.5)</td>
<td>51.2 (21.2)</td>
<td>102.5 (42.5)</td>
</tr>
<tr>
<td>Small N=2</td>
<td>26.5 (6.0)</td>
<td>22.8 (9.7)</td>
<td>45.5 (19.5)</td>
</tr>
<tr>
<td>T-statistic</td>
<td>1.22</td>
<td>1.22</td>
<td>1.22</td>
</tr>
<tr>
<td>P</td>
<td>&gt;.2</td>
<td>&gt;.2</td>
<td>&gt;.2</td>
</tr>
</tbody>
</table>
TABLE 15
Relation between offspring size and female parent size using offspring on parent regressions. Standard errors are in parentheses.

**Female offspring:**

N = 312  
$r = 0.103$  \( P = .06 \) that $r = 0.0$  
$r^2 = 0.01$  
Regression:  
Y-intercept $a = 0.733 (0.475)$  
slope $b = 0.432 (0.237)$  \( P = .072 \) that $b = 0.0$

**Male offspring:**

N = 166  
No significant correlation or regression \( (P > .1) \)
However, when we look at the size distributions of offspring, an interesting phenomenon appears. Fig. 17 shows the data for all eight logs involved in the parental size experiments, regardless of attack density. Offspring of small female parents appear to have a bimodal size distribution whereas offspring of large females tend to have the expected normal distribution. This bimodality seems to be much weaker in male offspring than females. It is very difficult to show statistically that a distribution is bimodal; the best one can do is to show that a distribution is more platykurtic (flattened) than a normal distribution, and such information is not very useful in the present context.

When the data in Fig. 17 are broken down into the two attack density treatments, another relationship appears. Female offspring (Fig. 18) of small maternal parents still show a stronger bimodality than offspring of large females, regardless of attack density, but male offspring (Fig. 19) show weak bimodality regardless of parental female size. Chi-square values shown in Figures 17-19 are the results of comparing the size distributions of offspring of large females with those of small females.

There are several possible causes of this bimodality in offspring size. First, there may be an emergence date effect on size, as with field populations, and offspring emergence dates may be linked to parent female size. Figs. 20-23 show
FIGURE 17

Size distributions of offspring classed by sex and size of female parents. Both attack densities are lumped. Chi-square values were found using frequency data.

Sample sizes are as follows:

Females from large parents = 187
Females from small parents = 125
Males from large parents = 108
Males from small parents = 58
OFFSPRING SIZES CLASSED BY PARENT FEMALE SIZE
BOTH ATTACK DENSITIES LUMPED
LARGE——, SMALL——
N=312 FEMALES

$X^2 = 28.0$
$P < .01$

OFFSPRING PRONOTUM WIDTH (MM)

OFFSPRING SIZES CLASSED BY PARENT FEMALE SIZE
BOTH ATTACK DENSITIES LUMPED
LARGE——, SMALL——
N=166 MALES

$X^2 = 11.9$
$P > .01$

OFFSPRING PRONOTUM WIDTH (MM)
Size distributions of female offspring classed by size of female parent and attack density at which parents were bred. Top graph is high attack density and bottom graph is low attack density. Chi-square values were found using frequency data.

Sample sizes were as follows:

Females from high attack density and large parents = 131
Females from high attack density and small parents = 89
Females from low attack density and large parents = 56
Females from low attack density and small parents = 36
OFFSPRING SIZES CLASSED BY PARENT FEMALE SIZE
HIGH ATTACK DENSITY
LARGE --- SMALL ---
N = 220 FEMALES

$X^2 = 27.6$
$P < .01$

OFFSPRING PRONOTUM WIDTH (MM)

OFFSPRING SIZES CLASSED BY PARENT FEMALE SIZE
LOW ATTACK DENSITY
LARGE --- SMALL ---
N = 92 FEMALES

$X^2 = 17.1$
$P > .01$

OFFSPRING PRONOTUM WIDTH (MM)
Size distributions of male offspring classed by size of female parent and attack density at which parents were bred. Top graph is high attack density and bottom graph is low attack density. Chi-square values were found using frequency data.

Sample sizes were as follows:

Males from high attack density and large parents = 71
Males from high attack density and small parents = 32
Males from low attack density and large parents = 37
Males from low attack density and small parents = 26
OFFSPRING SIZES CLASSED BY PARENT FEMALE SIZE
HIGH ATTACK DENSITY
LARGE——, SMALL-----
N=103 MALES

\[ \chi^2 = 14.1 \]
\[ P > 0.1 \]

OFFSPRING PRONOTUM WIDTH (MM)

OFFSPRING SIZES CLASSED BY PARENT FEMALE SIZE
LOW ATTACK DENSITY
LARGE——, SMALL-----
N=63 MALES

\[ \chi^2 = 12.2 \]
\[ P > 0.1 \]

OFFSPRING PRONOTUM WIDTH (MM)
FIGURE 20

Sizes of female mountain pine beetles in relation to emergence date. Vertical bars represent ± one standard error in size for beetles measured on that date. Data are from breeding logs 1-4.
FIGURE 21

Sizes of female mountain pine beetles in relation to emergence date. Vertical bars represent ± one standard error in size for beetles measured on that date. Data are from breeding logs 5-8.
FIGURE 22

Sizes of male mountain pine beetles in relation to emergence date. Vertical bars represent ± one standard error in size for beetles measured on that date. Data are from breeding logs 1-4.
FIGURE 23

Sizes of female mountain pine beetles in relation to emergence date. Vertical bars represent ± one standard error in size for beetles measured on that date. Data are from breeding logs 5-8.
offspring sizes by emergence date. Lack of significant correlations or regressions for these data ($P > .1$) indicates that this effect is not the cause of bimodality.

Second, the bimodality may have been produced by differences in food quality between replicate logs. This appears to be the case for both male and female offspring of small parentage bred at low density (logs 4 & 6). Table 16 shows that by comparing offspring size distributions between replicate logs, these two are the only cases in which offspring from replicate logs show different distributions. Thus, nutritional differences between logs might account for offspring bimodality at low attack density, but they do not account for the high attack density situation where there are, incidentally, many more data points.

The third possible reason for bimodality is suggested by the high attack density cases. Offspring on the large end of the bimodal distribution may have arisen from eggs laid on the sides of parental galleries where larvae were able to move away from competing galleries. It is clear (Fig. 12) that at high attack densities, only larvae on the outside edges of the perimeter adult galleries can extend their galleries uninhibited. Gallery overlap data were impossible to collect in my high attack density logs because, after bark removal, there was only a maze of boring dust and criss-crossing galleries. However, if this "position" effect were an important determinant of adult size, we would expect most
TABLE 16

Comparison of size distributions of offspring between replicate logs in the various treatment classes. A significant $X^2$ value indicates that the two replicate logs differ in the sizes of offspring that they produced.

