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A SIMULATION OF PREDATION BY NON-GAME BIRDS ON THE MOUNTAIN
PINE BEETLE (*DENDROCTONUS PONDEROSAE* HOPKINS)

by

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ABSTRACT

Available information on bird-lodgepole pine, bird-mountain pine beetle, and mountain pine beetle-lodgepole pine interactions was reviewed. A computer model was constructed for the purpose of simulating variations in these interactions. Three lodgepole pine stand structures and three sets of bird responses to changes in beetle density were simulated. It was determined that birds may be able to suppress beetle population growth and reduce maximum beetle density under 'typical' stand conditions, but could only prevent an epidemic when unrealistically high bird densities were assumed. Increasing base-line bird densities to levels which were realistically obtainable had effects similar to those obtained when predator efficiency was increased. No amount of avian predation could prevent a massive epidemic from occurring when stand conditions were such that beetle productivity was optimized. A mountain pine beetle epidemic, as well as bird functional and numerical responses, did not occur when a stand structure representing a preventive thinning was simulated. Preventive silvicultural methods such as thinning or reduction of rotation age, combined with practices such as retention of wildlife trees on clearcut sites in order to increase non-game bird densities, could help prevent endemic beetle populations from reaching epidemic levels.

RESUME

Le rapport revoit les données existantes sur l'interaction qui existe respectivement entre les oiseaux et le pin lodgepole (*Pinus contorta*), entre les oiseaux et le scotyle du pin de montagne (*Dendroctonus ponderosae*) et entre ce dernier et le pin lodgepole. On a élaboré un modèle informatique destiné à simuler différentes variations dans ces interactions. On a simulé trois différents peuplements des pins lodgepole et trois ensembles différents de réactions des oiseaux en réponse aux variations de densité de peuplement des scotyles. On a établi que les oiseaux étaient capables d'arrêter le développement des scotyles et d'en réduire la densité maximum dans certaines conditions précises de densité forestière, mais que ils ne pouvaient cependant empêcher le développement épidémique que si ces oiseaux étaient en nombre anormalement élevé. L'accroissement de la densité des oiseaux à des niveaux acceptables est censé avoir le même effet que celui qui est obtenu par une efficacité accrue des prédateurs. Même très élevée, la prédation par les oiseaux n'est pas capable d'empêcher le développement épidémique des scotyles lorsque la densité du peuplement forestier est telle que la multiplication de ces insectes s'en trouve favorisée au maximum. On a constaté que ni la multiplication effrénée des scotyles du pin de montagne ni les réactions fonctionnelles et numériques des oiseaux ne se produisaient lorsque l'on simulait une densité forestière obtenue après éclaircissage. Les méthodes sylvicoles préventives telles que l'éclaircissage ou l'abaissement de l'âge de rotation, combinées à des pratiques telles que le maintien d'arbres préférés par le dans les parties coupées à blanc, en vue d'augmenter la densité de population des oiseaux autres que le gibier, toutes ces méthodes pourraient contribuer à empêcher les populations endémiques de scotyles d'atteindre des niveaux épidémiques.

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1. INTRODUCTION

Irruptive insects infested more than 680,000 hectares of commercially valuable forest land in British Columbia in 1984. This represents an increase of over 500% since 1979 (Fiddick and Van Sickle 1980, Wood *et al.* 1985). Approximately 482,300 hectares, or roughly 71% of the total area, were infested by the mountain pine beetle.¹ The mountain pine beetle is considered the most serious enemy of lodgepole pine trees in western Canada (Safranyik *et al.* 1974, Safranyik 1984 personal communication), and the most significant insect problem in British Columbia. Since 1972 it has killed more than 172 million lodgepole pine trees. In 1984 alone the beetle killed approximately 41 million trees (Wood *et al.* 1985)(Figure 1).

A number of silvicultural, chemical, and biological methods have been suggested for the control or prevention of epidemics by irruptive insects (Safranyik *et al.* 1974, Amman *et al.* 1977, Hodgkinson *et al.* 1979, Safranyik *et al.* 1981, Manning *et al.* 1982, Takekawa *et al.* 1982, Moeck and Safranyik 1984). Biological methods include the use of pheromones, viruses, bacteria, parasitoids, and invertebrate and vertebrate predators (Hodgkinson *et al.* 1979, Takekawa *et al.* 1982, Moeck and Safranyik 1984).

¹Common names are used in the text. All scientific names appear in APPENDIX 1.

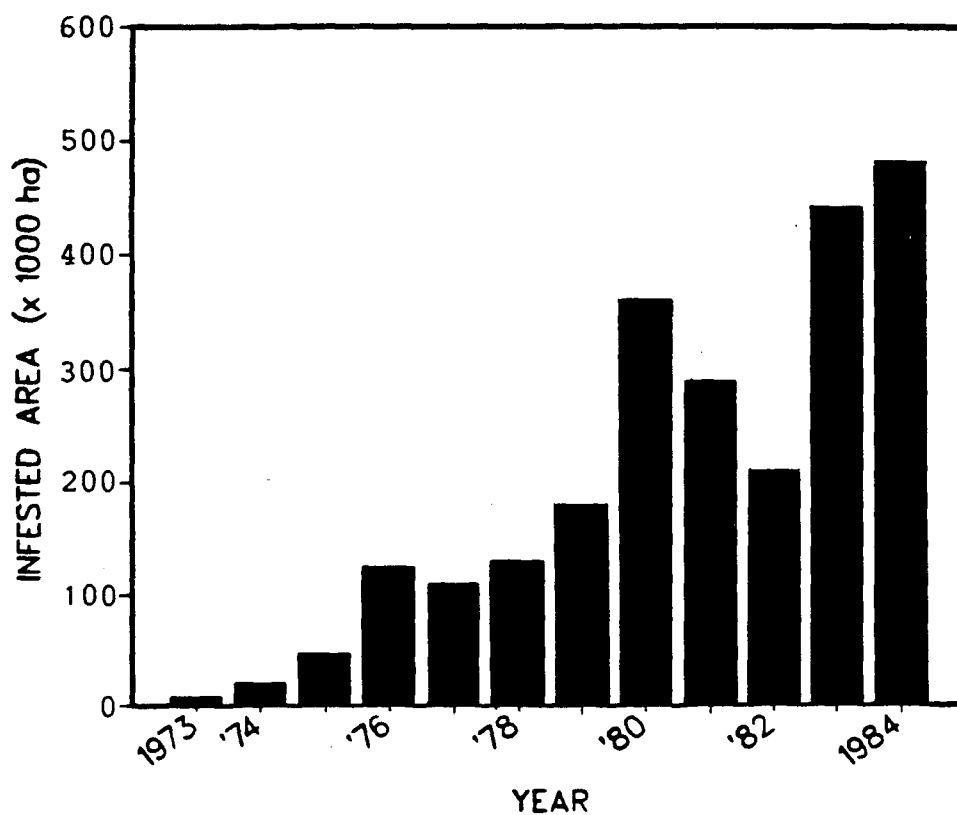


Figure 1: Area infested by the mountain pine beetle in British Columbia, 1970-1984 (Compiled from Forest Insect and Disease Survey file reports).

Birds have long been considered major vertebrate predators of forest insects. Boesenberg (*in* Otvos 1979) noted that birds were protected as early as 1335 by discerning Swiss authorities who recognized their value. Recent investigations by Torgersen and Campbell (1982), Campbell *et al.* (1983), and Takekawa and Garton (1984), supported by numerous earlier studies, have quantitatively demonstrated the consumptive abilities of insectivorous birds.

Determining the ability of birds to control forest insect populations (*i.e.* prevent epidemics), however, requires more than a knowledge of the number of insect larvae that a bird can consume. It also requires an understanding of insect life cycles and outbreak dynamics, the birds' responses to changes in insect abundance and distribution, and the manner in which both birds and their insect prey are affected by timber management practices.

1.1 OBJECTIVES

This study can be considered on two levels. First, it is a general examination of multiple resource management. In this sense, it examines the management of lodgepole pine stands to maintain timber production while simultaneously reducing stand susceptibility to insect attack, and enhancing local populations of insectivorous, non-game

birds. Second, it is a detailed study of the impacts of a class of vertebrate predators on invertebrate prey over a range of predator-prey densities and habitat conditions.

The mountain pine beetle was chosen as the subject of this investigation for the following reasons:

1. It is one of the most destructive coniferous forest insects, not only in British Columbia, but in the western United States as well.
2. Due to its destructive abilities there has been a considerable amount of research conducted on this species.
3. There are two distinct periods of avian predation (which may be referred to as the winter and summer periods) during the beetle's life cycle. They effect two different mountain pine beetle life stages; the overwintering larva and the attacking adult.
4. The birds responsible for predation during these periods represent, for the most part, two different avian Orders; the Piciformes (woodpeckers) and the Passeriformes (perching birds).
5. The predators from these different Orders also generally use two different methods of foraging; excavation and bark-gleaning.

With this insect and its avian predators in mind, the objectives of the study were:

1. To establish broad, general conceptual models describing the interactions of the insect, its avian predators, and forest stand structure through analysis of the literature and consultation with experts.
2. To document important problem areas in British Columbia where birds may be important controlling agents.
3. To examine some case histories from British Columbia to test the validity of the conceptual models, and to develop hypotheses for future testing.
4. To develop conditional statements that predict or describe the responses of the bird-insect system to forest management practices used in British Columbia.
5. To identify subject areas that require further research because data are incomplete or lacking.

1.2 SCOPE

The purpose of this study, in part, was to examine the possible impacts of relevant timber management practices used in British Columbia on bird/insect dynamics. This was accomplished through the construction and use of a computer simulation model. The model was designed to represent conditions that commonly occur in British Columbia where the mountain pine beetle is found (Figure 2). Unfortunately, the amount of information specific to the province often was extremely limited. Therefore, much of the data used in the

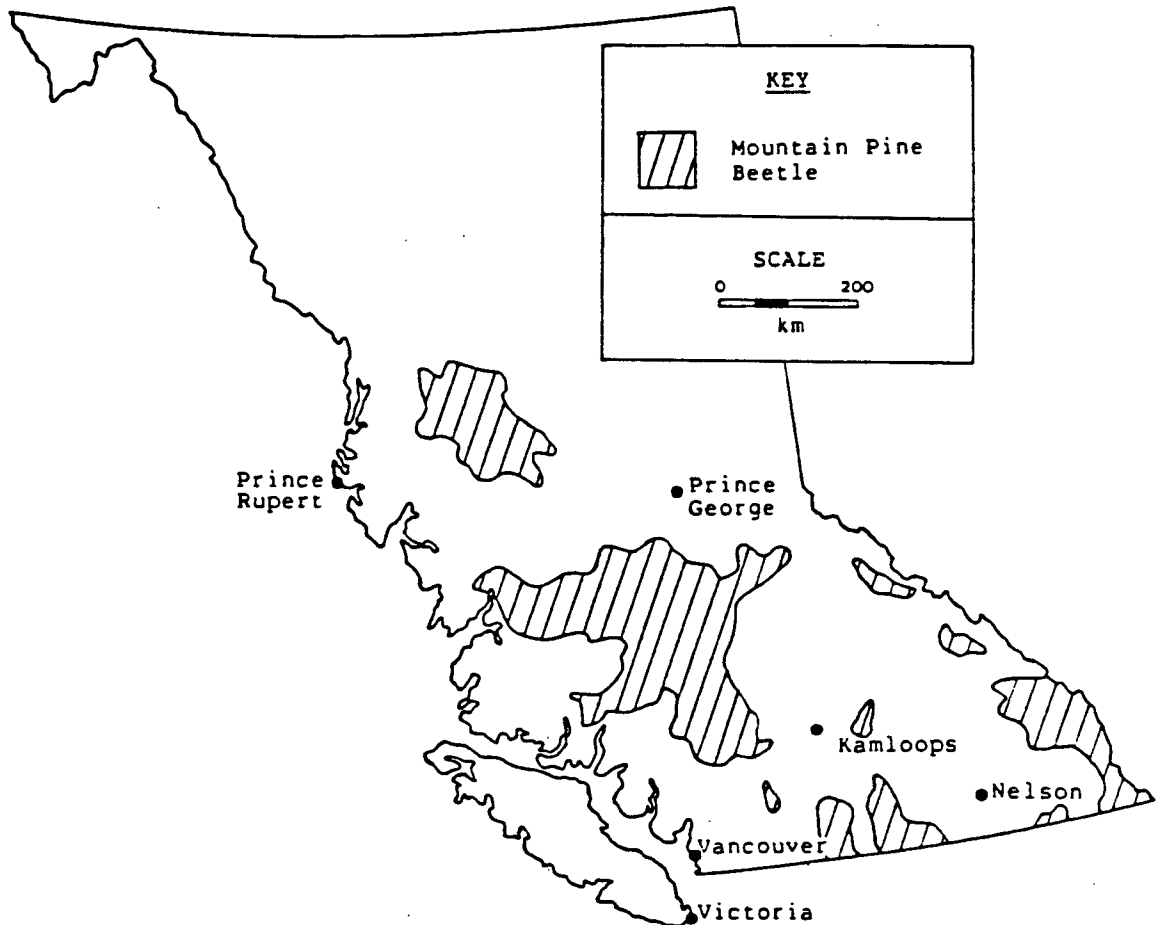


Figure 2: Location of mountain pine beetle infestations in British Columbia, 1970-1984 (compiled from Forest Insect and Disease Survey file reports).

construction of the simulation model came from research conducted in the western United States. These values were altered occasionally in an attempt to represent provincial conditions if sufficient background material was available to support the alteration.

2. APPLICABLE THEORY

2.1 INSECT EPIDEMIOLOGY

The forest ecosystem is home for a wide variety of insect species, most existing at low population densities that are relatively stable. However, populations of some species are capable of dramatic increases in a short period of time. These increases are referred to as outbreaks, irruptions, or epidemics. Widespread damage or destruction of valuable timber may occur, depending on the insect(s) involved. Species that possess this potential are termed 'irruptive' insects by entomologists, and 'pest' insects by the forest industry.

Irruptive insect species are often present in the forests at low, or endemic, levels. Biotic factors (*e.g.* predation) and abiotic factors (*e.g.* temperature) combine to hold them at these levels by imposing a density-dependent negative feedback such that population replacement approaches zero as density continues to increase. Berryman (1978) used the term 'tolerant' to describe factors that can control a population in this manner.

The effects of density-dependent factors on an insect population are shown in Figure 3. The horizontal line represents a replacement value of 1.0 (one offspring

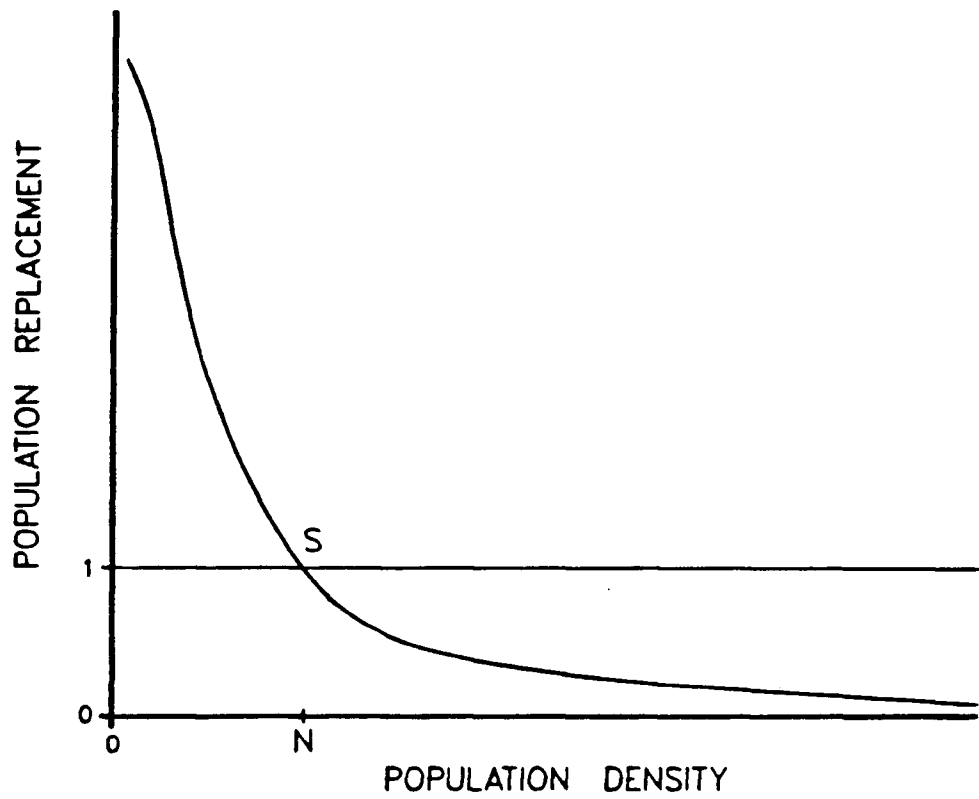


Figure 3: Influence of 'tolerant' control factors (Berryman 1978).

produced per parent). The point where the two lines intersect is the single, theoretically stable equilibrium of the population (S), corresponding to the insect density N. Populations having densities greater than N will have replacement values less than 1.0, and will decrease to S. Conversely, populations with densities less than N will have replacement values greater than 1.0, and will increase to S. This figure, and figures 4 through 7 do not include the theoretical "Allee" effect at very low population densities.