Female offspring:

<table>
<thead>
<tr>
<th>Treatment classes</th>
<th>$X^2$</th>
<th>d.f.</th>
<th>P</th>
<th>Log #'s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attack Density</td>
<td>Parent Size</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>Small</td>
<td>10.90</td>
<td>10</td>
<td>&gt;.1</td>
</tr>
<tr>
<td>High</td>
<td>Large</td>
<td>9.35</td>
<td>12</td>
<td>&gt;.5</td>
</tr>
<tr>
<td>Low</td>
<td>Small</td>
<td>24.77</td>
<td>11</td>
<td>&lt;.01</td>
</tr>
<tr>
<td>Low</td>
<td>Large</td>
<td>9.75</td>
<td>9</td>
<td>&gt;.1</td>
</tr>
</tbody>
</table>

Male offspring:

<table>
<thead>
<tr>
<th>Treatment classes</th>
<th>$X^2$</th>
<th>d.f.</th>
<th>P</th>
<th>Log #'s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Attack Density</td>
<td>Parent Size</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>Small</td>
<td>5.28</td>
<td>8</td>
<td>&gt;.5</td>
</tr>
<tr>
<td>High</td>
<td>Large</td>
<td>7.35</td>
<td>11</td>
<td>&gt;.5</td>
</tr>
<tr>
<td>Low</td>
<td>Small</td>
<td>19.47</td>
<td>5</td>
<td>&lt;.005</td>
</tr>
<tr>
<td>Low</td>
<td>Large</td>
<td>11.14</td>
<td>9</td>
<td>&gt;.1</td>
</tr>
</tbody>
</table>
adults in the bimodal distribution to be on the small end. Fig. 18 shows that just the opposite is the case; most are on the large end.

Further experimentation is needed to clearly demonstrate stronger bimodality in sizes of offspring of small females. If my observations are supported, one interesting explanation may be that small female parents (for example, from crowded conditions) may attempt to maintain some population variability in size, which in turn may be related to dispersal behavior. Some females may produce all the small offspring, or there may be a bimodal size distribution among offspring of any one female.

E. Summary

The breeding experiments have shown that: a) the number of offspring per female emerging from a log decreases with increasing attack density, b) small females tend to produce offspring with size distributions that are more strongly bimodal than offspring of large females, and c) female offspring of large females bred at high attack density tend to be larger than those of small females bred at the same density. Trends which are suggested from the data but which are not consistently statistically significant are: a) smaller offspring may result from higher attack densities and b) lower reproductive output may be a characteristic of smaller parent females. However, qualitative differences between
Experimental logs make the experiments difficult to interpret.
VIII. DISPERSAL

A. Introduction

Previous sections dealt with differences in tree characteristics and beetle reproductive and size measures between epidemic and endemic areas. This section compares dispersal behavior of beetles from each of the four sample areas and from the two experimental attack densities. I also compare variations in dispersal within each of these populations.

Atkins' studies with the Douglas-fir bark beetle (1966b, 1967, 1973a,b) show that an insect's fat content, which is weakly related to body size, is an important determinant of dispersal behavior. Studies on other insects also indicate that body size affects dispersal ability (Rose, 1972). My dispersal studies were designed, in part, to see whether the observed variability in sizes of D. ponderosae (see earlier sections) could be related to variability in dispersal capability.

I asked the following questions concerning mountain pine beetle dispersal: 1) What factors intrinsic to the beetles affect their dispersal behavior? 2) Is there any variation in dispersal characteristics within a group of beetles? 3) If
so, are there differences in the distribution of these characteristics between epidemic and endemic beetles? 4) Can factors affecting the observed differences between individuals of the field populations be determined through breeding experiments? 5) Do "pioneer" beetles exist, i.e., are early emerging beetles different in dispersal characteristics from the rest of the population?

The dispersal character studied was the response of flown individuals to host tree chemicals in the presence of light. This measure was chosen for two reasons. First, ample evidence exists for D. ponderosae concerning the use of tree chemicals in host selection. Pheromones appear to be only a second stage mechanism that is used by the bulk of dispersing individuals for finding the suitable hosts already detected by other dispersers. Therefore, response to host chemicals was felt to be a better measure of how populations would distribute themselves in space than responses to pheromones. Second, measurement of the flight potential of individuals (based on fat reserves or flight mill tests) may not be related to how far bark beetles will actually fly when in the presence of host stimuli. Thus, behaviors of pre-flown beetles were observed in the presence of tree chemicals.

The sequence of events in bark beetle dispersal are exemplified by the well-studied ambrosia beetle, Trypodendron lineatum, which has many dispersal characteristics of the mountain pine beetle. Details of these behaviors are
described by Chapman (1962), Francia and Graham (1966), Graham (1959, 1961, 1968), and Werner and Graham (1957). Dispersing T. lineatum leave overwintering sites sometime in late spring or early summer, and are initially photopositive (Daterman, Rudinsky and Nagel, 1965). They fly up toward the forest canopy but probably do not get above it. Early in the flight, beetles are not responsive to appropriate host tree chemicals even if the chemicals are present. However, after flying for some time, insects respond to such chemicals by becoming positively anemotactic and by flying upwind until the source is found. This threshold flight time required before the beetle changes to positive anemotaxis varies between individuals. Chemical concentration has also been found to affect beetle response (Graham, 1968). The mechanism which releases the beetles from photopositive domination of this anemotaxis appears to be increasing pressure from the formation of a gas bubble in the ventriculus during flight (Graham, 1961). This gas bubble mechanism, which was first noted by Chapman (1958), is similar to the one described by Wellington (1948) in spruce budworm larvae.

Mountain pine beetle appears to have the same dispersal behaviors, but the mechanism for initiating response to tree chemicals after some flight is unknown. Atkins (1961, 1966b) and Nijholt (1965, 1967, 1969) suggest for other bark beetle species that energetic limitations may be responsible. Therefore, it is important to know not only how far
individuals will fly given the chance, but also how far they need to fly before responding to tree chemicals. The flight threshold phenomenon is important in *D. ponderosae* even for the segment of the population that relies mainly upon pheromones for tree location, because it has been shown for this beetle that pheromones are attractive only in the presence of a tree chemical, alpha-pinene (see introduction).

The flight threshold phenomenon and its variation between individuals allows considerable flexibility in the distance insects will fly before initially attacking trees. Variability in flight distance within a population is significant, because various spatial distributions of susceptible trees will necessitate different flight patterns in order to make abundant insect colonization possible.

Several factors can cause variation in distance flown between individuals. First, the temperature threshold for flight may vary, releasing beetles sooner or later in the season than normal, when trees would be in different stages of attractiveness and susceptibility. This difference in spatial distribution of suitable hosts would cause a change in the distances flown by beetles before attacking. Second, the gas bubble pressure or flight time that is required to release photopositive domination of anemotaxis may vary. Third, the concentration of host chemicals needed for response, once the beetle is no longer photopositive, may vary.
One more justifying statement needs to be made concerning the active dispersal behaviors which I studied. It might be argued that passive dispersal by wind (as opposed to active dispersal by flight), is the most important dispersal stage. However, I would argue that since the beetles presently have complex active orientation mechanisms, the active dispersal stage is of evolutionary significance, even though only a small proportion of a beetle's flight time may be spent in active movement. The beetles probably fly actively out of the wind current when appropriate stimuli are sensed, much like aphids do (Kennedy and Booth, 1963).

Seven factors were studied to see what effects they had on dispersal characteristics of mountain pine beetle. These were: 1) sex, 2) geographic sampling location, 3) population type from which they were sampled (epidemic or endemic), 4) body size, 5) emergence date, 6) attack density of parents, and 7) flight history.

B. Methods

Beetle responses to tree chemicals were observed in a chamber (Fig. 24) similar to that described by Moeck (1970a) and Syed (1972), in a darkened controlled environment room kept at 70°F (21°C) and 60% R.H. The chamber frame had a hinged glass top over a test arena. A narrow beam of heat-filtered light was directed across the arena by a Nikon microscope light with a 6V tungsten bulb (#6V5ATB1) connected through a
FIGURE 24

The testing chamber for measuring the response of mountain pine beetle to chemical extracts from lodgepole pine. See text for full description.
To vacuum pump

Foam rubber

Light beam

Chemical injection tube

Hinged glass top
voltage regulator (to prevent intensity fluctuations) and a 7.5 amp Powerstat transformer set on 80 volts. Air was drawn across the field from right to left by a pump located outside the closed-environment room. Air speed in the test chamber was approximately 4 feet per second. The width of the chemical-bearing airstream in the chamber was determined by putting dry ice in hot water inside the chemical injection tube. The resulting thick, white clouds permitted easy tracing of the course of the airstream.

Because of logistic problems with measuring responses of flying beetles, all response tests were made using pedestrian beetles which had been pre-flown (to be described). Other workers have shown that behavior of pedestrian beetles in the laboratory is qualitatively the same as that of flying beetles in the field (e.g. Moeck, 1970b).

Experimental insects were put into the test chamber at point A in Fig. 24 and were allowed to wander freely. Most insects moved toward the light and encountered the air stream. At this point, they had to make a choice between the light or the airstream. Their resulting behaviors were recorded as one of five categories: 1) no turning or hesitation; kept on moving toward light, 2) a brief pause in movement but no turning; ended up at light, 3) turned slightly (<45° from initial direction of movement) toward chemical source but continued on to light, 4) oriented toward chemical source (turned >45°), 5) turned toward chemical source and walked
upstream. These responses were assigned the values 1 to 5, respectively. Fig. 25 shows representative responses for some of these categories. Each insect was tested six consecutive times, three times with the control or blank air stream (no tree chemicals in injection tube) and then three times with tree chemicals present.

All tree chemicals used in my 1973 experiments were taken from a 95-year-old lodgepole pine tree of 9.75 inch diameter cut at the epidemic Terrace Creek study area on 1 June, 1973. This tree was untouched by mountain pine beetle but was on the edge of a group of trees which were infested. Thus, it came as close as possible to what I could determine was a susceptible tree. A 30 inch long section was removed, transported back to Vancouver within 28 hours, and stored in a cold room at 1° C. Extracts were taken from this log for ten days starting 11 June with a technique described by Syed (1972). A 4 inch square piece of bark was stripped off the source log and immediately placed in a closed chamber. The only air outlet from this chamber ran through a Pyrex U-tube immersed in liquid nitrogen. The air was drawn from the chamber containing the bark sample and all volatiles passed into the U-tube and were solidified on its sides. The low temperature of liquid nitrogen (-196 to -210° C) insured that most volatiles were trapped. After two hours of pumping, the solidified bark extract was transferred to a flint-glass vial and stored at -10° C until needed. Tree chemicals were added
Examples of the paths followed by three typical beetles in runs through the test chamber in the presence of lodgepole pine extract. Numbers represent the different behavior classes which were assigned to these beetles (see text).
to the injection tube by dropping 0.05 ml of bark extract onto pure cellulose filter paper inside a small tin foil cup. The extract was added to the filter paper outside the controlled environment room to avoid contamination of the air in the room. Both tin foil and dry filter paper were present during blank airstream trials. In all experiments, the concentration of tree extracts was kept constant. No attempt was made to test the effect of changing host chemical concentration on beetle behavior.

Experimental insects were derived from two sources: field samples from the four study areas and offspring from the breeding experiments. All groups were tested in the same way. Insects were collected the day they emerged from their host logs and were immediately sexed, roughly sized by eye, and split up into three flight time groups. Each flight time group had the full range of individual sizes present that day. Each insect was then subjected to its pre-selected flight regime of 0, 15, or 30 minutes, with some variation (Table 17).

Insects were flown prior to tests in the behavioral chamber by tethering them by the dorsal thorax surface to thin copper wire with Lepage's household cement. The other end of the copper wire was looped and this loop was pierced by a pin stuck into a styrofoam board, permitting free circular movement of the insect. Flying insects were exposed to fluorescent lighting from above and a 100 watt incandescent
TABLE 17

Distributions of total flight times of insects used in dispersal experiments. Data are in minutes.

<table>
<thead>
<tr>
<th>Time</th>
<th>Number</th>
<th>Time</th>
<th>Number</th>
<th>Time</th>
<th>Number</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>144</td>
<td>10</td>
<td>4</td>
<td>24</td>
<td>1</td>
</tr>
<tr>
<td>1</td>
<td>9</td>
<td>11</td>
<td>1</td>
<td>25</td>
<td>2</td>
</tr>
<tr>
<td>2</td>
<td>11</td>
<td>12</td>
<td>1</td>
<td>26</td>
<td>2</td>
</tr>
<tr>
<td>3</td>
<td>8</td>
<td>13</td>
<td>3</td>
<td>27</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>2</td>
<td>14</td>
<td>3</td>
<td>28</td>
<td>1</td>
</tr>
<tr>
<td>5</td>
<td>3</td>
<td>15</td>
<td>152</td>
<td>29</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>1</td>
<td>16</td>
<td>9</td>
<td>30</td>
<td>144</td>
</tr>
<tr>
<td>7</td>
<td>1</td>
<td>17</td>
<td>4</td>
<td>31</td>
<td>5</td>
</tr>
<tr>
<td>8</td>
<td>2</td>
<td>18</td>
<td>2</td>
<td>32</td>
<td>2</td>
</tr>
<tr>
<td>9</td>
<td>3</td>
<td>19</td>
<td>1</td>
<td>33</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20</td>
<td>2</td>
<td>34</td>
<td>1</td>
</tr>
</tbody>
</table>
light from straight ahead. A slight flick of the copper wire usually initiated flight. Not all beetles flew for their allotted time without interruption; most stopped at least once and had to be restarted by giving their wires a flick. Clocks were stopped during such times of flight interruption. After flight, insects were removed from their wires and placed under small petri dishes until used some minutes later in the test chamber. Insects chosen for zero flight were treated in exactly the same way as the others, including being tethered and hung on wire, except they were not allowed to fly. Prior to these dispersal experiments, all insects probably had flight experiences in their cages between emergence and collection times. Therefore, the experimental flight times should be interpreted only as relative, not absolute, measures of flight experience. Motion pictures of two tethered beetles showed that the equivalent distances covered in 30 minutes of flight were 0.7 miles for one beetle and 1.3 for the other.

After tethered flight, each insect was run through the test chamber (described above) and its responses to blank and chemical air streams were recorded. Animals which were not photopositive (about 4% of those tethered) were not used in the tests. Each tested insect was saved for later exact sizing. Each insect was tested with only one flight time; the same insect was never reused because of habituation to the experimental apparatus.

With this experimental design it was possible to test for
differences in flight time thresholds between different groups of beetles. Such differences were then related to sex, population type, attack density, body size and emergence date.

Experiments were done in both 1972 and 1973, but only the 1973 data are discussed. The 1972 data are not as trustworthy because I had stored the beetles at 2° C for several days between emergence and testing. This storage time resulted in decreased viability and activity.

C. Results

526 beetles were tested, 267 from field populations and the rest from breeding experiments. All dispersal data were analyzed using single and multiple regression and analysis of variance. To meet the assumptions of these statistical tests, response data were normalized using the dummy-Y variate technique (Gilbert, 1973) and Y-residuals were found to be normally distributed.

Each insect had three runs in the control airstream and three in the chemical-bearing stream, and the first noticeable fact about the data is a marked habituation of insects to the testing apparatus. For both the control and extract trials, responses were less intense in the second run than the first, and also in the third than the second (Table 18). For each insect, various measures of response were calculated, some of which took this habituation into consideration. These were:
TABLE 18

Data on the habituation of insects to the dispersal response apparatus. Data are means (and standard errors) of responses which were numbered from one to five (see text). First, second and third responses refer to the different runs for the same insect.