Some controlling factors do not function at all population densities, and have been termed 'intolerant' by Berryman (1978). Bird predation, for instance, eventually loses its effectiveness as insect densities continue to increase. Predation, initially producing a negative feedback, becomes an inverse density-dependent process producing a positive feedback on the insect population (Morris 1963, Berryman 1982). As a result, the rate of replacement begins to increase (Figure 4). When the population replacement curve again intersects the line representing a replacement value of 1.0, a second equilibrium point, U, corresponding to insect density T, is established. This second equilibrium point, unlike S, has been shown to be unstable (Morris 1963, Takahashi 1964, Holling 1973, Berryman 1981). Insect populations with densities less than T will have replacement values less than

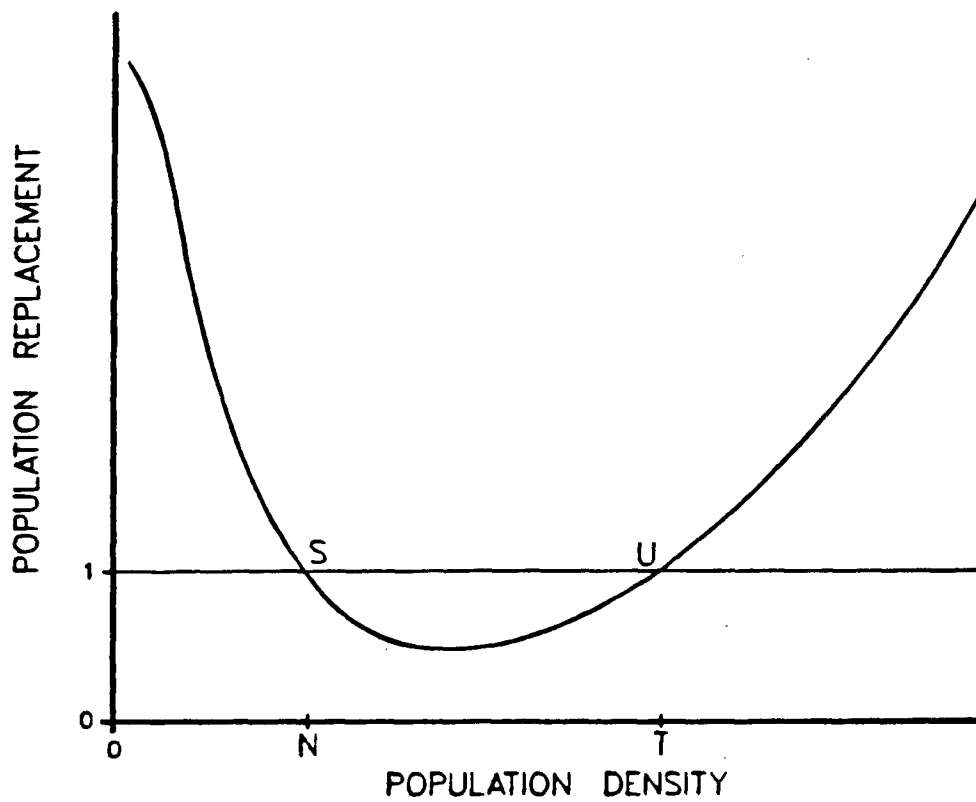


Figure 4: Influence of 'intolerant' control factors (Berryman 1978).

1.0, and will decrease to S (density N). Populations with densities exceeding T will continue to increase. The density T is thought to separate the domain of endemic from epidemic behavior (Berryman 1982)

Insect population growth does not continue infinitely. Competition for limited resources eventually returns population replacement to 1.0 (Morris 1963, Takahashi 1964 Berryman 1981), as illustrated in Figure 5. Populations that exceed the outbreak threshold density T will increase to the stable point S_2 (density N_2).

Figure 6 illustrates the dynamics of an insect outbreak if a constant environment is assumed. However, if the same population was subject to a different set of environmental factors, a similar replacement curve with different equilibrium points would result. Differences in habitat quality could have the effect of increasing or decreasing the population replacement curve relative to the line where replacement equals 1.0. For example, a population would stabilize at a greater density in a more favorable environment than in a less favorable one (Figure 6, lines A and D, respectively).

Including the effects of habitat variability on replacement and population density enables examination of outbreak dynamics in three dimensions. Figure 7 is an example of an equilibrium manifold (Holling *et al.* 1977).

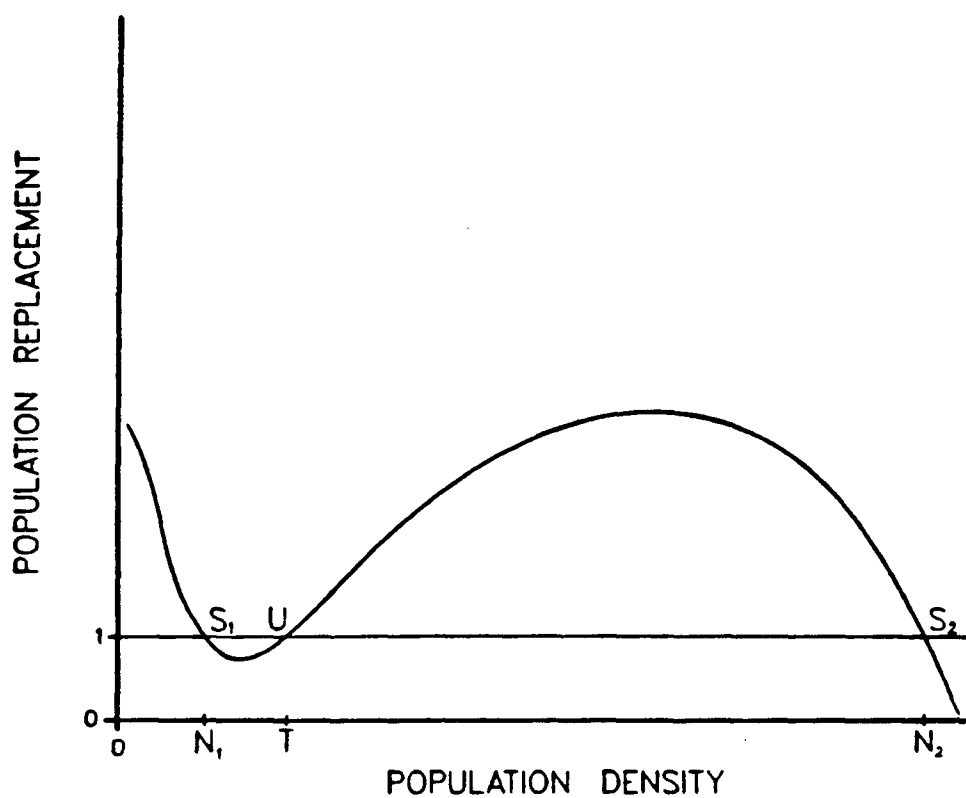


Figure 5: A population replacement curve with three equilibria (Berryman 1978).

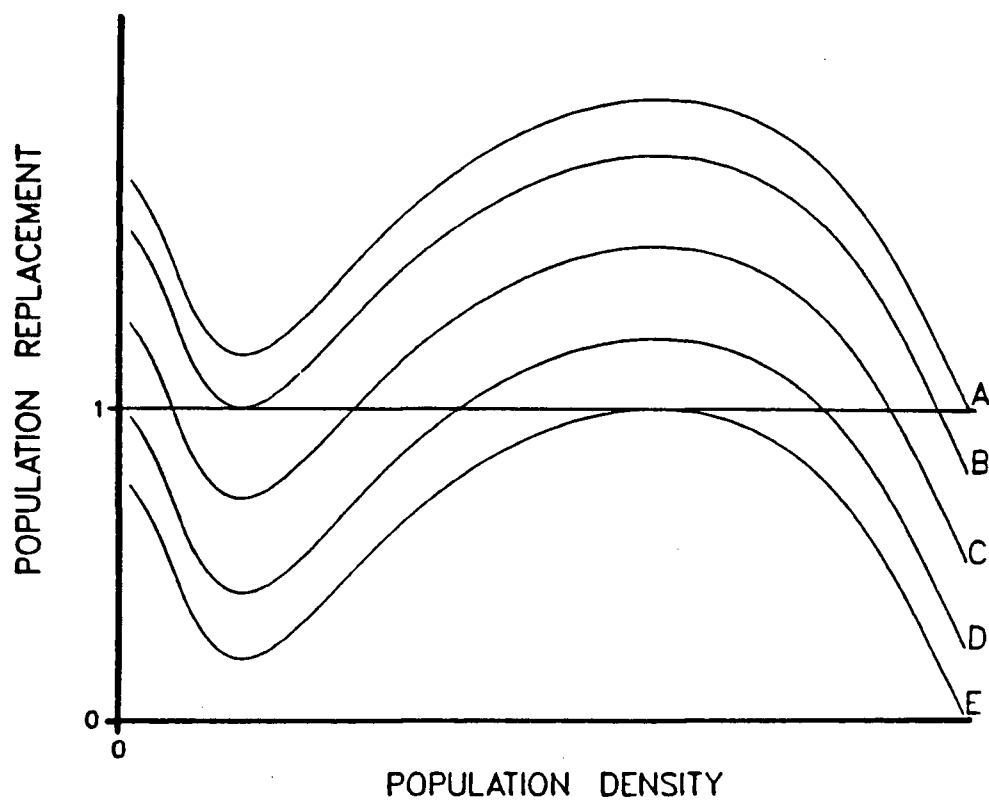


Figure 6: A series of population replacement curves illustrating the effects of different habitats on number of equilibria (Clark *et al.* 1977).

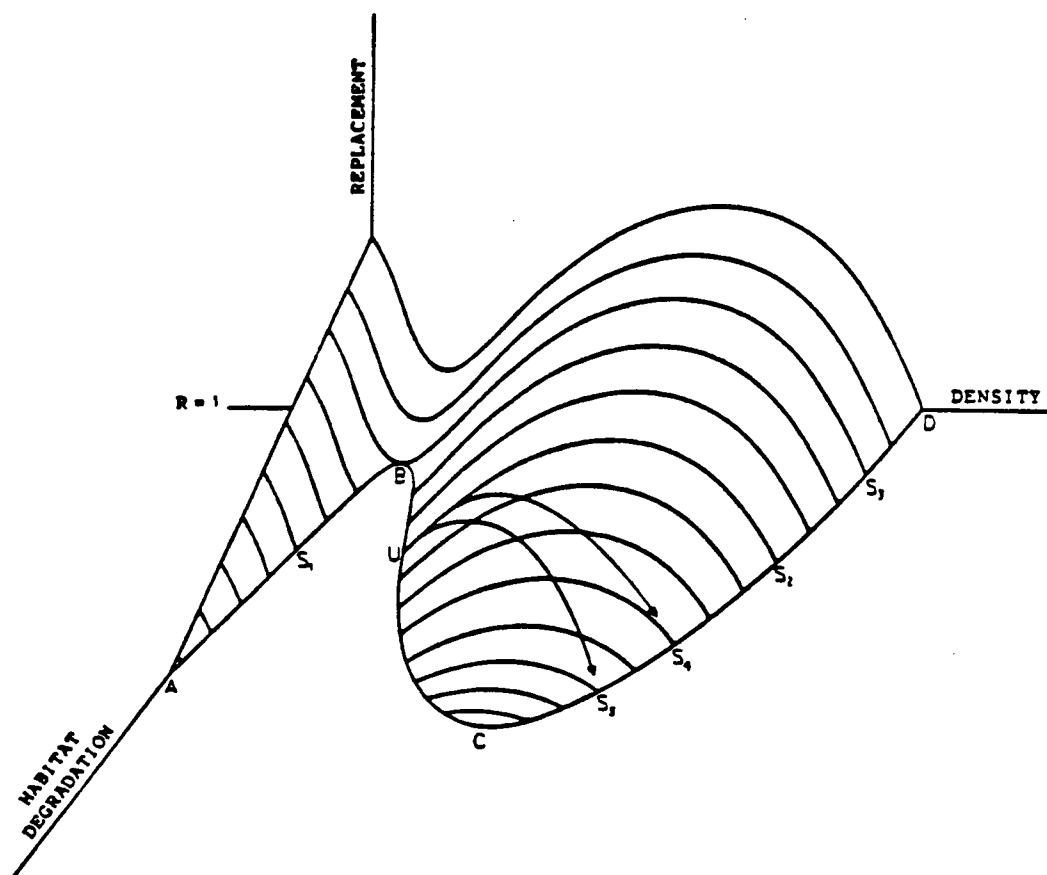


Figure 7: An equilibrium manifold illustrating population responses to habitat degradation (Berryman 1978).

The equilibrium points S_1 , S_2 , and U of Figure 6 are now part of a continuum of equilibrium values from A to D on the plane where replacement equals 1.0. Points along the lines A-B and C-D are stable, while points on the line B-C are unstable.

A population at the lower, stable equilibrium S_1 can now follow two paths into the epidemic domain. First, it may respond to an improvement in habitat quality and move from S_1 to B. At this point the population crosses the epidemic threshold and moves to S_3 where it stabilizes. The second path involves a large increase in density, perhaps through insect immigration. The population would move from S_1 directly to U, and would then move to and stabilize at point S_2 .

During the course of an epidemic many insects, through their own feeding activity, reduce the suitability of their habitat. Should this occur the trajectory of the population growth would be diverted to S_4 or S_5 , depending on the extent of habitat degradation. A continuation of habitat degradation at this time would move the population toward C. At this point population replacement would fall below 1.0, and the epidemic would begin to collapse.

2.2 PREDATOR RESPONSES TO CHANGES IN PREY DENSITY

Solomon (1949) divided a predator's responses to the changes in its prey's density into two major components. The term functional response was used to describe a change in the number of prey captured per predator. This may also be viewed as a change in the proportion of the predator's diet represented by a particular prey species. A change in the density of predators in response to a change in prey density was termed a numerical response.

2.2.1 THE FUNCTIONAL RESPONSE

Three basic forms of the functional response were proposed by Holling (1959). A Type I response was a direct linear response in which the predator's search rate was constant, and the number of prey taken increased in direct proportion to the prey density (Figure 8, graph A). At some prey density the predator became satiated, or the time spent searching for and handling the prey had been reduced to a minimum. The number of prey taken then became constant. A Type I response was found to be typical of filter-feeding invertebrates.