Sample size = 526 insects

Responses to Controls (blank air)

<table>
<thead>
<tr>
<th>First</th>
<th>Second</th>
<th>Third</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>1.260</td>
<td>1.219</td>
</tr>
<tr>
<td>S.E.</td>
<td>0.0315</td>
<td>0.0273</td>
</tr>
</tbody>
</table>

Responses to Extract

<table>
<thead>
<tr>
<th>First</th>
<th>Second</th>
<th>Third</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean</td>
<td>2.640</td>
<td>2.144</td>
</tr>
<tr>
<td>S.E.</td>
<td>0.059</td>
<td>0.056</td>
</tr>
</tbody>
</table>
1) First response to extract
2) First extract response minus first control response
3) Average of the three extract responses,
4) Measure 3) minus average of three control responses,
5) Weighted averages of the three extract responses, where weightings were .6, .3, .1 on the first, second and third responses, respectively, and
6) Number 5) minus the same weighted average of control responses.

The weightings of the fifth measure were chosen because of habituation. All statistical analyses were performed using these six response indices. Since all of them gave the same answers, I will henceforth only refer to a general dispersal response measure and data will be presented only for the fifth measure.

The first step in the analysis was to determine which blocks of data could be lumped and which had to be kept separate. The best prediction of dispersal response for all the data was found in a multiple regression with emergence date, sex, size and flight as the independent variables (regression data in Table 19). Field and breeding experiment beetles were compared using analysis of covariance and the slopes and intercepts for this multiple regression were not different (P > .1). Thereafter, these two data blocks were lumped. Male data were compared with female data and it was found that the probability of the intercepts of the best
**TABLE 19**

Multiple regression data of dispersal response measure discussed in text on emergence date, sex, size and flight time. Standard errors are in parentheses.

N = 526 insects

<table>
<thead>
<tr>
<th>Independent variable</th>
<th>Slope</th>
</tr>
</thead>
<tbody>
<tr>
<td>Emergence date</td>
<td>-0.060(0.009)</td>
</tr>
<tr>
<td>Sex</td>
<td>-0.296(0.118)</td>
</tr>
<tr>
<td>Size</td>
<td>-0.763(0.353)</td>
</tr>
<tr>
<td>Flight time</td>
<td>0.281(0.057)</td>
</tr>
</tbody>
</table>

**Intercept** = 4.451 (0.626)

Regression Mean square = 23.19
Residual Mean square = 1.11

\[ F = 20.9 \quad P < .001 \text{ that slope} = 0.0 \]
multiple regression (emergence date, size and flight time as X-variates) being the same was <0.005 (between-block M.S./residual M.S. = 8.6, 1 & 521 d.f.). Therefore, males and females were considered separately in all subsequent dispersal data analyses.

Data were then blocked into three flight time classes, short, medium and long defined as 0-9, 9.1-22, and 23-34 minutes, respectively. These class boundaries are reasonable considering the distributions of flight times in my experiments (Table 17). For data blocked by flight times and sex, the regression of response on emergence date was the most significant (Tables 20 & 21). Taking beetle size into account did not increase predictability, but males did show a weak non-significant (P > .1) negative slope of response on size, much as Atkins (1966b) found. Sizes squared and cubed were also tried in order to account for volume changes but these did not give any more significant results than the linear size measure.

The probable reason that size did not significantly help to predict dispersal response is that insects of the same size may not have had the same energy reserves. Atkins (1967, 1973a) found that Douglas-fir beetles spent a variable length of adult life underneath the bark before emerging. Fat content of this beetle was related to this length of time. Thus, my beetles which emerged on the same date and were in the same size class might not have had the same energy
### TABLE 20

Data for regressions of female dispersal response #5 (see text) on emergence date, by flight class as shown in Fig. 26. Standard errors are in parentheses.

**Females:**

**Overall regression, all flight classes lumped:**

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>$r$</td>
<td>$r^2$</td>
</tr>
<tr>
<td>327</td>
<td>0.205</td>
<td>0.04</td>
</tr>
</tbody>
</table>

Y-intercept $a = 2.679(0.113)$
Slope $b = -0.0385(0.010)$ $P < .001$ that $b = 0.0$

**Short flight:**

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>$r$</td>
<td>$r^2$</td>
</tr>
<tr>
<td>102</td>
<td>0.175</td>
<td>0.031</td>
</tr>
</tbody>
</table>

Y-intercept $a = 2.201(0.177)$
Slope $b = -0.027(0.012)$ $P < .03$ that $b = 0.0$

**Medium flight:**

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>$r$</td>
<td>$r^2$</td>
</tr>
<tr>
<td>117</td>
<td>0.167</td>
<td>0.028</td>
</tr>
</tbody>
</table>

Y-intercept $a = 2.684(0.191)$
Slope $b = -0.0341(0.0175)$ $P = 0.05$ that $b = 0.0$

**Long flight:**

<p>| | | |</p>
<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>$r$</td>
<td>$r^2$</td>
</tr>
<tr>
<td>108</td>
<td>0.272</td>
<td>0.07</td>
</tr>
</tbody>
</table>

Y-intercept $a = 3.119(0.199)$
Slope $b = -0.0545(0.0186)$ $P < .005$ that $b = 0.0$

*(males' data on next page)*
TABLE 21

Same as Table 20 but data are for males only instead of females.

Males:

Overall regression, all flight classes lumped:

<table>
<thead>
<tr>
<th>N</th>
<th>r</th>
<th>P</th>
<th>r²</th>
<th>a</th>
<th>s</th>
<th>P</th>
<th>b</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>199</td>
<td>0.408</td>
<td>&lt; .01</td>
<td>0.16</td>
<td>3.63</td>
<td>-0.094</td>
<td>&lt; .001</td>
<td>0.0</td>
<td></td>
</tr>
</tbody>
</table>

Short flight:

<table>
<thead>
<tr>
<th>N</th>
<th>r</th>
<th>P</th>
<th>r²</th>
<th>a</th>
<th>s</th>
<th>P</th>
<th>b</th>
<th>P</th>
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</thead>
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<tr>
<td>82</td>
<td>0.383</td>
<td>&lt; .01</td>
<td>0.147</td>
<td>3.369</td>
<td>-0.0866</td>
<td>&lt; .001</td>
<td>0.0</td>
<td></td>
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</tbody>
</table>

Medium flight:

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<th>P</th>
<th>r²</th>
<th>a</th>
<th>s</th>
<th>P</th>
<th>b</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>65</td>
<td>0.522</td>
<td>&lt; .01</td>
<td>0.27</td>
<td>3.928</td>
<td>-0.115</td>
<td>&lt; .001</td>
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<td></td>
</tr>
</tbody>
</table>

Long flight:

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<th>P</th>
<th>r²</th>
<th>a</th>
<th>s</th>
<th>P</th>
<th>b</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>52</td>
<td>0.248</td>
<td>.08</td>
<td>0.06</td>
<td>3.52</td>
<td>-0.0655</td>
<td>.050</td>
<td>0.0</td>
<td></td>
</tr>
</tbody>
</table>

but additional regression on X² is significant, P < .005
reserves. If energy stores do affect responses to hosts in mountain pine beetle as they do in the Douglas-fir beetle (Atkins 1966b), then lack of control for fat reserves added to the variability in my data.

The regressions in Fig. 26 (data in Tables 20 & 21) establish that so-called pioneer beetles do exist; the earlier a beetle emerges, the more likely it is to respond to tree chemicals after a given length of flight time. One explanation for this decrease in response with lateness of emergence may be that my tree chemicals changed during storage. Syed (1972) suggested that auto-oxidation may occur in ponderosa pine logs or extracts that have been stored for 2 to 6 weeks and he found that attractiveness of these chemicals to *D. ponderosae* changed. However, his results may have been biased by using beetles from different parts of the emergence period in the tests with tree chemicals stored for different lengths of time. In any case, my results do not indicate a change in attractiveness over time because, according to data presented earlier, there was no difference in the responses, within emergence date groups, between field beetles and breeding experiment offspring. These two groups of beetles were tested from 4 to 18 July and 30 Aug. to 20 Sept., respectively. If the tree chemical samples had decreased in attractiveness with increasing time since the sample tree was cut, there should have been lower responses among breeding offspring than field populations. This was not the case, so
FIGURE 26

The relation in mountain pine beetle between tendency to respond to extracts of lodgepole pine and beetle emergence date. Regressions are broken down by sex and flight history class. Statistics for these relationships are given in Tables 20 and 21.
FEMALES
N = 327
R = -0.205
P < .001

LONG FLIGHT
MEDIUM
SHORT FLIGHT

MALES
N = 199
R = -0.41
P < .001
the differences in responses of beetles from different emergence dates (shown in Fig. 26) were due to differences in beetles, not tree samples.

The regressions in Fig. 26 are significant; the correlation coefficients are in Tables 20 & 21. However, the low proportion of the variance accounted for is disappointing. Residual variance may be due to variation in energy stores (above) or to the heritability of dispersal behavior. Data on the existence of the latter phenomenon are discussed by Dingle (1968) and Rose (1972) though they do not establish whether their inheritance mechanisms are genetic or physiological. I was not able to obtain data on this inheritance because of the time required for dispersal experiments in relation to the constraints imposed by emergence date effects on dispersal.

For females in Fig. 26, significant differences were found in Y-intercepts for the regression lines of each flight class but there was no difference between slopes (Table 22). In other words, all three lines were parallel with different intercepts. This means that the longer a female beetle emerging on a given date flies, the greater is the probability that her flight threshold will have been passed and that she will attack a tree with appropriate chemicals. This supports the theory derived from Graham (1961). However, my observations do not provide any information concerning the mechanism for operation of the flight time threshold; it could be gas bubble formation or drainage of energy stores. The
TABLE 22

Testing for the difference in slopes and intercepts between the regression lines shown in Figure 26 for females.

**Test for difference between intercepts:**

\[ F = \frac{\text{between block mean square}}{\text{residual mean square}} \]

where data are blocked by the three flight time classes.

\[ F = \frac{12.6058}{1.046} = 12.05 \quad P < .001 \]

Therefore, these lines have different intercepts.

**Test for difference between slopes:**

\[
\begin{align*}
\text{Individual Regr. Sum of Squares} & \quad 2.4656 + 3.9057 + 9.79 = 16.16 \quad 3 \text{ d.f.} \\
\text{Combined S.S.} & \quad 14.83 = 14.83 \quad 1 \text{ d.f.} \\
\text{Regr. x blocks S.S.} & \quad \underline{1.33} \quad 2 \text{ d.f.}
\end{align*}
\]

\[ F = \frac{1.33/2}{\text{residual M.S.} = 0.635} = 0.65 \quad P > .5 \]

Therefore slopes are not different for females.
later a female emerges from the host tree, the longer she will have to fly to reach the same probability of responding. This means that insects coming out later in the emergence period will fly farther out and tend to spread out more than earlier beetles.

For males in Fig. 26, regressions and correlations are significant but there are no significant differences between intercepts or slopes of lines for the three flight time classes (Table 23). This means that male beetles respond equally well to host chemicals no matter what their flight history up to the moment of encounter. And, as with females, there is a decrease in response with increasing lateness of emergence.

Data were then broken down by sex, experimental attack density, and population type (epidemic or endemic) in order to test for differences in dispersal characteristics between these groups. These tests were made by comparing the slopes and intercepts of regressions of response on emergence. Unfortunately, when data were disaggregated into this many groups, the only regressions that could be compared were male epidemic and endemic beetles and there was no significant difference (P > .1) between these two regressions. For each of the other pairs of comparisons, at least one of the regressions was not significantly different from zero, (P > .2) eliminating the possibility of comparison. Therefore, there is no evidence for intrinsic differences in dispersal between
TABLE 23

Same as Table 22 except that data are for males.

Test for difference between intercepts:

\[ F = \frac{2.2768}{1.1998} = 2.03 \quad P > .1 \]

Therefore, the intercepts are not different.

Tests for difference between slopes:

<table>
<thead>
<tr>
<th>Term</th>
<th>Sum of Squares</th>
<th>Degrees of Freedom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Combined S.S.</td>
<td>46.66 = 46.66</td>
<td>1 d.f.</td>
</tr>
<tr>
<td>Regr. x blocks S.S.</td>
<td>1.90</td>
<td>2 d.f.</td>
</tr>
</tbody>
</table>

\[ F = \frac{1.90}{2} /\text{residual M.S.} = 0.79 \quad P > .5 \]

Therefore slopes are not different for males.
epidemic and endemic beetles, or between offspring of parents bred at high or low density.

D. Discussion

The dispersal test results have interesting ecological implications. First, it is known that mountain pine beetle females are the initial searchers for hosts and diggers of galleries; males arrive afterwards by homing in on the female pheromone and a tree terpene (Renwick and Vite, 1970). My observed lack of effect of flight time on male behavior fits these observations. Males are as responsive to tree chemicals when they first emerge as they are after having flown for 30 minutes. Therefore, males are ready to respond to females as soon as they encounter their pheromones in the presence of alpha-pinene. Also, males have a higher positive response early in the emergence period than do females, for any flight time. Near the middle of the emergence period (Fig. 8), intensity of male response drops below that of females.

In my experiments, insects which emerged earliest had greater responses after a given flight time than beetles emerging later. This is apparently the opposite of female Douglas-fir beetle behavior; Atkins (1966b) found late emergers to be more likely to attack trees. His apparent use of beetles without flight histories might be interpreted as the cause of the difference, but my short flight class shows a negative slope and most flight times in this class were zero.
We need to consider the effects of sequences of attacks on the relationship between emergence date and tendency to respond to tree chemicals in order to discern why these two species have opposite responses to emergence date. First, let us translate the axes of Fig. 26 into a different measure of dispersal. The present measure shows that, for a given emergence date, a female will have a certain probability of responding to host chemicals after a short flight. If she flies longer, that probability increases. The later her emergence date, the longer she will have to fly in order to reach that same probability of responding. Therefore, we can translate the relationship shown in Fig. 26 to a changing slope relation between average distance flown and proportion of the population responding to tree chemicals (Fig. 27a). This means that during the course of *D. ponderosae* emergence, insects will first tend to attack trees close in to the source tree and later will tend to fly out farther before responding to tree chemicals. This should produce a slowly expanding series of concentric waves of attacking beetles through the emergence period (Fig. 28a).