In a Type II, or hyperbolic, functional response (Figure 8, graph B) the number of prey taken diminished progressively. This produced an inverse density-dependent mortality over the range of prey densities. This type of

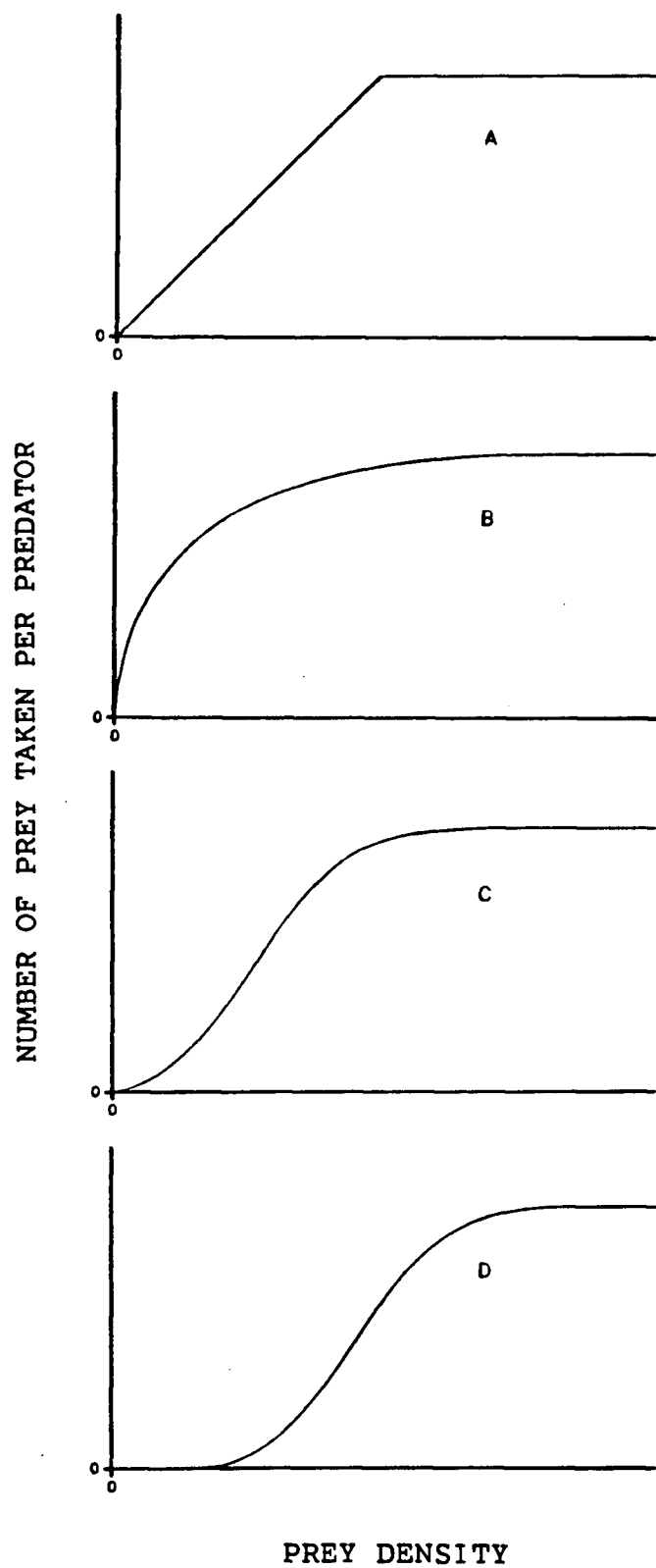


Figure 8: Four types of predator functional responses to changes in prey density (Holling 1959).

This type of response was common in predatory insects. Figure 8 (graph C) illustrates a Type III (or sigmoid) functional response. The number of prey taken initially increased as prey density increased, then decreased in much the same manner as the Type II response, because of satiation and/or handling time effects. The resultant prey mortality was density-dependent at first, then became inversely density-dependent as prey density continued to increase. Studies by Betts (1955), Baldwin (1960), and Mook (1963) documented the Type III response in some insectivorous birds.

Holling (1959) originally proposed two forms of the Type III response (Figure 8, graphs C and D). In form C, the response of the predators was immediate. The second form (D) included a time-lag effect. This modification has since been used to accomodate effects such as prey switching (Murdoch 1969), changes in predator feeding behavior (Kendeigh 1947, Morris *et al.* 1958, McCambridge and Knight 1972), electivity (Ivlev 1961), search image formation (DeRuiter 1952, Tinbergen 1960), critical prey density (Kendeigh 1947, Tinbergen 1960, Beaver 1967), and minimum prey size (Kendeigh 1947, Tinbergen 1960, Koplin and Baldwin 1970).

The proportion of the prey population taken by predators representing each of Holling's original response types is shown in Figure 9. The Type I and Type II responses

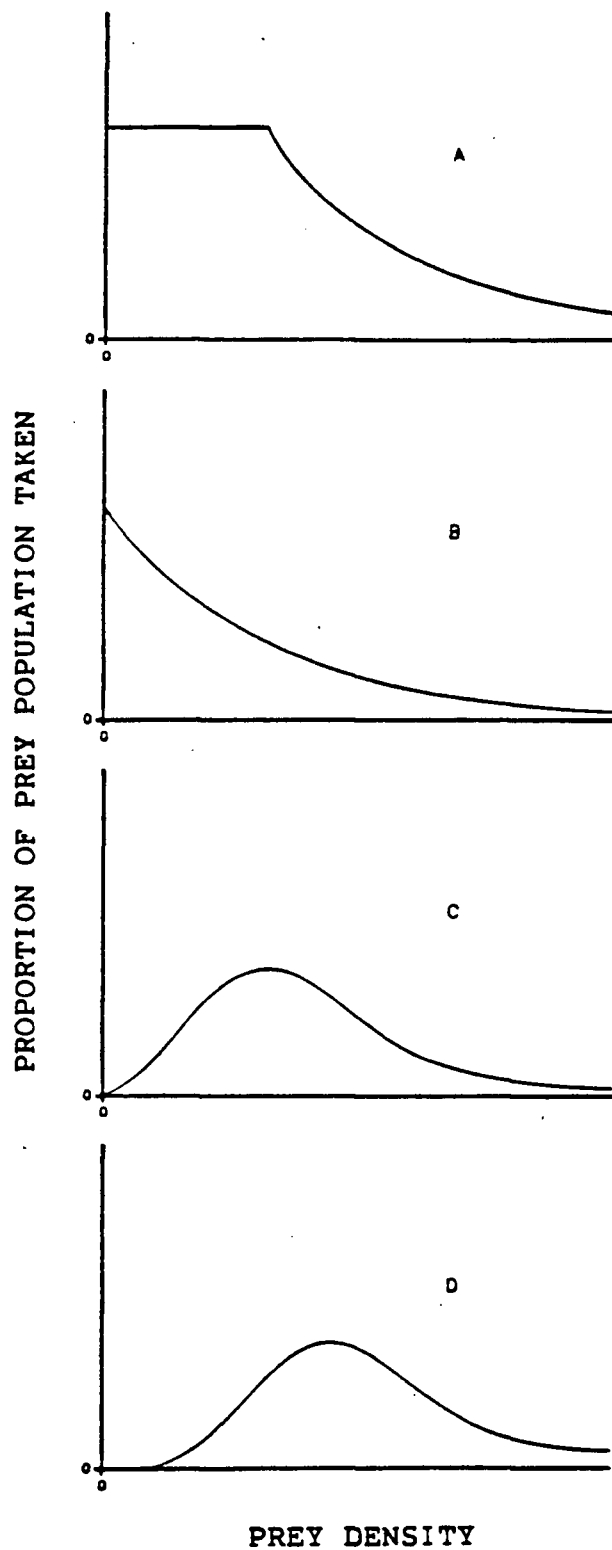


Figure 9: Proportion of prey taken per unit time by predators exhibiting the functional responses illustrated in Figure 8 (Holling 1965).

(A and B) allow a constant or increasing proportion of the prey to survive as prey density increases. This creates a positive feedback on the population. Therefore these response Types cannot have a regulating effect on the prey population (Berryman 1981). However, in the Type III response the predator initially takes an increasing proportion of the prey population. This creates a density-dependent negative feedback on the prey when its density is low. The initial density-dependent mortality is critical to the concept of biological control in that Type III predators, if they react quickly to prey population increases, may be able to prevent insect densities from moving beyond the threshold density shown in Figure 4.

2.2.2 THE NUMERICAL RESPONSE

The numerical response of a predator can take three basic forms (Figure 10). Curves A , B and C represent a direct numerical response, no response, and an inverse response, respectively. All three response types have been reported for avian predators of irruptive insects (Kendeigh 1947).

The direct response can occur in three ways: through aggregation of the predator, through an increase in predator survival, or through an increase in predator reproduction. Increase through aggregation is the most commonly reported

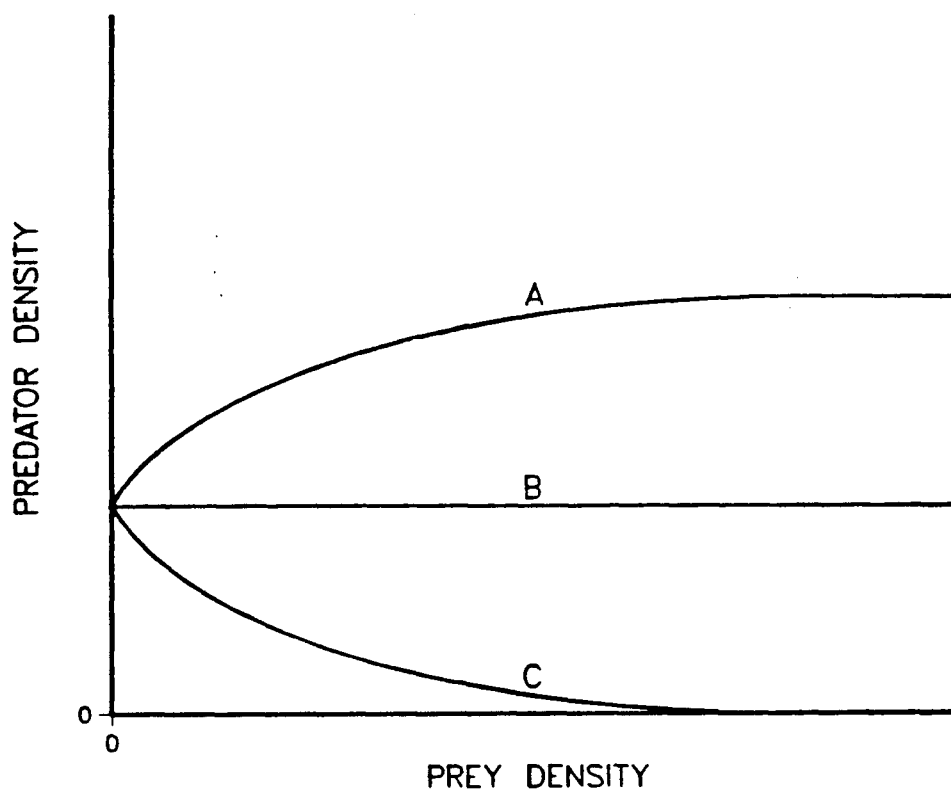


Figure 10: Three types of predator numerical responses to changes in prey density (Elseth and Baumgardner 1981).

form of direct response. It can occur temporarily, or on a daily or seasonal basis. Blackford (1955), for example, found that several species of woodpeckers entered a burned area each day to feed on the beetle larvae in the dead trees, and returned to their roosts in the nearby unburned woods in the evening.

During an outbreak of the eastern spruce budworm Kendeigh (1947) noted temporary increases in the numbers of savannah and white-crowned sparrows, and several species of warblers. These birds were present for a few days only, and appeared to have taken advantage of the available food source as they passed through the area during migration.

During the same study Kendeigh described the breeding bird population of the area as being composed of a nucleus of permanent residents, and a larger number of birds that remained only for the summer. He suggested that the initial influx of migratory birds consisted predominantly of those that had nested in the area the previous spring. The later-arriving migrants may have included a large proportion of birds that were raised in the area the previous spring. Those late-arriving birds that found sites still available established territories of their own. The three bird species that exhibited the greatest numerical response were seasonal species.

As noted by Kendeigh (1947), the seasonal bird population was composed mostly of birds that had nested in the area the previous spring, plus some birds that were raised in the area that spring. The following year a larger number of birds returned to the area. In this manner the breeding season population increased during the epidemic. The upper limit on total bird density may have been fixed by factors such as a limited number of nest sites or maximum compression of territories.

Otvos (1965) proposed an alternative process through which bird density could increase during the course of a bark beetle infestation. As the infestation progressed, an increasing number of trees were killed by the insects. This resulted in an increase in the number of potential nest sites available to the woodpeckers.

Numerical responses may also occur due to increases in bird reproduction. Lack (1955) found that the clutch size of British titmice increased in years when caterpillars were more abundant. MacArthur (1958) described the population ecology of five species of warblers in eastern Canada. He found that the clutch size of the bay-breasted warbler was significantly larger during spruce budworm outbreak years, but he did not have sufficient data to make similar comparisons for the other species.

Predator functional and numerical responses can occur simultaneously. In Figure 11 the functional responses are plotted as the proportion of the prey population taken per predator. The numerical responses are plotted as predator density. The combined impact (total effect) on the prey population is calculated by multiplying the corresponding values of the functional and numerical responses.

The total effect of the Type I and Type II responses produces a density-dependent mortality only if the direct numerical response occurs simultaneously. The Type III response, however, is capable of producing density-dependent mortality even if an inverse numerical response occurs. Therefore, it appears that the Type III predators (vertebrates) are the only ones capable of exerting control over the populations of their prey through both functional and numerical responses.

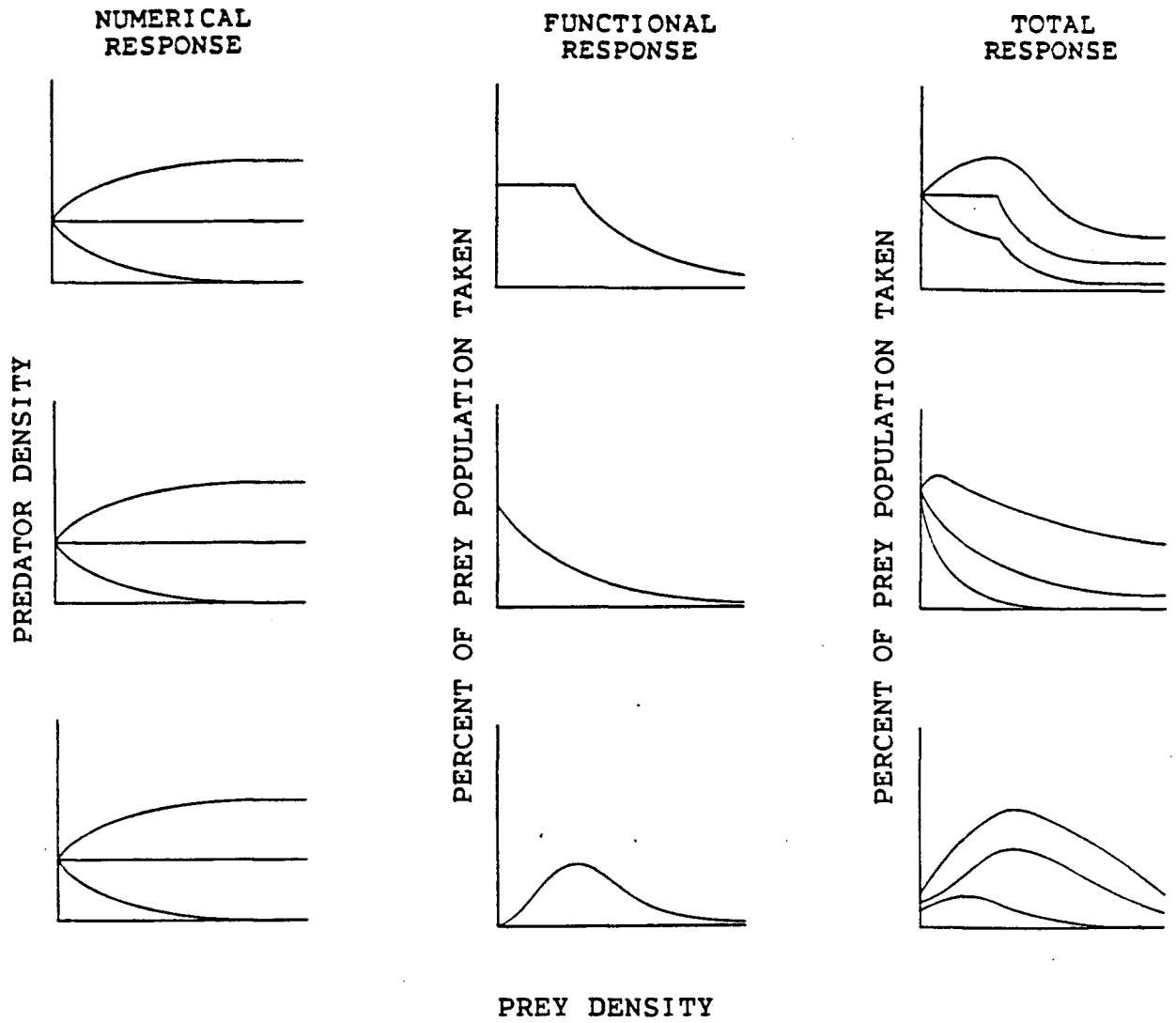


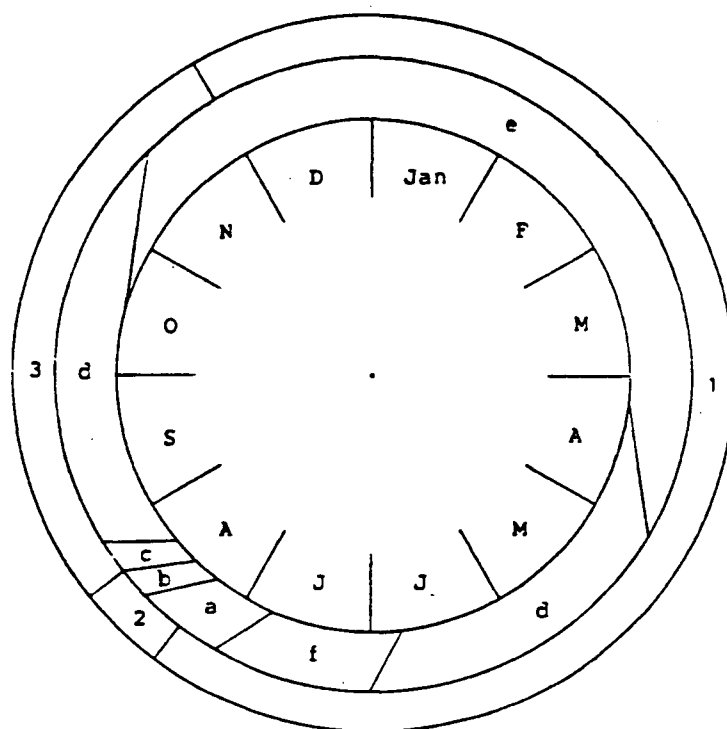
Figure 11: Total predator responses to changes in prey density (Elseth and Baumgardner 1981).

3. GENERAL CONSIDERATIONS FOR MODEL DEVELOPMENT

3.1 THE INSECT

3.1.1 LIFE CYCLE

The mountain pine beetle usually has a 1-year life cycle (Figure 12). Adults emerge between late July and mid-August (Reid 1962a), and fly to uninfested trees where the females bore through the outer bark and begin construction of an egg gallery in the tree phloem. At this time the attacking beetles also inoculate the host tree with one or more species of blue stain fungi. The fungi are important in slowing down the tree's resin responses, enabling the females to build egg galleries. During gallery construction the females combine two chemicals, *trans*-verbenol and *exo*-brevicomin, from their bodies with host-tree monoterpenes such as *alpha*-pinene, *beta*-phellandrene, and myrcene to create a pheromone that attracts more beetles to the tree (Vite and Pitman 1968, Cole *et al.* 1981, and Borden *et al.* 1983). Once mated, the females lay 40 to 80 eggs each (Peterman 1974, Safranyik *et al.* 1974), though more than 200 eggs per female has been recorded in British Columbia (Reid 1962b). Depending on climate, weather, and date of initial emergence an adult female may re-emerge, attack a new tree, mate, and lay more



KEY	
Life Cycle Stages	
a:	Adult
b:	Flight and attack
c:	Egg
d:	Larva
e:	Larval dormancy
f:	Pupa
Susceptibility To Avian Predation	
1:	Woodpeckers only
2:	All predator species
3:	Low susceptibility to all species

Figure 12: Mountain pine beetle life cycle.

more eggs. This phenomenon is considered rare north of Montana (Amman and Cole 1983) though it was observed near Invermere, B. C. by Reid (1962a).

Eggs hatch after about two weeks (Reid and Gates 1970). The larvae feed on the tree phloem (or inner bark), and move at approximately right angles to the vertical egg gallery (Amman and Cole 1983). The mountain pine beetle develops through four larval instars before pupation. Depending on date of hatch the brood may develop from egg to teneral (immature) adult before becoming dormant for the winter (Reid 1962a). All eggs and most of the small larvae that enter the winter are killed by cold temperatures (Amman 1973). Adults that emerged and attacked late in the summer may survive through the winter if temperatures are mild, otherwise few adults emerge for a second summer (Amman and Cole 1983).

In April or May the surviving larvae resume feeding, excavate a cell in the bark or sapwood, and pupate. The pupae mature in one to two weeks. Following a period of relatively high temperatures and abundant sunshine the beetles emerge. All beetles from a common chamber emerge through one hole in the bark (Reid 1963). Most beetles emerge in a period of about one week (Reid 1962a, Stallcup 1963, Rasmussen 1974), though the emergence period may last over four weeks.

3.1.2 FACTORS INFLUENCING EPIDEMICS

The exact nature of the processes that shift mountain pine beetle populations from endemic to epidemic levels are only partially understood. During epidemics even the largest, most vigorously growing trees may be overcome by mass attack (Safranyik *et al.* 1974, Safranyik 1984 personal communication). Beetle production in these trees is high, resulting in population growth. At endemic levels, however, there is usually an insufficient number of beetles present to infest the large trees. Consequently, the population remains at a constant level or declines.

Two general theories to explain the transition from endemic to epidemic behavior have evolved. One involves prior infestation by secondary bark beetles, particularly engraver beetles. A small number of mountain pine beetles may survive in and emerge from trees initially infested by the engraver beetles. When several of these infested trees are situated close together the combined number of emerging mountain pine beetles may be sufficient to successfully attack a large, uninfested tree nearby (Amman 1978, Raffa and Berryman 1980, Amman and Safranyik 1985).

In the second theory, the pine beetles attack large trees which are under stress, and can therefore be successfully infested by a smaller number of beetles. Some of the possible sources of tree stress include diseases such

as root rots (Stark and Cobb, Jr. 1969, Raffa and Berryman 1980, Gara *et al.* 1985), rusts, and dwarf mistletoe (Schmitz 1985 personal communication), smog (Stark and Cobb, Jr. 1969), insect defoliation (Amman and Safranyik 1985), drought (Safranyik *et al.* 1974, Amman 1978, Berryman and Stark 1985), seasonal and ontongenal declines in tree vigour (Safranyik *et al.* 1974, Amman 1978), and lightning strikes (Raffa and Berryman 1980, Berryman and Stark 1985, Schmitz 1985 personal communication). Furthermore, factors such as tree diseases and lightning strikes often affect small, isolated groups of trees (Schmitz and Taylor 1969, Schmitz 1985 personal communication). This isolation would assist in the local concentration of the mountain pine beetle population.

Once the beetle population begins to expand, the spread of the epidemic may be significantly influenced by site weather, elevation, latitude, and the extent of the available food source. The rate of mountain pine beetle development varies with temperature (Reid and Gates 1970, Safranyik *et al.* 1974). Cool summer temperatures may extend the life cycle to two years (Reid 1962a). This longer life cycle exposes the immature stages to mortality factors for longer periods of time (Safranyik *et al.* 1974). Cool summers may also cause adult emergence and flight to occur later than normal. Eggs laid by these late-emerging adults may not

hatch before the onset of winter. The probability of these eggs surviving through the winter is extremely low in western Canada except along British Columbia's southern coast (Safranyik *et al.* 1974). Exposure to summer temperatures of about 38 °C for long periods of time will kill all stages, however the critical temperature for short time periods is 43.3 °C (Safranyik *et al.* 1974). Optimum weather conditions for mountain pine beetle population growth are a moderately warm autumn, mild winter, moderate weather in the spring and early summer, and hot, dry weather in July and August (Reid 1963).

When determining beetle development and/or survival it is important to consider the elevation and latitude of the site. These two factors can have a major influence on temperature as indicated by Hopkins' Bioclimatic Law (Hopkins 1920). Reid (1962a) found that broods of the mountain pine beetle raised at Invermere, B.C. (elevation 835 m) developed from egg to teneral adult between July and September, while broods raised in the Banff area (elevation 1366 m) where temperatures averaged six to eight degrees lower reached only the fourth instar stage in the same time period.

Amman (1973) studied mountain pine beetle populations at four elevations (1923, 2130, 2450, and 2573-2750 m) and determined that eggs constituted 12% of the winter

population at 1923 m, and 90% at 2573-2750 m, which also indicated slower development at higher elevations. In addition, Amman (1973) found that survival rates changed with elevation. Parent adult winter survival, for instance, was 67% at the lowest elevation compared to 12% at the highest elevation. As a result of lower total beetle survival fewer trees were killed at the higher elevations.

Site latitude can also influence the mountain pine beetle life cycle. Reid (1962a) found that no beetle spring flights occurred in the Invermere study area though he stated that they were "common" in the more southern regions. Amman *et al.* (1973) found that tree mortality from beetle attack at 2830 m at 40° N was equal to mortality at 2615 m at 43° N (Amman *et al.* 1973). In British Columbia Safranyik *et al.* (1974) considered their climate-based mountain pine beetle hazard map to be valid from 770 m at the northern limit of the beetles' distribution to 1230 m in southern B.C.

The beetles' food source is the phloem of the tree. The amount of phloem is considered to be the primary factor in determining brood survival and production (Amman 1969, Amman 1972a, Amman 1972b, Berryman 1976). In general, the number of eggs laid, the size of late instar larvae, and the ratio of emerging beetles to parent attacking beetles are all greater in trees with thick phloem (Amman and Pace 1976,

Amman *et al.* 1977, Amman and Cole 1983). Because phloem thickness is positively correlated to tree diameter (Amman 1969), and is also related to good tree vigour (Cole 1973) large, vigorous trees produce more beetles than do small and/or non-vigorous trees. A large number of trees in a stand, however, does not necessarily produce an increased supply of phloem. Trees in dense stands generally have thinner phloem than those grown in more open stands (Amman *et al.* 1977). There exists a trade-off, then, between the amount of phloem available per tree and the total amount available in the stand. For lodgepole pine stands in general, the mountain pine beetle is food (phloem) limited where developmental temperatures are optimum, and limited by climate at high elevations or at the northern latitudinal limits of the its occurrence (Amman 1969, Amman and Cole 1983).

3.1.3 PAST HISTORY AND CURRENT TRENDS

In British Columbia mountain pine beetle activity was first recorded in 1910 (Manning *et al.* 1982). The areas where damage historically has been the greatest are the Chilcotin Plateau, and the south-central and south-eastern interior. In recent times infestations have increased significantly, especially in the Chilcotin Plateau of the Cariboo Forest District.

Approximately 2/3 of the infestations mapped in 1984 were twenty hectares or less in area; and on about 2/3 of the mapped area less than 30% of the susceptible host trees were attacked. Furthermore, the ratio of overwintering progeny to parent beetles ranged from 0.6 to 25.0 in the Kamloops, Cariboo and Nelson Regions (Wood and Van Sickle 1984b). A factor of 4.1 or greater indicates a rising population. Overall, there is a great potential for expanding and intensified attacks in the three Regions listed above.

3.2 THE HOST TREE SPECIES

3.2.1 LOGEPOLE PINE CHARACTERISTICS

The mountain pine beetle has been observed to infest ten native pine species (Wood 1963) and five exotic pine species (Furniss and Schenk 1969). In British Columbia the primary host tree is lodgepole pine (Reid 1962a, Amman and Cole 1983, Safranyik 1984 personal communication). Ecologically, this species is moderately drought resistant, shade intolerant, an aggressive pioneer species (Krajina *et al.* 1982, Angove and Bancroft 1983), and susceptible to fire. Trees may produce seed by the age of five years. The cones mature in one year, and are often, though not always, serotinous, increasing the ability of the species to invade

and regenerate a site after a fire (Arno 1980)

Lodgepole pine can be classified as a seral, persistent seral, or climax species depending on site location (Volland 1985). It is seral where conditions allow the establishment and growth of shade-tolerant species. On sites where disturbances occur periodically or where the environment is only marginally suited for the establishment of competing species, lodgepole pine is considered a persistent seral species (Volland 1985). It may be classified as a climax species when cyclic wildfires have removed the seed source of shade-tolerant competing species, or edaphic conditions are such that no other species can become established on the site (Pfister *et al.* 1977, Volland 1985). Wildfires are considered to be the factor most responsible for the establishment and structure of extensive, even-aged lodgepole pine stands common in western Canada and the western United States (Brown 1973).

In British Columbia clearcutting is the most commonly used method for harvesting lodgepole pine (Anonymous 1981, Schmidt and Alexander 1985). The slash that remains after harvesting is usually wind-rowed and burned. This treatment exposes mineral soil and simultaneously opens any serotinous cones on the site. Site regeneration generally relies on natural reseeding, though some areas are seeded or planted.

3.2.2 TREE AND STAND SUSCEPTIBILITY

When the mountain pine beetle is present at epidemic levels individual tree susceptibility to attack depends initially on tree diameter at breast height (DBH), and ultimately on tree vigour. In other words, a tree may be attacked because of its size but, once attacked, its survival depends on its ability to resist the attack. During an infestation, attacking mountain pine beetles appear to exhibit a 'preference' for the larger diameter trees in a stand (Hopping and Beall 1948, Cole and Amman 1969, Safranyik *et al.* 1974). Research by Shepherd (1966) has shown that attacking beetles are attracted to large, dark objects silhouetted against a lighter background, indicating that attack may be based at least partly on visual cues. However, Cole *et al.* (1981) suggested that the beetles may also respond to olfactory stimuli in the form of terpenes that occur in greater quantities in larger trees.

Burnell (1977), in his theory on mountain pine beetle aggregation, assumed that there was a small number of pioneer or first attacking beetles, and that each susceptible tree had a threshold number of pioneer beetles required to induce mass attack (aggregation of a large number of beetles) of the tree. The initial response of a tree to pioneer beetle attack is an extensive flow of resin from ducts severed by the boring activity of the beetles. If

the attacked tree is resistant and vigorously growing its response may be rapid and massive enough to overwhelm the pioneer beetles, and prevent their establishment. A non-resistant tree of low vigour will produce only a limited resin response, and the pioneer beetles will have sufficient time to release the aggregating pheromone that initiates mass attack. Once mass attack has begun the tree has little chance of survival.

Safranyik *et al.* (1974) examined attacked trees in two beetle-infested stands and found that the cumulative annual growth of some trees declined much more with time than others. The slow-growing, 'non-resistant' trees were found to suffer greater mortality than faster growing, 'resistant' trees.

Using a different approach, Waring *et al.* (1980) defined tree vigour as the current growth (in grams of stemwood produced) per square meter of crown leaf surface. Mitchell *et al.* (1983) examined trees in three infested stands and, using Waring's definition, compared tree vigour to beetle-caused tree mortality. They found that mortality increased noticeably when trees produced less than 80 grams of stemwood per square meter of foliage. Individual trees with vigour ratings of 100 grams or more of stemwood produced were rarely attacked or killed.

Stand susceptibility to mountain pine beetle epidemics is greatly influenced by stand age, diameter distribution, stand density, and overall stand resistance and vigour as defined above. Four other variables (weather, elevation, latitude, and food supply) were discussed in section 3.1.2.