In the Douglas-fir beetle, the opposite appears to be the case. Atkins' (1966b) finding that early emergers tend to be weaker responders implies that pioneering beetles will have to fly farther than late emergers before attacking trees (Fig. 27b). If late emergers needed to sense pheromones before attacking, then the bulk of the population would be
FIGURE 27

The relation between average distance flown and the proportion of beetles responding to tree chemicals and attacking. Top graph is for *D. ponderosae* and bottom one is for the Douglas-fir beetle.
A

Proportion of Population Responding to Tree Chemicals

Average Distance Flown

Dendroctonus ponderosae

Early emergers

Late emergers

B

Proportion of Population Responding to Tree Chemicals

Average Distance Flown

Dendroctonus pseudotsugae

Early emergers

Late emergers
A hypothetical sequence of attacks over space by D. ponderosae and the Douglas-fir beetle. Numbers represent the order in which trees at various distances from the source tree (in the center) are attacked.
drawn farther out from the source tree than in the mountain pine beetle. If late emergers did not require pheromones, then the sequence of attacks would be starting far away and working inward, instead of vice versa, as in D. ponderosae (Fig. 28b).

The ecological significance of these opposite patterns of attack in D. ponderosae and D. pseudotsugae might be found in the different types of preferred hosts when insects are at endemic levels. D. ponderosae attacks only standing, relatively healthy trees whereas the Douglas-fir beetle prefers greatly weakened or recently fallen trees (McMullen and Atkins, 1961; Rudinsky, 1970). The number of insects required to overcome host resistance is lower in the case of the Douglas-fir beetle because of the weaker trees attacked. As noted above, first attacking beetles in this species, if we assume random directionality of movements, will attack trees farther away from the original host than will D. ponderosae. This means that the initial concentration of beetles on trees will be lower in D. pseudotsugae than in D. ponderosae because there will be fewer beetles per unit area at a given distance purely due to diffusion. Subsequent concentrations of beetles would depend on the relative effective distances of each species' respective pheromones and how much response behavior is altered by the changing volatile host chemical concentrations caused by increasing numbers of attacks. Since first-attacking mountain pine beetles infest trees close in,
they would be assured of "filling up" these trees first and then attacking more distant ones later. Individual Douglas-fir beetles, on the other hand, could spread fairly thinly and still have high reproductive success because of the weak trees attacked. This thinning of the population also reduces the probability of offspring suffering from too much intraspecific competition.

A tradeoff is implied in the above discussion: average dispersal distances required before responding to hosts must be short enough to insure a large enough number of attacking beetles to overcome resistance of trees, and yet long enough to find suitable hosts. The shorter flight distance of pioneer mountain pine beetles, when compared with the Douglas-fir beetle, reflects the relative importance of having greater numbers of attacking insects for overcoming the relatively healthy hosts. The longer distance required by pioneering Douglas-fir beetles emphasizes the need to search for distant (and perhaps rarer) hosts and de-emphasizes the requirement for numerous attacking beetles per tree.

Nothing is known about directionality of dispersal in mountain pine beetle, but it is clear that two different types of factors, internal and external, affect how far *D. ponderosa* will disperse before attacking trees. I have established that the dispersal characteristics of male and female *D. ponderosa* are weakly affected by their emergence dates. Early emergers are more prone to respond than later
emergers after the same flight time. For females, flight history affects tendency to respond to host chemicals, but for males it does not. Body size was shown to have no effect on the dispersal characteristics measured, but works of other people suggest that fat content (only weakly related to size) may be more important. One external factor in dispersal is the tree chemical complex, for which my test samples constituted only one point in the range of concentrations probably encountered by beetles in the field. Other workers have also shown pheromones to be a significant determinant of flight behavior and its termination, but some further questions need to be investigated. Is a pheromone a more effective attractant in the presence of higher concentrations of appropriate host chemicals? What are the attractive distances over which pheromones operate? And finally, do late emerging beetles have the same response to pheromones in a given concentration as do early emergers, or is there a changing pattern as I have found in response to tree chemicals?
IX. GENERAL DISCUSSION

The basic life history adaptations of mountain pine beetle give us some hints about the selection pressures on this species. The most interesting problem deals with energy limitations and mortality during dispersal. Data on this problem are difficult to obtain but the general feeling among bark beetle ecologists is that mortality during dispersal is high because of inability to find suitable hosts (e.g. 30-50%, Amman and Baker, 1972). However, I believe that host discovery cannot be a very serious problem. Female *D. ponderosae* do the initial searching for trees, take the brunt of the initial host resistance, and do all the gallery digging. The female also has a greater energy demand (for egg production) than the male. I argue that if energy were very often limiting in the course of dispersal or if even a small proportion of females were lost searching for hosts, the pioneering role would be held by the males, as is the case with most *Ips* species. In these species, the male does the searching, initial gallery construction, and pheromone production, which attracts the rest of the population.

One possible argument against this reasoning in *D. ponderosae* is that such a large number of beetles are needed to kill healthy host trees that no individual could afford to have an offspring sex ratio that would produce
mostly pioneer males; there would be too few females to reproduce the genotype. A test of this argument is to see whether there are any *Ips* species that attack healthy trees. I am aware of no such case.

Early emerging or pioneer females might be at a disadvantage. Dispersal mortality might be higher in this group than in later emergers because there is no pheromone to follow to suitable hosts and when trees are initially attacked, their resistance mechanisms are more likely to overcome beetles. However, there may be an advantage in being among pioneering beetles if, under normal summer conditions, there is a greater probability of early attackers being able to successfully produce a second brood than later emergers. This increase in productivity of pioneer beetles could only be significant if it can be shown that earliness of emergence is, in any sense, heritable. For example, the offspring of early attackers on fairly weak hosts may develop sooner than later arrivals, assuming that early-laid larvae do not stop feeding and developing at some point while the later larvae "catch up". If all these assumptions are true, then early emergers are probably related from one generation to the next and the disadvantages of being a pioneer beetle may be outweighed by the increased probability of successfully producing two broods.

Another aspect of the emergence period in mountain pine beetle is its timing relative to the changing stresses on
lodgepole pine. Since the beetle prefers relatively healthy trees, one would expect the timing of attacks to be adjusted within the season so that the bulk of attacks would occur when trees were weakest. However, Reid and Shrimpton's (1971) data show that tree resistance is just past its peak when most mountain pine beetles normally attack in these areas. The beetles simply may not be able to shift emergence and attack any later because of the minimum time needed for larval development to overwintering size. A less likely but more elegant explanation for this seemingly premature attack time is that the increased payoffs of occasionally being able to produce a second brood outweigh the risks of attacking while trees are more vigorous. Also, mass attack behavior helps reduce these risks. The kind of evolutionary shift in emergence and attack period which is assumed possible in the above discussion has been shown to occur in the fall webworm (Morris and Fulton, 1970a). These investigators found that heat requirements for development and diapause termination were genetically controlled.

Several testable hypotheses arise from the previous few paragraphs. 1) Offspring of early emerging beetles will emerge earlier than the bulk of the population. 2) Most of the successful second broods will be fruits of these early emergers. 3) Heat requirements for larval and pupal development may be under genetic control. 4) Males will be the pioneer or searching sex in bark beetle species where high
mortality is suffered during the dispersal stage and where relatively weak trees are utilized.

The evidence for bark beetles in general is that populations are essentially oviposition-site limited owing to narrow host tree physiology tolerance ranges (Berryman, 1972; Rudinsky, 1962). Since these populations are limited by abundance of suitable trees, outbreaks of insects can actually be construed as normal developments following "outbreaks" of susceptible trees. This interpretation fits the mountain pine beetle-lodgepole pine system quite well because of the even-aged stand characteristic of lodgepole and the relation of tree age to susceptibility. When large areas of even-aged lodgepole reach susceptible ages, there are abundant sites for reproduction and the beetles reproduce quite successfully.