Outbreaks of mountain pine beetle rarely develop in stands with an average age of less than 60 years. The phloem on the young trees is too thin for high beetle productivity, and mortality factors such as freezing and desiccation are greater in smaller trees (Safranyik *et al.* 1974, Amman *et al.* 1977, Amman and Cole 1983). Assuming that the smaller trees are the younger trees, stands with an average age of 60 to 80 years are considered intermediate risks, and stands greater than 80 or 90 years old present the greatest potential for infestation (Safranyik *et al.* 1974, Amman *et al.* 1977).

In general, large trees produce more beetles than do small trees because of their greater average phloem thickness. The ratio of emerging to attacking beetles is usually less than one in trees smaller than 25 cm at DBH, but may be as great as six or eight in trees greater than 40 cm DBH (Safranyik *et al.* 1974, Amman *et al.* 1977). Therefore, stands with a high proportion of large diameter trees are more susceptible to infestation.

Stand density influences average tree phloem thickness. Generally, low density stands have a greater proportion of large diameter trees with thick phloem, and so are more susceptible to outbreaks. High-density 'doghair' stands of lodgepole pine rarely undergo infestation.

Both Safranyik *et al.* (1974) and Mitchell *et al.* (1983) related stand susceptibility to the proportion of the stand made up of 'resistant' or 'vigorous' trees as defined previously. Safranyik *et al.* (1974) found that the number of resistant trees in a stand varied both seasonally and over the 'life' of the stand. Seasonally, the number of resistant trees increased until July, then decreased. Over the stand life the proportion of resistant trees increased until an age of 40 to 60 years, then rapidly decreased (Figure 13). The maximum level of stand resistance was found to be positively correlated with the maximum current annual increment and the culmination of basal area growth, assuming a fully stocked stand.

Mitchell *et al.* (1983) related individual tree vigour as defined by Waring *et al.* (1980) to leaf area index and basal area, then compared the results to the beetle-caused mortality on several stands. Those stands with leaf area indices of approximately 1.0, and basal areas of roughly 15.0 square meters per hectare had the lowest mortalities. However, Waring *et al.* (1980) pointed out that the results

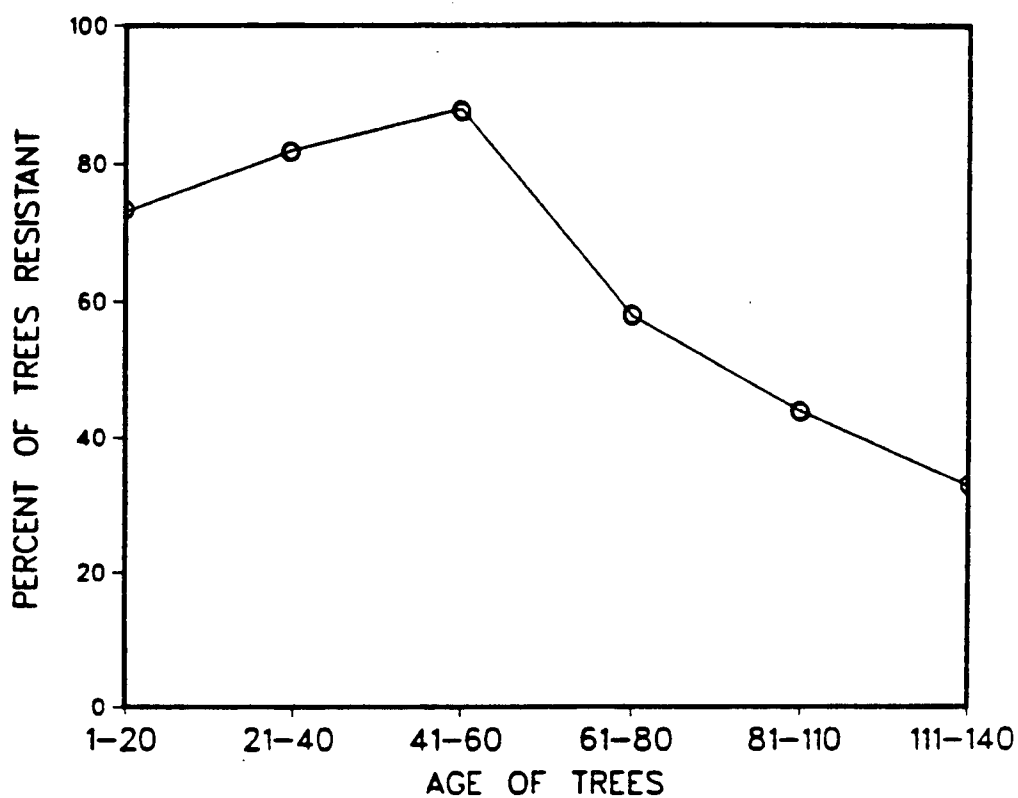


Figure 13: Change in frequency of resistant lodgepole pine trees for different aged stands (Safranyik *et al.* 1974).

were preliminary, required further research, and should not be used as a guide for stand management.

3.2.3 MOUNTAIN PINE BEETLE EFFECTS ON TREES AND STANDS

Attack of a tree by the mountain pine beetle produces one of three results: successful resin response by the tree, a 'strip' (partial) attack, or death of the tree. If the tree's resin response (section 3.2.2) is successful the beetle is 'pitched out' of the tree. Residual pitch tubes on the bole of the tree may be the only indication that the tree was once attacked.

In some cases, the beetle is only partially successful in its attack. This results in a 'strip' attack in which only a vertical section on part of the tree is infested. Although strip attacks may occur in 15% of the attacked trees in a stand (Wood and Woensdregt 1981) the dynamics of this type of attack are currently not well understood. It is known that trees may survive a strip attack, however their resistance to further attack may be lessened (Rasmussen 1974, Burnell *et al.* In Press).

Beetle colonization will be successful if the tree's resin response is insufficient to contain the fungi and beetles. Following germination the fungal spores penetrate live phloem and xylem cells. The fungi interfere with water conduction and the tree's defensive resin response. Also,

well-developed blue-stain fungi cause the tree to dry rapidly in the winter after attack, but remain more moist the following summer, reducing beetle mortality due to desiccation (Amman *et al.* 1977). The growing fungi move rapidly in a vertical direction, but slowly in a horizontal direction. The beetle larvae, however, feed more or less horizontally, thus spreading the fungi. In this manner the combined action of the beetle-fungi association essentially girdles the tree.

As an infestation progresses the mountain pine beetles generally attack the largest remaining live trees. However, overall population productivity declines as the beetles are forced to attack smaller trees, and the outbreak eventually collapses. The overall effect of a mountain pine beetle infestation is a proportionately greater mortality in the larger DBH classes (Figures 14 and 15), and a reduction in average stand diameter.

3.2.4 SILVICULTURAL APPROACHES TO REDUCING SUSCEPTIBILITY

It has been suggested that the susceptibility of a stand to attack by mountain pine beetle can be reduced through silvicultural methods. Stands should first be ranked according to susceptibility, and those with the greatest probability of outbreak given treatment priority.

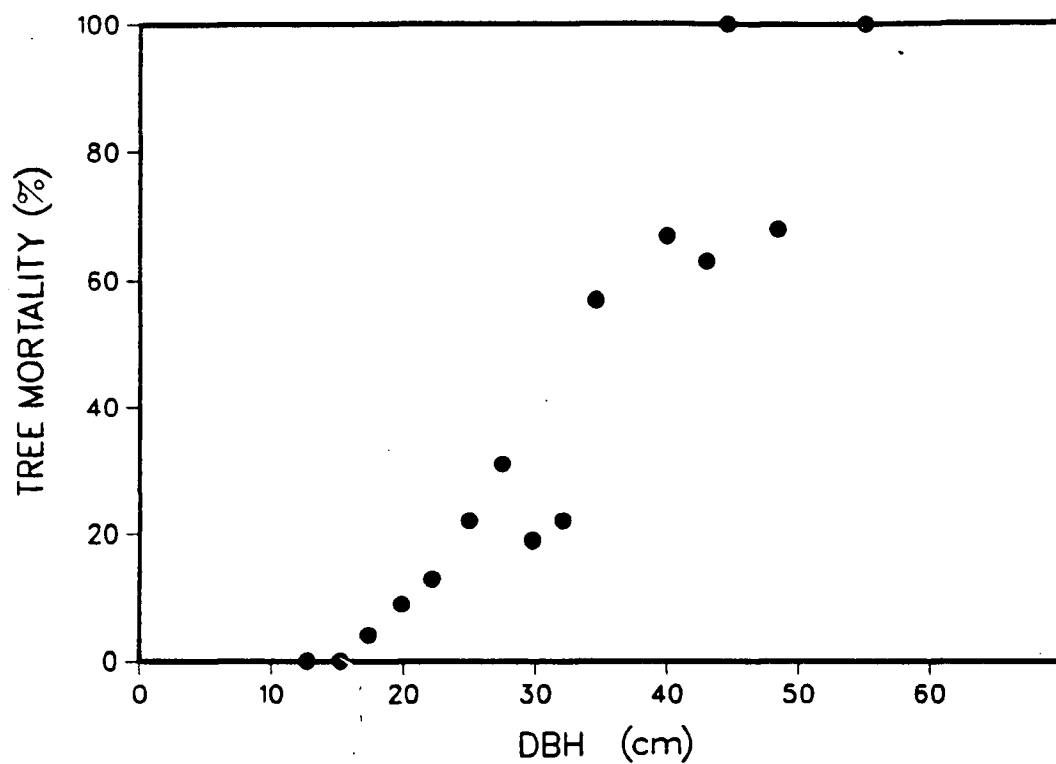


Figure 14: Mortality in a lodgepole pine stand attacked by the mountain beetle in relation to tree DBH (Hopping and Beall 1948).

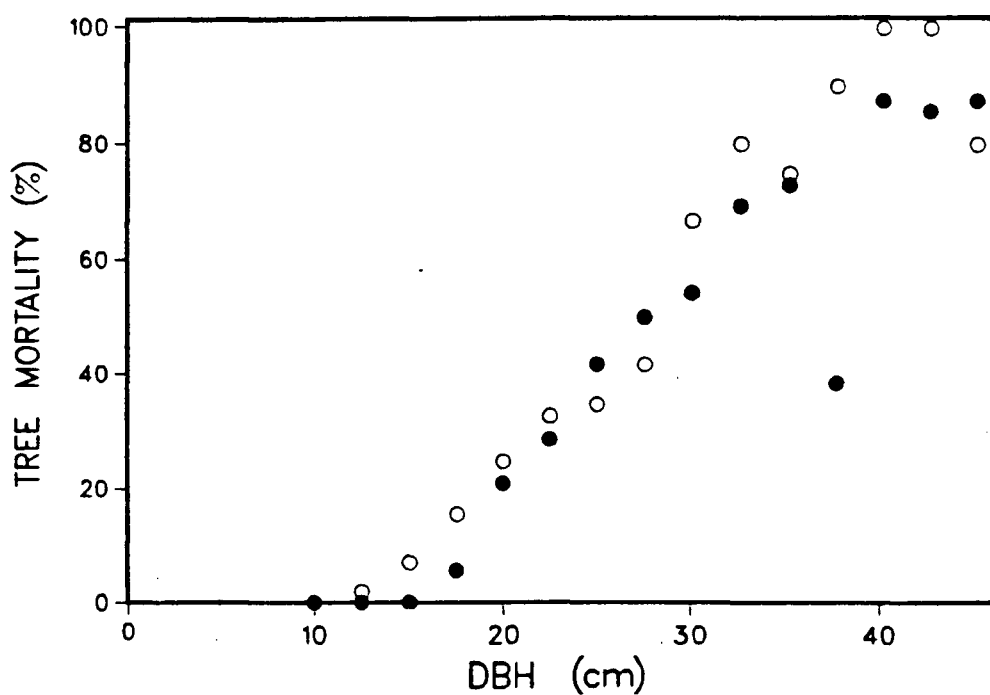


Figure 15: Mortality in two lodgepole pine stands attacked by the mountain beetle in relation to tree DBH (Cole and Amman 1969).

In areas where lodgepole pine stands are chronically susceptible to beetle outbreaks the replacement of pines by a non-host species may be the best option. In some areas, lodgepole pine is not the climax species but persists in the stand because of its competitive abilities and/or a limited climax species seed source (Pfister *et al.* 1977, Volland 1985). In these areas conversion to the climax species should be encouraged. Clearcutting, however, often results in site conditions that preclude the establishment of shade-tolerant replacement species. Therefore, an extensive planting campaign would probably be necessary.

Thinning from above is a second alternative. In this method the most susceptible trees would be removed, and the residual pine stems would act as nurse trees providing shade and shelter to aid the establishment of the new, climax species. There are two possible drawbacks. First, planting may be necessary and second, the residual stems may be subject to stem collapse or windthrow.

An alternative to total replacement of lodgepole pine is the creation of mixed-species stands (Safranyik *et al.* 1974, Amman *et al.* 1977). This option has several advantages. First, the insect susceptibility of mixed species stands is lower than that of pure stands. Even if the mixed species stands were attacked, the loss in terms of residual stocking would be less than that of a pure stand

(Amman *et al.* 1977). A mosaic of age classes would also help prevent the simultaneous development of outbreaks over large areas (Safranyik *et al.* 1974). One possible drawback would be the complex management necessary for the maintenance and harvesting of such stands.

In some stands, conversion to or introduction of a second species may not be possible. In this case, the two best available options are thinning (either pre-commercial or commercial), or a reduction of the rotation age. The mountain pine beetle appears to show a preference for larger diameter trees (Cole and Amman 1969, Safranyik *et al.* 1975) and survives and reproduces better in their thicker phloem. Therefore, removal of these larger trees would reduce the potential for infestation. Safranyik *et al.* (1974) and Amman *et al.* (1977) agreed that the removal of trees greater than 20 cm at DBH would reduce stand susceptibility.

The potential for a mountain pine beetle outbreak increases with stand age, particularly after age 80 years. Safranyik *et al.* (1974) indicated that tree and stand resistance is greatest between the ages of 40 and 60 years. Therefore, a reduction in rotation age could also reduce the susceptibility of a stand to mountain pine beetle attack.

One final option available is to do nothing to prevent or control infestations, and allow them to run their natural course (Amman 1976). The many openings created by the death

of the lodgepole pine trees would allow natural succession to take place. Douglas-fir would become dominant at lower elevations, and Engelmann spruce and subalpine fir at higher elevations (Pfister *et al.* 1977). Standing wildlife trees (or snags) would provide perches for some raptors, and nest sites for cavity-nesting birds (Amman *et al.* 1977, Lester 1980). Fallen logs would provide nest sites for ground-nesting birds, and bedding and cover for various large and small mammals (Thomas 1979). However, doing nothing does have its negative effects. An outbreak in one stand may spread to another stand where the do-nothing option is not acceptable. The option also results in a large amount of unused timber. Finally, the dead trees add to the build-up of the stand's fire fuel load (Brown 1973).

3.3 THE AVIAN PREDATORS

3.3.1 PREDATOR IMPACTS

To date nineteen species of birds have been identified as predators of the mountain pine beetle (Table 1). During the winter, when the larvae are beneath the bark, only birds of the woodpecker family can feed effectively on them. Woodpeckers have numerous special adaptations that enable them to find and remove wood-boring insects. They have sharp, chisel-like bills that allow excavation through live

Table 1: Avian Predators Of The Mountain Pine Beetle

<u>BIRD SPECIES</u>	<u>SOURCE</u>
Common nighthawk	1
Pileated woodpecker	5
Hairy woodpecker	1, 4, 5, 6, 7
Downy woodpecker	4, 5, 6, 7
Black-backed woodpecker	6
Three-toed woodpecker	1, 6
Western wood pewee	4
Olive-sided flycatcher	4, 7
Empidonax ssp.	4
Clark's nutcracker	4
Mountain chickadee	4
White-breasted nuthatch	4
Red-breasted nuthatch	1
Pygmy nuthatch	4
Brown creeper	4
American robin	4
Townsend's solitaire	4
Mountain bluebird	2, 3
Yellow-rumped warbler	4

1: Rust 1929

2: Blackman 1931

3: Beal 1939

4: Stallcup 1963

5: Amman 1973

6: Lester 1980

7: Otvos and Stark 1985

or dead wood, and their strong neck muscles and thick skull absorb the shock of the blows. The extremely long, barb-tipped tongue can be extended far beyond the bill in order to locate and withdraw insects from deep within the tree. The sharp-clawed feet, usually with two toes forward and two toes back, are designed for clinging to bark. The feet and stiff, tapered tail feathers stabilize the bird, and contribute to the efficiency of the pecking action. (Bent 1939, Jackman 1975).

Amman (1973) reported the predation of overwintering mountain pine beetle adults by the hairy and downy woodpeckers. Mortality due to the woodpeckers varied depending on elevation. Woodpeckers consumed an estimated 54% of the parent adults at high elevations (2573-2750 m), 37% at 2450 m, and 21% at 2130 m. Woodpecker-caused mortality was not measured at 1923 m, but was assumed to be small. Amman suggested that woodpecker predation was greatest at high elevations because the larvae were larger and more numerous. Furthermore, preference for the parent adults over the larvae may have been due to the smaller size of the larvae. Studies on woodpecker predation of the Engelmann spruce beetle (Koplin and Baldwin 1970) and evening grosbeak predation of the eastern spruce budworm (Blais and Parks 1964) appear to support Amman's observations concerning the influence of prey size.

In Montana, Lester (1980) studied woodpecker predation in 8 stands with different mountain pine beetle population densities. The most common woodpecker species during the winter were the three-toed, hairy, and black-backed woodpeckers. Though no stomach samples were taken, Lester made some estimates of brood mortality due to woodpeckers based on bark disturbance. Woodpecker feeding disturbed approximately 10% of the bark on beetle-attacked lodgepole pines. Most of the bark removal was in patches of less than or equal to 6.45 cm^2 in area. Bark beetle larvae in phloem adjacent to areas disturbed by woodpeckers may die from desiccation and increased exposure to cold temperatures (Otvos 1979). Lester (1980) estimated that the zone of such indirect influence was 1.3 cm wide around the area of bark removal. Based on estimated direct consumption by woodpeckers, and the indirect effect of the zone of influence of disturbed bark, she estimated that woodpeckers were responsible for about 30% of the total beetle brood mortality.

Cole (1981) examined risks and causes of mortality in pre-epidemic, epidemic, and post-epidemic populations of the mountain pine beetle in 23-cm, 30-cm, and 38-cm tree diameter classes. The probability of larval mortality from woodpeckers was lowest in 38-cm trees regardless of infestation stage, decreased with infestation stage in the

30-cm tree diameter class, and increased with infestation stage in the 23-cm stage. Cole suggested that snow depth, bark thickness, and beetle densities may have been important factors in tree selection by woodpeckers.

There have been no studies conducted in British Columbia specifically aimed at determining the impact of winter feeding by woodpeckers on mountain pine beetle populations. However, observations made by Moeck, Otvos, and Whitney (1984 personal communication), and unpublished data made available by Safranyik (1984 personal communication) are relevant to this topic. Dr.'s Moeck and Whitney, in their research on the mountain pine beetle, required information about overwintering mortality. In early studies they made estimates or counts of beetle brood size in the autumn, only to return in the spring to find the bark chipped off by woodpeckers and the brood destroyed. From their descriptions and descriptions offered by assistants, it appeared that hairy and three-toed woodpeckers were active in the area. On some trees the bark had been removed down to about snowline, while on others the birds had evidently worked the same tree as the snow melted and removed the bark down to ground level. The observations of Dr.'s Moeck, Otvos, and Whitney concerning the size of trees that the woodpeckers fed on appear to agree with the observations made by Lester (1980). She found that the

woodpeckers chose trees with an average DBH of 24.9 cm (± 5.1 cm).

During some earlier investigations Dr. Safranyik also found it necessary to 'cage' trees with wire in order to prevent woodpeckers from destroying the brood. The spring brood densities in bark areas protected from woodpeckers averaged 40, 30.2, 20.2, and 27 larvae per 80 square inch sample unit at 4 tree heights. Densities of corresponding unprotected areas averaged 25, 16.4, 9.2 and 8 larvae per sample unit. Though these values cannot be related to mountain pine beetle population densities they can be used as an indication of the impact that moderate bark disturbance by woodpeckers can have on brood survival.

During the beetles' short flight and attack period in the summer, they are susceptible to predation by a larger number and variety of bird species than during the winter. Studies conducted by Rust (1929 and 1930) and Stallcup (1963) examined the birds that feed on the beetles at this time. In his first study, Rust (1929) found that the common nighthawk was the most important predator. Ten nighthawk stomachs contained two to 289 (avg. 76) adult pine beetles representing, in the latter case, 20% of the total volume of food consumed. The three-toed and hairy woodpeckers were next in importance, averaging about 2.7 and 1.5 beetles per stomach, respectively.

One year later Rust (1930) found that the importance of the species in terms of beetles consumed was reversed. The three-toed and hairy woodpeckers averaged 74.7 and fourteen beetles per stomach, respectively. The fourteen nighthawks averaged only five beetles per stomach. Rust suggested that the change may have occurred because the heaviest concentration of the mountain pine beetle moved six to ten miles west of the area investigated the previous year. The woodpeckers moved with the infestation, while the nighthawks stayed near their established breeding grounds.

Stallcup (1963) examined not only the number of beetles taken per bird, but also the densities of the bird and mountain pine beetle populations. Based on stomach contents, bird and beetle densities and weights, and the assumption that the birds consumed daily a quantity of food equal to about 25% of their body weight, Stallcup calculated that the birds could have consumed a maximum of 2358 adult beetles per acre. This figure represented 11.6% of the estimated mountain pine beetle population. In terms of the proportion of the bird stomach contents represented by beetle fragments, the most important bird species were the red-breasted nuthatch, western wood pewee, brown creeper, pygmy nuthatch and Empidonax flycatchers.

3.3.2 HABITAT REQUIREMENTS

Based on the available information, the most important avian predators of the mountain pine beetle during its flight period are the mountain bluebird, common nighthawk, hairy and three-toed woodpeckers, pygmy and red-breasted nuthatches, brown creeper, and western wood pewee.

The first two species feed by flycatching (capturing insects on the wing). These birds are responsible for catching the beetles as they seek new trees to attack. Both birds exhibit a preference for open habitats (Godfrey 1979, Thomas 1979), so their effectiveness in dense lodgepole pine stands would be limited. Though they share the same feeding method the nesting requirements of the two species are quite different. The mountain bluebird is a secondary cavity nester (Thomas 1979). It requires a cavity in a tree for nesting but cannot excavate its own, so it must depend on natural cavities or those excavated by other birds. The common nighthawk does not require trees for nesting. In fact, it builds no nest but simply lays its eggs on the ground, preferably on sand, gravel, or rock. Information from the Vertebrate Zoology Division of the British Columbia Provincial Museum indicated that both of these species occur in the interior of British Columbia, and may be raising young at the time of beetle flight.

The woodpeckers, nuthatches, and brown creeper do most of their summer feeding by gleaning insects from the bark of tree trunks and limbs. These birds would feed on the beetles as they emerged from trees and as they landed on new trees. The female mountain pine beetles do not simply bore into a tree as soon they land. They examine the bark, avoid smooth areas, and usually bore into the tree in bark crevices or under scales (Rasmussen 1974). The examinations usually last less than 30 minutes each but this would give the bark-gleaning birds time to locate the beetles before they bored into the tree.

Censuses conducted in Montana by Lester (1980) indicated that the three-toed and hairy woodpeckers were the most common woodpeckers during the breeding season in mountain pine beetle-infested lodgepole pine stands. She found a total of eight hairy and eleven three-toed woodpecker nests. Seven of the eight hairy woodpecker nests were found in aspen or birch. Nine of the eleven three-toed woodpecker nests were in lodgepole pine, seven of which had been killed by the mountain pine beetle. One of the conclusions made by Lester (1980) was that the three-toed woodpecker, because of its ability to use lodgepole pine as a nest tree, would have the greater ability to follow the infestation as it spread to new areas. The hairy woodpecker nests more often in softwoods (Thomas 1979, Lester 1980),

and may not show as great a response to the beetle outbreak.

Both nuthatches have the ability to excavate their own nest cavities (Thomas 1979). Of the two species listed the red-breasted nuthatch is more common in lodgepole pine communities (Austin and Perry 1979, Thomas 1979). Information from the Provincial Museum indicated that both species are resident in the interior, and may be raising young during the beetle flight period.

The brown creeper is considered a secondary cavity nester (Thomas 1979). This species usually shows a preference for older, undisturbed stands (Austin and Perry 1979, Verner 1980). Provincial Museum data shows this species to be a resident of the interior, but there is little additional information concerning periods of nesting or fledging.

Provincial information concerning the western wood pewee is also limited. It can be found in a wide variety of conifer habitats but prefers to nest in older stands (Thomas 1979). Information from the Provincial Museum indicates that it will nest in mixed lodgepole pine/aspen stands in the interior. Nest records indicate breeding as early as June 22 and as late as August 6.

The hairy and three-toed woodpeckers are the most important predators of the mountain pine beetle during the winter (Amman 1973, Lester 1980), though the black-backed

woodpecker may also be important (Lester 1980). During the winter, nest tree requirements no longer limit bird densities. Furthermore, territories are not defended during the winter, so feeding by mixed-species flocks of up to six birds may be observed (Baldwin 1960). Provincial Museum records indicate that the three woodpecker species listed can be found in the interior throughout the winter, though detailed habitat information is scarce.

3.3.3 AVIAN RESPONSES TO TIMBER HARVESTING

As noted in section 3.2.1. the most common method of harvesting lodgepole pine in the interior is clearcutting. This method, through its rapid removal of the overstory and simultaneous creation of a large open site, can have drastic effects on bird populations. Eight bird species were listed as important predators of the mountain pine beetle. Two of these, the mountain bluebird and common nighthawk, would probably benefit from a clearcut. Both require large, open areas for feeding. The common nighthawk, which nests on the ground in open habitats, would probably benefit most. The mountain bluebird requires a tree cavity in which to nest. If nest sites were available adjacent to the clearcut it would benefit from the open feeding area. In the study by Austin and Perry (1979) the mountain bluebird was absent from the mature and stagnated lodgepole pine stands, but did

occur in the recently clearcut area.

Three species, the red-breasted and pygmy nuthatches and the brown creeper, would be adversely affected by a clearcut. Austin and Perry (1979), Schwab (1979), Scoullar (1980) and Peterson (1982) agreed that the red-breasted nuthatch is associated with mature forest stands. It was also the only species of the three listed found to nest in senescent lodgepole pine stands (Austin and Perry 1979). Szaro and Balda (1979) and Scott (1979) indicated that the pygmy nuthatch would decrease on logged stands. The brown creeper was associated with mature, but not senescent or harvested, stands (Austin and Perry 1979, Verner 1980).

Woodpecker response to clearcutting appeared to depend on whether or not wildlife trees were left on the site. Studies in ponderosa pine communities in Arizona by Scott and Oldemeyer (1983) and in mixed pine-hardwood forest in Texas by Dickson *et al.* (1983) indicated that by leaving some wildlife trees on clearcut areas the negative impact of the cut on woodpeckers (and cavity nesters in general) could be lessened.

Only one study, that of Szaro and Balda (1979) examined the impact of logging on the western wood pewee. This species was absent from uncut and clearcut stands, reaching its greatest density on partially cut stands. Evidently, a moderate decrease in stand density proved most beneficial.

4. STRUCTURE OF THE SIMULATION MODEL

The basic structure of the mountain pine beetle-bird simulation model has been outlined in a simplified flow diagram (Figure 16). In the figure the numerals associated with some of the variables identify the sources (Appendix 2) used to determine the value or values of that variable.

4.1 LOGGEPOLE PINE STAND STRUCTURE

Following the examples of Klein *et. al.* 1978, Cole and McGregor 1983, and others the stand structure and density was determined by the number of trees in each of six diameter classes; 12.7-17.5, 17.6-22.6, 22.7-27.7, 27.8-32.8, 32.9-37.8, and 37.9-42.9 cm at breast height. For convenience these are referred to as the 15, 20, 25, 30, 35, and 40-cm DBH classes. Trees with a DBH of 12.6 cm or less were not included in the model because they are rarely attacked (Hopping and Beall 1948, Amman and Cole 1969, Safranyik 1984 personal communication). Trees larger than 43 cm DBH were not included because specific information on insect attack density, insect survival, tree mortality, etc. was extremely limited or non-existent.

The stand area (ha) is set prior to simulation. A review of Forest Insect And Disease Survey file reports for the province of British Columbia, and for the Cariboo, Kamloops, and Nelson Forest Regions indicated that

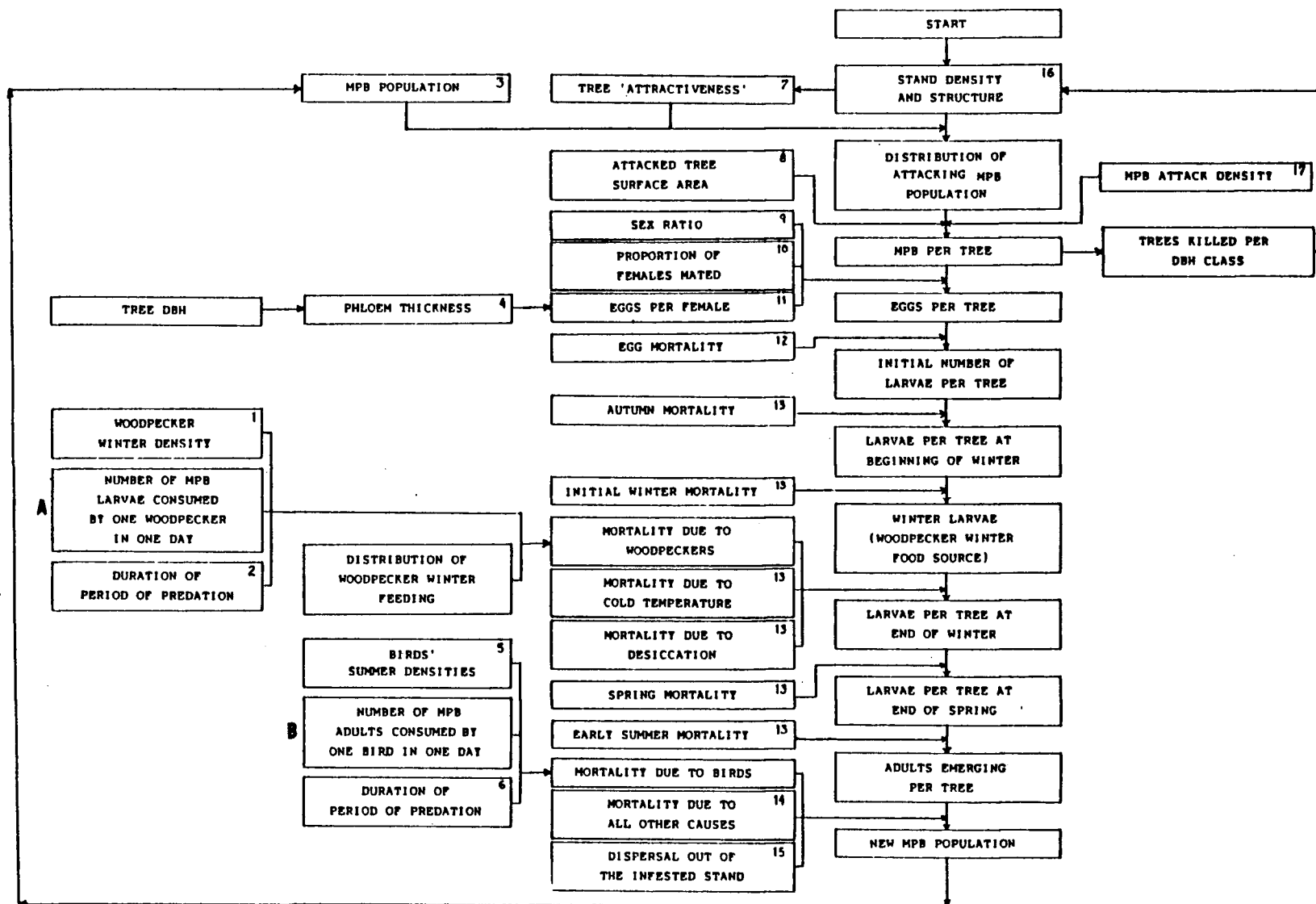


Figure 16: Basic flow diagram of the simulation model.

infestations range from a few to greater than 400 hectares in area, Most, however, are less than 50 hectares. The stand area used for all simulations was 20 hectares, after Manning *et al.* (1982).