Foresters in the United States have recently become aware of this concept and have proposed that natural fires in lodgepole stands be left to burn out naturally (L.L. Loope and G.D. Amman, pers. comm., 1972). They hope that by breaking up the spatial distribution of age classes into a mosaic, there will be lower probabilities of mountain pine beetle outbreaks. However, this reasoning assumes that after some number of years, the stands of suitable trees will be small enough to support only small *D. ponderosae* populations and will be separated by bands of unsuitable trees wide enough to keep mountain pine beetle dispersal between stands very low. However, until we know more about how far these beetles
disperse, the proposal seems a slow, risky, and costly way of testing ideas.

One aspect of the dynamics of insect populations which has received little attention is the role of within-population variation. Albrecht (1962) shows that locusts which are subjected to changes in density produce offspring with higher phenotypic variability than the parental generation. This has been interpreted as a means for increasing the survival of genotypes in the face of environmental uncertainties. The apparent bimodality of offspring size that I found in mountain pine beetles might also be interpreted in this way. Another example of this general nature concerns the western tent caterpillar. Wellington (1964, 1965) has shown that within-population variability in vigor and dispersal characteristics enable this species to colonize habitats of different severities. Variability among offspring of one female increases the probability of her genotype surviving. The within-population variability in dispersal characteristics of my mountain pine beetles also suggests that an advantage may be gained by maintaining within-population heterogeneity, if the distribution of suitable hosts is unpredictable in time and space.

Many mountain pine beetle characteristics seem to be the product of selection at low, or endemic, levels. There are highly refined mechanisms for sensing suitable hosts and attracting other members of the population to such hosts.
Such characteristics are most advantageous when insect populations are low and there are few suitable trees. Thus, the critical questions for bark beetle ecologists may not be "Why does this species fluctuate in numbers so widely?" but "How does this species persist in times of low suitable host abundance?" Related to this point, Watt (1971) noted that many ecological theories are biased by data from relatively few, well-studied species. Additionally, these species are ones that have attracted our attention by achieving high densities or by fluctuating widely.
X. SPECULATIONS ON LODGEPOLE FITNESS

Gilbert and Hughes (1971), Hughes and Gilbert (1968), and Gilbert and Gutierrez (1973) have pointed out the significance of the adjustment of relationships between plant and herbivore populations. They suggest for their aphid and host plant situations that reproduction and dispersal to new plants occur in such a way as to optimize certain fitness measures. It is interesting to look in a similar manner at the interaction of mountain pine beetle with lodgepole pine.

Safranyik et al. (1974a) have noted that most mountain pine beetle outbreaks in this century in western Canada have taken place in tree stands about 80 years old. This age is remarkably close to foresters' rotation age for a lodgepole pine stand on an average site (70 ft at 80 years), as indicated by normal yield tables (Smithers, 1962). The general term rotation age refers to the age at which it is best to harvest a stand and is defined by some (e.g., Stanek, 1966; Smithers, 1962) as the age at which mean annual increment reaches its maximum. Although there is some controversy over how rotation age should be determined, the correct definition is unimportant here; the concept which is significant is that mountain pine beetle outbreaks normally occur in tree stands of about the age at which foresters believe they can maximize long term wood production.
The simplest explanation for this peculiar phenomenon is that trees keep from being susceptible as long as is feasible and that bark beetles attack these trees as early as it is possible to achieve some degree of success; i.e., when trees begin to grow old and weak. If this senescence age is fairly consistent between stands, then the observed phenomenon would be explainable. However, I hypothesize that there is a more subtle evolutionary explanation; lodgepole may have adjusted its age of increased susceptibility to mountain pine beetle so that tree stands are decimated before they produce so many seeds that individual tree reproductive fitness decreases due to overcrowding in the next generation. This hypothesis suggests that *D. ponderosae* is more than a "natural thinning agent" for lodgepole pine; it is a removal agent which acts in its own interest and that of the trees.

The evidence which led to this hypothesis deals with the reproductive characteristics of lodgepole pine. As noted in introductory section III, lodgepole is a prolific seed producer and is well known for its tendency to overstock and cause stagnation, or early termination in growth. One important characteristic of these overcrowded stands is that seed production is greatly reduced due to crown suppression; only a few per cent of the trees in such stands ever produce cones. There is thus an advantage for individual trees to become susceptible to mountain pine beetle after they have produced enough seed to insure some survival of offspring;
stands will have greater probabilities of being killed by mountain pine beetle and the fires which are essential for seed release will come through the stand much sooner. The reason this is an individual selection mechanism and not a population one is that there is almost no spreading of seeds in a stand; most seeds fall within a 200 foot radius of the parent tree (Boe, 1956; Dahms, 1963). This means that a tree producing a large number of seeds will cause competition and reduced reproductive success mainly among its own offspring. Thus, the basic idea behind the hypothesis at hand is that trees welcome "harvest" at the point of diminishing reproductive returns.

The kind of evolutionary adjustment in beetle and tree characteristics which this hypothesis requires is easily imaginable. Selection pressures between these species have been and still are intense, since mountain pine beetle's major host is lodgepole pine and in most regions this beetle is the main source of the tree's mortality other than senescence. The kinds of questions which are interesting to pursue deal with the consequences for lodgepole of altering the normal age (80) at which trees become susceptible to and are "harvested" by mountain pine beetle. For instance, what would happen over a number of tree generations if lodgepole evolved much more potent resistance mechanisms, keeping beetle populations low until many years later than usual? Conversely, what would be the consequences of the mountain pine beetle's evolving
greater ability to withstand tree resistance mechanisms, thereby lowering the normal tree age at which outbreaks normally occurred?

These questions can be answered by taking a closer look at natural lodgepole reproduction. Natural reproduction is purposely distinguished here from man-enhanced reseeding practices because of obvious problems in dealing with the evolutionary questions at hand. Information is needed on seed viability, factors affecting seed loss, and numbers of seeds available in stands of various ages and densities.

Several independent factors affect annual production of serotinous cones of interior lodgepole. More middle-aged trees produce cones than older or younger trees (Fig. 29), (Crossley, 1956a; Latham, 1965). The number of cones per tree (Fig. 30) increases exponentially with tree diameter, due to the increase in crown volume as trees grow (Crossley, 1956a; Latham, 1965). Fig. 31 shows that the proportion of trees in a stand which bears cones also goes up with diameter (Bates, 1930; Crossley, 1956a). Tree diameters at given ages are in turn greatly affected by stand density (Alexander et al., 1967; Dahms, 1967; Smithers, 1962; Trappe and Harris, 1958). Some data on this effect (from Lee, 1966) are shown in Fig. 32 for trees with a site index of 70 ft at 80 years. Crown suppression due to crowding also decreases the number of cones on a tree (Baker, 1950; Bates, 1930; Clements, 1910; Smithers, 1962).
FIGURE 29

The relationship between tree age and proportions of trees bearing any cones for lodgepole pine. Data are from Crossley (1956a) and Latham (1965).
PROPORTION TREES BEARING CONES

CROSSLEY (1956A) AND LATHAM (1965)
FIGURE 30

The relation between tree diameter and the number of cones per tree for lodgepole pine. Data are from Crossley (1956a) and Bates (1930).
CROSSLEY (1956A) AND LATHAM (1965)

# CONES/TREE

0 3 6 9 12 15

AVERAGE DIAMETER (IN.)
FIGURE 31

The relation between tree diameter and the proportion of trees in a stand of lodgepole pine that bears any cones, assuming that all trees are of the same age. Data are from Crossley (1956a).
FIGURE 32

The relation between lodgepole pine stand density and average diameters at given ages from 20 to 150 years. Data from ages 20 to 100 are directly from Lee (1966) and data from ages 110 to 150 are extrapolations from other curves of Lee (1966).
NORMAL YIELD TABLE, LEE (1966)
BY STAND AGE

DIAEMTER (IN.)