The stand age was modelled as approximately 100 years; an age when almost all lodgepole pine stands are susceptible to mountain pine beetle attack. To avoid the complex and confounding affects of topography the stand was assumed to be level.

4.2 MOUNTAIN PINE BEETLE POPULATION DISTRIBUTION

The size of the initial beetle population is set before the simulation begins. For all simulations an initial density of 750 beetles per hectare was used (Klein *et al.* 1978, Burnell *et al.* In Press).

Once stand characteristics and initial beetle density are established, the beetle population is distributed among the host trees. Distribution is based on the proportion of the trees in the stand represented by each diameter class (P_i), and the 'attractiveness' value (A_i) for the i th diameter class. The A_i values were determined by calculating $(DBH^6)_i$, then re-scaling the figures such that the value for the largest class was equal to 0.95. 'Relative attractiveness' values (RA_i) were then calculated by

$$RA_i = A_i / A_i \text{ maximum.} \quad (1)$$

The 'total attractiveness' (TA_i) of each diameter class was then equal to

$$TA_i = RA_i P_i \quad (2)$$

The proportion of the mountain pine beetle population assigned to the i th diameter class (PB_i) was calculated by

$$PB_i = TA_i / \sum TA_i \quad (3)$$

and the actual number of beetles assigned to each class (NB_i) was equal to

$$NB_i = PB_i (ALLBET) \quad (4)$$

where ALLBET was the total mountain pine beetle population in the stand. In this manner the beetles were concentrated in the large diameter trees at the beginning of the infestation, and progressively shifted to the smaller trees as the larger ones were killed.

4.3 LODGEPOLE PINE MORTALITY

Tree mortality depended on the beetle attack density and the surface area of the attacked portion of the tree. Mean attack density was initially set at a relatively low value of 58 attacks per m^2 because, theoretically, the beetles, when at endemic levels, attack trees of lower than average vigour (section 3.1.2), and fewer beetles are necessary to kill the tree. Attack density then increased, and became asymptotic at 75 attacks per m^2 by the third year of the infestation. This number is an approximation of the optimal attack density for the mountain pine beetle (Berryman *et al.* 1985). Overall population productivity decreases at both lower or higher attack densities due to a low number of eggs produced, and the effects of within- and between-brood competition, respectively (Reid 1963). The attack density increased from zero to ten percent, depending on the size of the attacking beetle population (Klein *et al.* 1977).

Mountain pine beetles usually concentrate their attacks in the lower 2.4 to 4.6 metres of a tree (Rasmussen 1974, Lester 1980), though this figure varies with tree diameter and the stage of the infestation (Shepherd 1965, Safranyik 1968, Klein *et al.* 1978, Safranyik 1984 personal communication). In the model the attacked surface area of a tree (ASRF) is calculated by

$$\text{ASRF} = -3.78 + (0.3221 \text{ DIAM}_i) \quad (5)$$

where tree diameter at breast height is measured in centimeters, and surface area in square metres. This equation was derived from measurements recorded by Lester (1980). As the infestation progresses the attacked surface area is increased by approximately ten percent due to the increased height of attack. Due to the lack of data no attempt was made to stratify the attack densities by diameter class. The number of attacks required to kill a tree was calculated by multiplying the attacked surface area by the attack density. The total number of trees killed per diameter class, TREKIL_i , was then equal to

$$\text{TREKIL}_i = \text{TOTTAT}_i / \text{TATT}_i \quad (6)$$

where TOTTAT_i was the total number of attacking beetles in the diameter class, and TATT_i was the number of attacks per tree. Partial or 'strip' attack dynamics (section 3.2.3) are currently not well understood or documented and were not included in the model. The number of dead trees in each DBH class was removed from the pool of live trees per DBH class at the end of each yearly iteration of the model, thus setting stand conditions for the next year.

4.4 MOUNTAIN PINE BEETLE PRODUCTIVITY

The number of eggs laid in each tree was dependent on the number of females present and the number of eggs produced per female. The proportion of the beetle population that was female (PROFEM) varies considerably with tree diameter and the stage of infestation (Amman and Cole 1983), and was calculated by

$$\text{PROFEM}_i = 0.6919 - (0.0035 \text{ DIAM}_i) \quad (7)$$

from Burnell *et. al.* (In Press).

The number of eggs laid per female can vary greatly, from one or two to more than 200 in one instance (Reid 1962b). Values usually range between 40 and 80 eggs per female (Peterman 1974, Safranyik *et al.* 1974). Female fecundity was found to be related to the thickness of the host tree phloem (Amman and Cole 1983) which, in turn, was related to tree diameter (Amman 1969, Amman 1972a, 1972b). In the model, females in trees with thin phloem (approximately 1.0 mm) produced 40 eggs, while those in trees with thick phloem (4.6 mm) produced a maximum of 80 eggs.

Data on the proportion of the female population that is mated are currently unavailable. In the model it was assumed that 95 % of the females were successfully mated. Egg hatch

varies between 82% and 98 %, depending on the diameter of the attacked tree and the stage of the infestation (Reid 1962b, Amman and Cole 1983).

4.5 MOUNTAIN PINE BEETLE MORTALITY

Researchers have examined a wide variety of factors that cause mountain pine beetle mortality (Reid 1962b, Amman 1973, Cole 1974, and Amman and Cole 1983). Unfortunately, all factors exhibit considerable variation depending on elevation, latitude, tree diameter, and the stage of the infestation. This model did not attempt to simulate each individual factor. Instead, with a few exceptions described below, a general mortality rate was applied to the beetle population in each tree at the beginning of autumn, winter, spring, and summer. These basic mortality rates were modified by tree diameter and population density to account for such effects as crowding and the lower insulative property of thinner bark.

During the winter, three individual mortality factors were simulated in addition to the general winter mortality. These included mortality due to cold temperatures, desiccation, and woodpecker predation. The first two factors were selected because they are the major sources of mortality during the winter. They were simulated in a similar manner to the general mortality rates, varying in

relation to tree diameter and population density. Woodpecker predation, a major focus of the model, was calculated in a more complex manner, as illustrated in the flow diagram (Figure 17).

The three major factors that determine mortality due to woodpeckers during the winter are the number of birds present, the length of the period of predation, and the number of larvae one bird consumes in a day. Woodpecker winter population densities (WPSTD) varied with the number of larvae available in the winter. The birds exhibited a direct numerical response as described in section 2.2.2. The duration of the period of predation (WINTER) was fixed at 123 days to approximate the period of greatest predation between December 1 and March 31.

Four major steps were required to calculate the number of larvae each bird consumed in a day. First, the daily energy requirement in kilocalories per gram of bodyweight (WKGD), is calculated by

$$\text{WKGD} = 0.64 - (0.008 \times \text{TEMP}) \quad (8)$$

where TEMP is the average winter temperature in degrees centigrade. This equation was derived from measurements recorded by Koplin (1967). The second step is

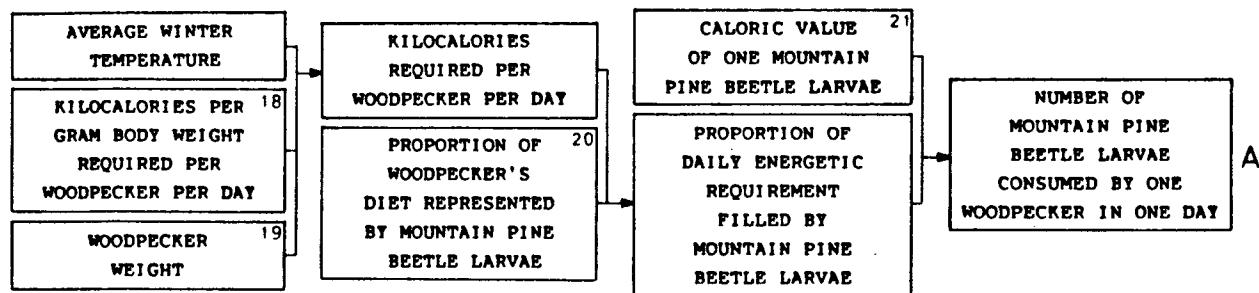


Figure 17: Simplified flow diagram of sequence used to determine larvae consumption by winter woodpeckers.

$$\text{WPKD} = \text{WKGD} \times \text{WPWT} \quad (9)$$

where WPWT is the woodpecker's weight in grams, and WPKD is the number of kilocalories required per day per bird to maintain body weight. In the third step, WPKD is multiplied by the proportion of the bird's diet made up of mountain pine beetle larvae (DIET) to determine the proportion of the woodpecker's daily caloric requirement filled by beetle larvae. Changes in DIET follow a sigmoid functional response as described in section 2.2.1. To derive the number of larvae consumed by one woodpecker in one day (CATAWP), the number of kilocalories in the woodpecker's diet obtained from larvae is divided by the caloric value of one larva to determine the number of larvae consumed by one woodpecker in one day (CATAWP). The equation

$$\text{CATAWP} = \text{CATWPD} \times \text{WINTER} \times \text{WPSTD} \quad (10)$$

where CATWPD is the number of larvae consumed by all woodpeckers in the stand in one day, determined the number of larvae consumed by all woodpeckers in the stand during the winter (CATAWP).

Once the number of larvae consumed by woodpeckers has been calculated it is necessary to determine the source of

the larvae; that is, the number of larvae removed from each tree, and the number of trees per DBH class from which the larvae were removed. Unfortunately, there is a surprising dearth of information in this area, considering the visibility and recurrence of bark removal by woodpeckers.

Bark removal by woodpeckers may be related to bark beetle density (Hutchinson 1951, Beaver 1967, McCambridge and Knight 1972, Lester 1980). When insect densities are great small groups of woodpeckers have been known to work on only a few trees until most of the bark has been removed (Massey and Wygant 1954). Estimates of the percentage of the bark beetle brood destroyed by woodpecker feeding activity ranged from 13% (Koplin and Baldwin 1970) to 98% (Massey and Wygant 1954, Knight 1958). Therefore, it is assumed that, through bark removal and subsequent feeding, woodpeckers remove 20% to 80% of the pine beetle brood in a tree, depending on initial winter larval density. Ten percent of the brood is assumed to be protected from woodpeckers by snow, suffering mortality from desiccation only. The balance of the brood undergoes mortality from both desiccation and cold temperatures.

To calculate the number of woodpeckered² trees it was first necessary to determine the number of larvae removed

²"Woodpeckered" is a term used by some authors to indicate a tree from which bark has been removed through a woodpecker's feeding activity.

from each diameter class each winter. For simplicity, it was assumed that the distribution of woodpecker winter feeding (DSTWPF) was proportional to the distribution of larvae available at the start of the winter. DSTWPF was determined by

$$DSTWPF_i = WSLRVH_i / WSLRVT \quad (11)$$

where WSLRVH_i is the number of larvae available per hectare during the winter in the *i*th DBH class, and WSLRVT is the total number of larvae available per hectare. Multiplying DSTWPF_i by the total number of larvae consumed each winter (CATWWH), yielded the number of larvae consumed per hectare per DBH class during the winter (CCWPH). Dividing this figure by the number of larvae removed from each tree determined the number of woodpeckered trees per hectare in each DBH class (WPTRHA). Lastly, the equation

$$UWPTH A_i = TREKHA_i - WPTRHA_i \quad (12)$$

where TREKHA_i is the number of trees killed that year in the *i*th DBH class, determined the number of non-woodpeckered trees per hectare per DBH class. Larvae in the woodpeckered trees were subjected to greater mortality from desiccation and cold temperatures due to bark removal than those in

non-woodpeckered trees (Otvos 1979).

The beetles that survived spring and early summer mortality represent the emerging adult beetle population. Following emergence, they die from 'flight-period' mortality factors, disperse out of the stand, or survive and remain in the stand to attack new trees. The impact and extent of mortality during the flight and attack period is largely unknown. This mortality may result from a variety of factors including fish, shrews, ants, bats, birds, vehicle windshields, forest fires, etc. In the model there are two forms of flight period mortality: birds, and other causes. Mortality from other causes was assumed to be a constant at ten percent. Mortality due to summer birds was calculated in a similar manner (Figure 18) to woodpecker-caused mortality in the winter. Specific energetic information concerning the red-breasted nuthatch and the brown creeper (two of the three summer bird species modelled) was not available. Therefore, a general metabolic equation (Kendeigh 1970) was used to determine the daily energetic requirement (in kilocalories) per bird (CALB_i) through the equation

$$\text{CALB}_i = 1.5720 (\text{BIRDW})^{0.6210} \quad (13)$$

where BIRDW is the bird's weight in grams. A similar equation

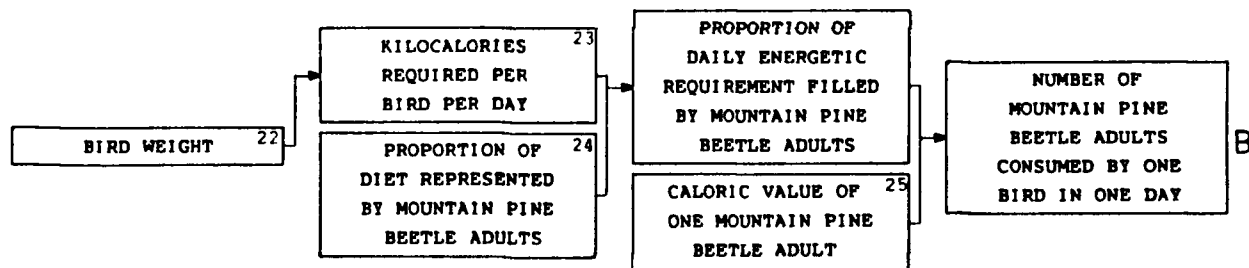


Figure 18: Simplified flow digram of sequence used to determine beetle consumption by summer birds.

$$CALB_2 = 0.5404 (BIRDW^{0.7545}) \quad (14)$$

was used to calculate daily energetic requirements for the non-Passerine woodpecker (Kendeigh 1970). $CALB_1$ and $CALB_2$ were multiplied by a correction factor of 1.5 to convert standard metabolic requirements to an approximation of existence level requirements. This correction was unnecessary for winter woodpeckers because it had already been included in the calculations by Koplin (1967). As in the winter calculations, the proportion of the diet represented by mountain pine beetles was used to determine the proportion of the daily energetic requirement filled by adult pine beetles. This figure, divided by the caloric value of one adult beetle, yielded the number of beetles consumed per bird per day. As in winter calculations this figure was multiplied by the number of birds in the stand and the duration of period of predation to determine the total number of adult beetles consumed by summer birds.

Beetles not killed in flight were subjected to dispersal out of the stand. Again, no actual figures are available, though Canadian and U.S. research on this subject continues (Safranyik 1985 personal communication). In the model, dispersion is dependent on the average DBH of the stand. Briefly, dispersion from the stand is at its lowest

level (1%) when many, large host trees are easily available. As the infestation progresses and large, preferred trees become scarce, dispersion increases, becoming asymptotic at 40%. Beetles remaining in the stand after dispersal form the mountain pine beetle population for the next iteration of the model.

A listing of the basic mountain pine beetle simulation model and a glossary of the variables used in the model are found in Appendices 3 and 4.