INITIAL STOCKING DENSITY
TREES/ACRE
The proportion of seeds (at about 25 to 40 seeds per cone) which become saplings the next generation is determined by several factors. Initially, seeds are released from cones by fires, as noted earlier. Approximately 50% of these seeds are viable (Bates, 1930; Clements, 1910; others) but only 1 out of 278 of the viable ones actually roots successfully on burned ground (Lotan, 1964). Squirrels are a major source of seed loss and most cones do not survive their intense harvesting more than 25 years (Crossley, 1956a).

All these agents of cone loss are fairly constant, acting independently of tree densities. However, as can be seen from the data referred to in the preceding two paragraphs, most factors affecting cone production are density-dependent, typically giving rise to sequences of events as follows. Let us assume that there is only one fire in a stand per generation. Lodgepole in a fairly open stand, say 250 trees per acre, will produce many seeds. If a fire burns the stand when it is 90 years old, there may be enough seed available to produce a very dense stand, say 4,000 trees per acre. This new stand, being crowded, will have smaller trees with smaller crowns than the previous generation. The new number of seeds produced at any age will be much smaller than in the previous generation as will the number of saplings in the following generation if this stand is burned before it becomes too old. This will lead to an oscillation in numbers of trees per acre through several generations.
A simple simulation model was constructed using the functional relationships just described. In addition, stands of different ages were given various probabilities of having fires according to estimates of J. Murraro (pers. comm.). Stands from 10-40 years old were somewhat likely to be burned, 50-90 year stands were fairly immune, and older stands were very susceptible, becoming more so with age. The basic structure of the model was to calculate, for every ten years, the number of seeds produced by a stand of trees in a one acre plot. These calculations were made for every ten year period until the stand was decimated either by fire or by mountain pine beetle. At this point the viable seeds were summed up and surviving saplings were calculated. These new saplings became the start of the next generation and the calculations for every ten year period were carried out in the same way as before. This process was repeated for ten generations. Various fitness measures were calculated each generation, including number of seeds surviving to reproduce, population size, offspring per grandparent, etc.

The model had four main assumptions: 1) There are three causes of tree mortality: mountain pine beetle, senescence, and fire. 2) There is only one fire in the stand each generation, either immediately after bark beetles decimate the stand or at some randomly determined time. Such fires kill all trees (if not already dead from beetles) and release lodgepole seeds. 3) External populations of bark beetles and
lodgepole pine do not affect the simulated populations. 4) Bark beetles do no damage to lodgepole until the decade of outbreak, when all trees in the stand are killed.

This simulation model allowed exploration of the possibility that some tree (not beetle) fitness measures are being optimized in the mountain pine beetle-lodgepole pine system. Simulated numbers of seeds closely approximated field data. Several random sequences of fires were tested in the model and ages at which stands became vulnerable to beetles were varied from 50 to 150 years. The results of this series of simulations show that there may be something meaningful in the observation that most outbreaks of mountain pine beetle occur in stands of tree species, including lodgepole, of about 80 years of age.

Two tree fitness measures show a peak near the age of beetle harvest which is normally observed in nature. These are numbers of surviving saplings per reproducing grandparent (Fig. 33) and numbers of surviving saplings per total tree-years during each generation (Fig. 34). Ten other fitness measures (such as offspring per reproducing parent and offspring per tree at time of harvest) all either increased or decreased monotonically with age of susceptibility. The most reasonable fitness measure for lodgepole is offspring per reproducing grandparent because of the time lag involved in determination of genotype survival. If one were to look only at offspring per parent one would find that the later a stand
The simulated relation between numbers of saplings produced per grandparent (reproducing trees two generations back) and the age at which lodgepole stands become susceptible to mountain pine beetle attack. This is one example of the curves showing this relationship when only one set of random numbers representing probabilities of fires is used.
SAPLINGS PER REPRODUCING GRANDPARENT

OVERTEN GENERATIONS

AVERAGE FITNESS

BY BEETLES (YEARS)

TREE AGE AT HARVEST

0 40

15 30

60 80 100 120

150
FIGURE 34

The simulated relation between numbers of saplings produced per tree per year per generation and the age at which lodgepole stands become susceptible to mountain pine beetle attack. This is one example of the curves showing this relationship when only one set of random numbers representing probabilities of fires is used.
AVERAGE FITNESS OVER TEN GENERATIONS

SAPLINGS PER TOTAL TREES PRESENT

TREE AGE AT HARVEST BY BEETLES (YEARS)
is harvested, the larger is the number of offspring per parent surviving due to the larger seed crop and low sapling mortality. However, in such crowded conditions, very few of those offspring would reproduce, and, since fitness measures perpetuation of genotype, a fitness measure involving a one-generation time lag would be more appropriate. The number of saplings surviving per total tree-years per generation has a local maximum at 90 years, drops and then rises again (Fig. 34). This drop is caused by the sharply increased probability of fires in stands aged 90 years and older.

Changes in the probabilities of fires occurring changed quantitative values of these various fitness measures but only slightly altered the shapes of the curves (Fig. 35). Two other fitness measures, numbers of seeds produced per generation and average population size per generation also showed peaks at 80-90 years. However, present ecological theory does not support the notion that these are reasonable fitness measures and thus we must rely on the two more likely measures of numbers of surviving saplings per reproducing grandparent and per tree-year.

Since these are reasonable fitness measures and since they fit the observation of ages at which lodgepole stands are normally killed by D. ponderosae, it may be that by adjusting its age of susceptibility, lodgepole is maximizing these reproductive fitness measures. This conclusion assumes that susceptible age can be at least partially inherited, either
FIGURE 35

An example of how one of the fitness measures changed when different probabilities of fires as a function of stand age were used.
genetically or physiologically.

Since some fitness measure can usually be found to fit just about any hypothesis or observation, the above hypothesis is not totally substantiated. Lodgepole may, in actual fact, not be maximizing any of the predicted fitness measures. However, the evidence suggests that it is worth considering the postulated concept as a possible explanation of the observed behavior of the *D. ponderosae*-lodgepole pine system. A test for the hypothesis might be to look at lodgepole pine in the northern part of British Columbia, where mountain pine beetle is not and never has been present, and see whether reproductive characteristics are different or whether another natural harvesting agent is present.

The concept that plant species may be using their insect predators to their own advantage is a useful one to pursue. In the *D. ponderosae*-lodgepole pine system, the bark beetles are probably attacking trees as soon as good attack success is insured, while the trees may have adjusted this age so that their own reproductive outputs are maximized. Other plant-herbivore systems may be more complicated to analyze in this manner; lodgepole has unusually simple characteristics (pure, even-aged stands, shade intolerance, and fire-released seeds). However, it is a viewpoint which should be used to explore the significance of the timing of "outbreaks" of herbivores on their hosts.
LITERATURE CITED


Wellington, W.G. 1948. The light reactions of the spruce budworm, Choristoneura fumiferana Clemens (Lepidoptera: Tortricidae). Can Ent. 80:56-82.


Publications (continued)