5. SIMULATION RESULTS AND DISCUSSION

5.1 SIMULATED SCENARIOS

Nine scenarios, with different combinations of stand structure and bird responses, were simulated (Figure 19). The three stand structures were control ('normal'), senescent, and thinned. The control stand had a diameter distribution considered typical for stands commonly attacked by the mountain pine beetle (Cole *et al.* 1976), and represented an approximation of an 'average' lodgepole pine stand. The senescent stand had a more tightly even-aged, single-storied structure, with most of the trees concentrated in the larger DBH classes. Density was slightly less than that of the control stand. In the thinned stand tree densities in the 15 and 20 cm-DBH classes were the same as those in the control stand. Densities in the 25, 30, 35, and 40-cm classes, however, were reduced by 95% based on the suggestions of Safranyik *et al.* (1974), and Amman *et al.* (1977) for reducing stand susceptibility to beetle attack (section 3.2.4).

Three combinations of bird functional and numerical responses were also simulated. As a control, the maximum bird densities and the maximum proportion of mountain pine beetle larvae or adults in the birds' diets were approximations of 'normal' conditions for each stand

		STAND STRUCTURE		
		Control	Senescent	Thinned
PREDATOR RESPONSE	Normal	1	4	7
	Efficient	2	5	8
	2 X Control Density	3	6	9

Figure 19: Diagram of 3 X 3 factorial design used in the simulations.

structure, as were the insect densities at which the maximum responses occurred. The second combination of responses simulated more efficient avian predators whose functional and numerical responses attained their maximum values at approximately half the beetle density required by the normal predators. In the third set of combinations the functional response was assumed to be normal, but the bird densities were double those that occurred in the control stand. The last two combinations of responses were simulated in order to compare changes due to increased predator efficiency to those caused by increased density alone. Initial values of some key variables are found in Appendix 5.

5.2 THE CONTROL STAND

5.2.1 SCENARIO 1: NORMAL PREDATOR RESPONSES

The mountain pine beetle population achieved its greatest density in the control stand in this scenario (Figure 20). Maximum late summer density (65,777 adult beetles per hectare) occurred in year nine of a sixteen year infestation. The extended duration of the outbreak was due, ultimately, to the density and structure of the stand. Initial population growth was slow because of poor food quality (thin phloem) resulting from a high stand density (Amman *et al.* 1977), and a greater number of trees in the

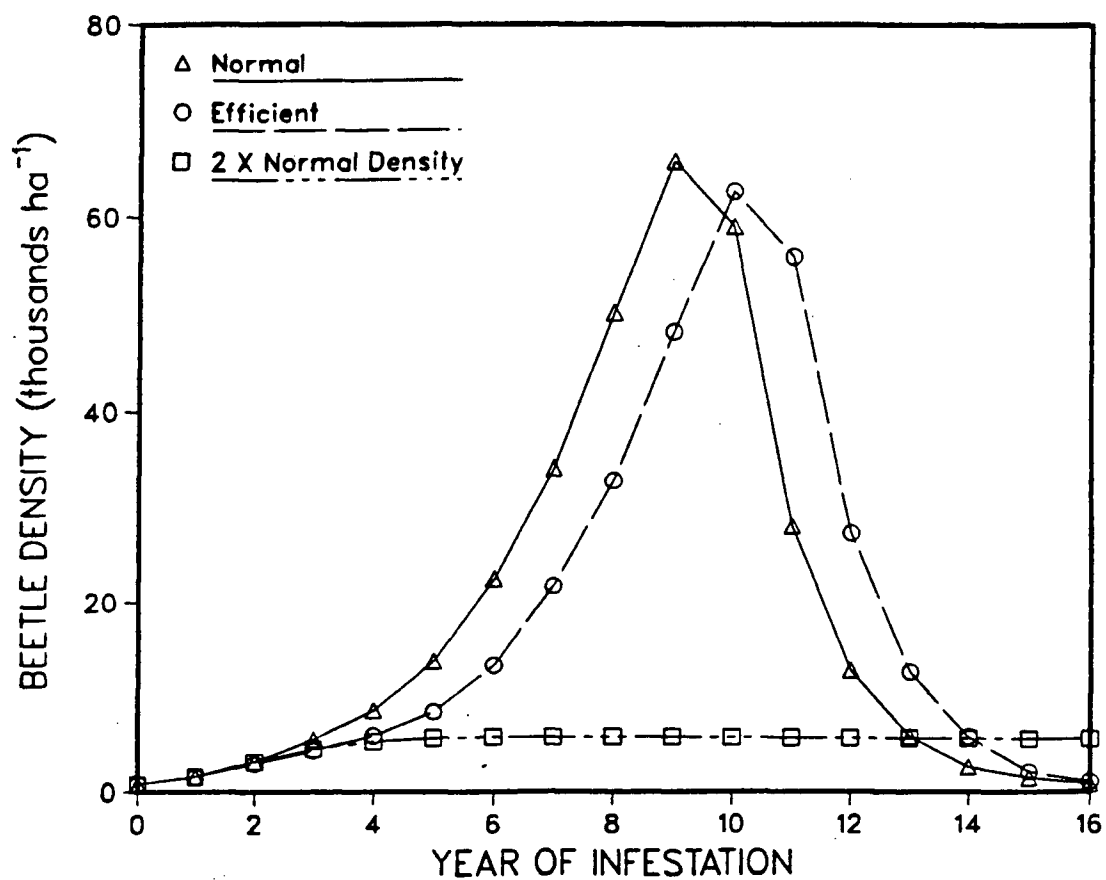


Figure 20: Yearly mountain pine beetle autumn density in the control stand.

smaller diameter classes (Cole and Amman 1980). Because expansion was slow, the beetle population did not rapidly deplete its food supply, enabling the population to persist in the stand for a long period of time.

By the end of the infestation approximately 325 trees per hectare, or roughly 17% of the original stand, had been killed by the beetles (Figures 21 and 22). Tree mortality increased with diameter, ranging from 3% in the 15-cm DBH class to 65% in the 40-cm class (Figure 23). This pattern commonly occurs during mountain pine beetle outbreaks (see Figures 13 and 14).

Winter woodpecker densities attained a maximum of 25 birds per 100 hectares in year five of the infestation, corresponding to a winter larval density of 93,011 larvae per hectare (Figures 24 and 25). At this time, the woodpeckers first achieved their peak consumption of 21,108 larvae per hectare per winter. However, the maximum percentage larval consumption, 26% of the winter larval population, occurred in the previous year, corresponding to a population of 59,711 larvae per hectare (Figure 26).

Total summer bird density for the three species simulated reached a peak of 50 individuals per 100 hectares in year seven of the outbreak, corresponding to a beetle density of 38,464 beetles per hectare (Figures 27 and 28). The maximum consumption of 329 adult beetles during the

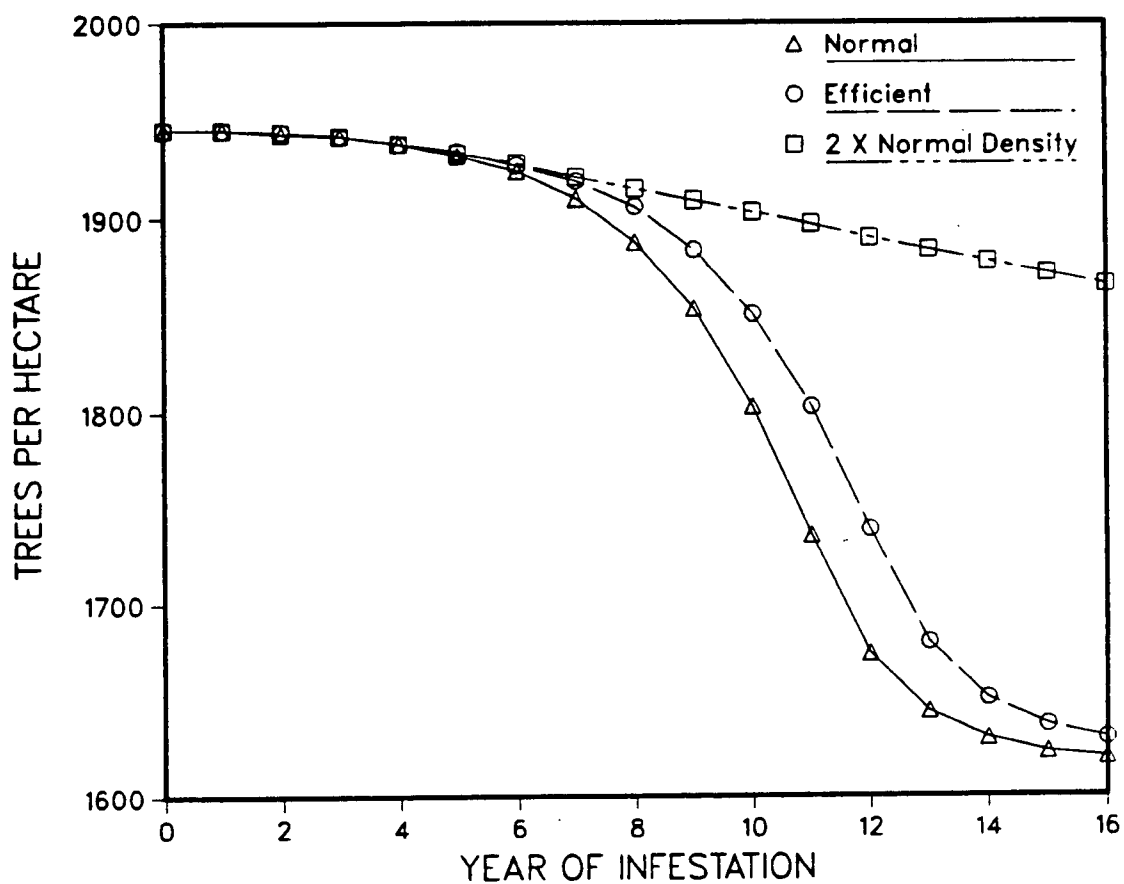


Figure 21: Yearly total stand density for the control stand.

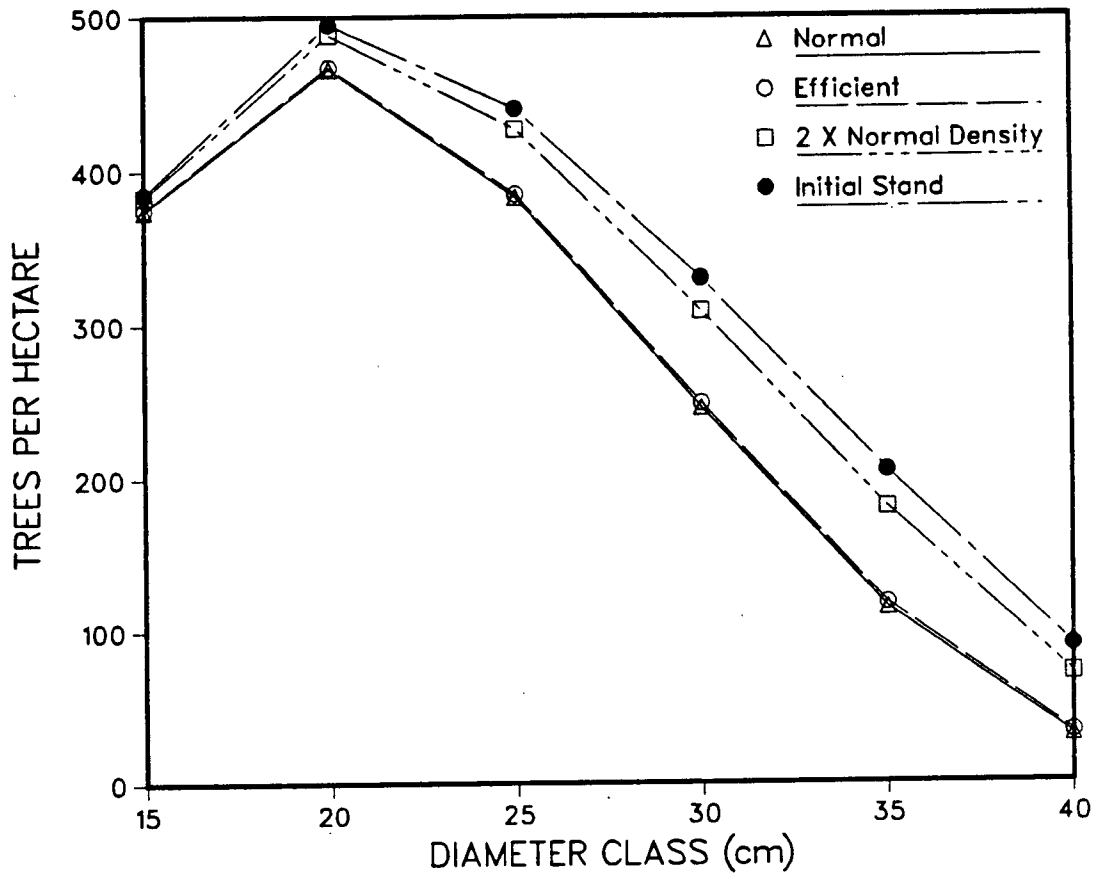


Figure 22: Initial and final stand structures for the control stand.

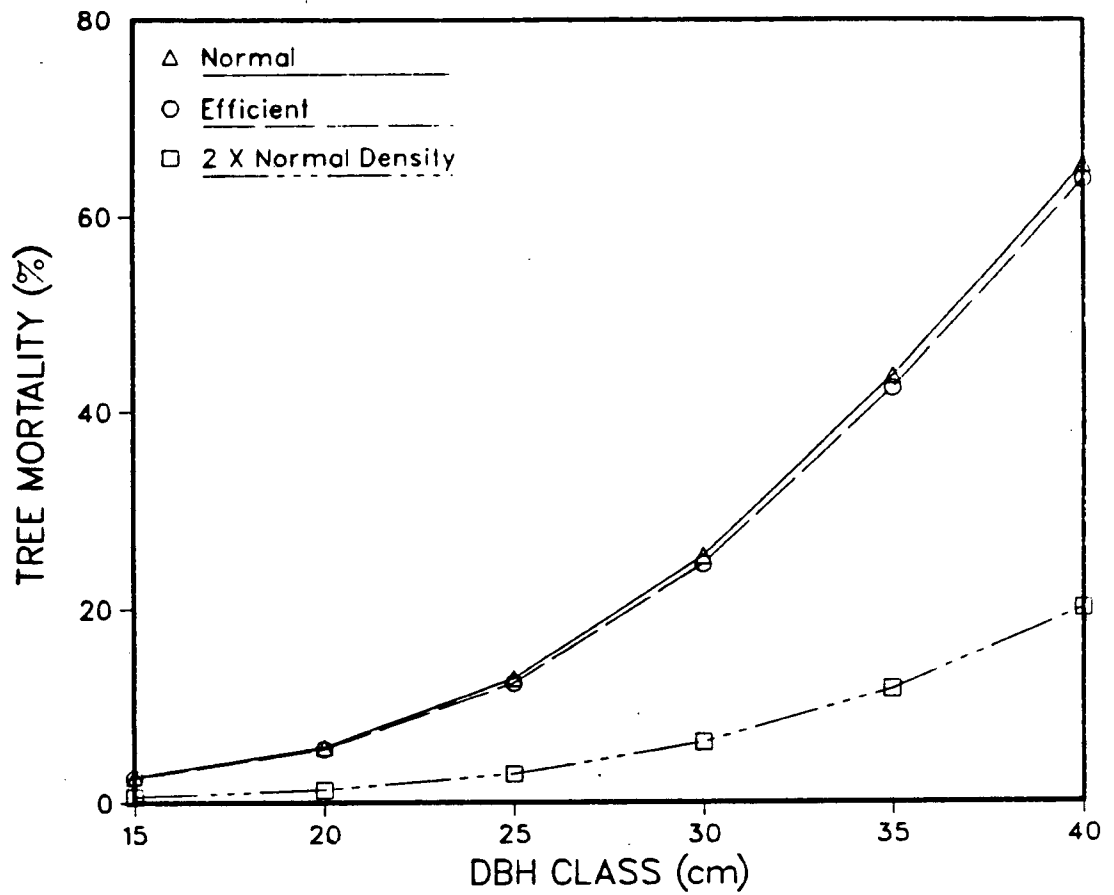


Figure 23: Total tree mortality for each diameter class in the control stand.

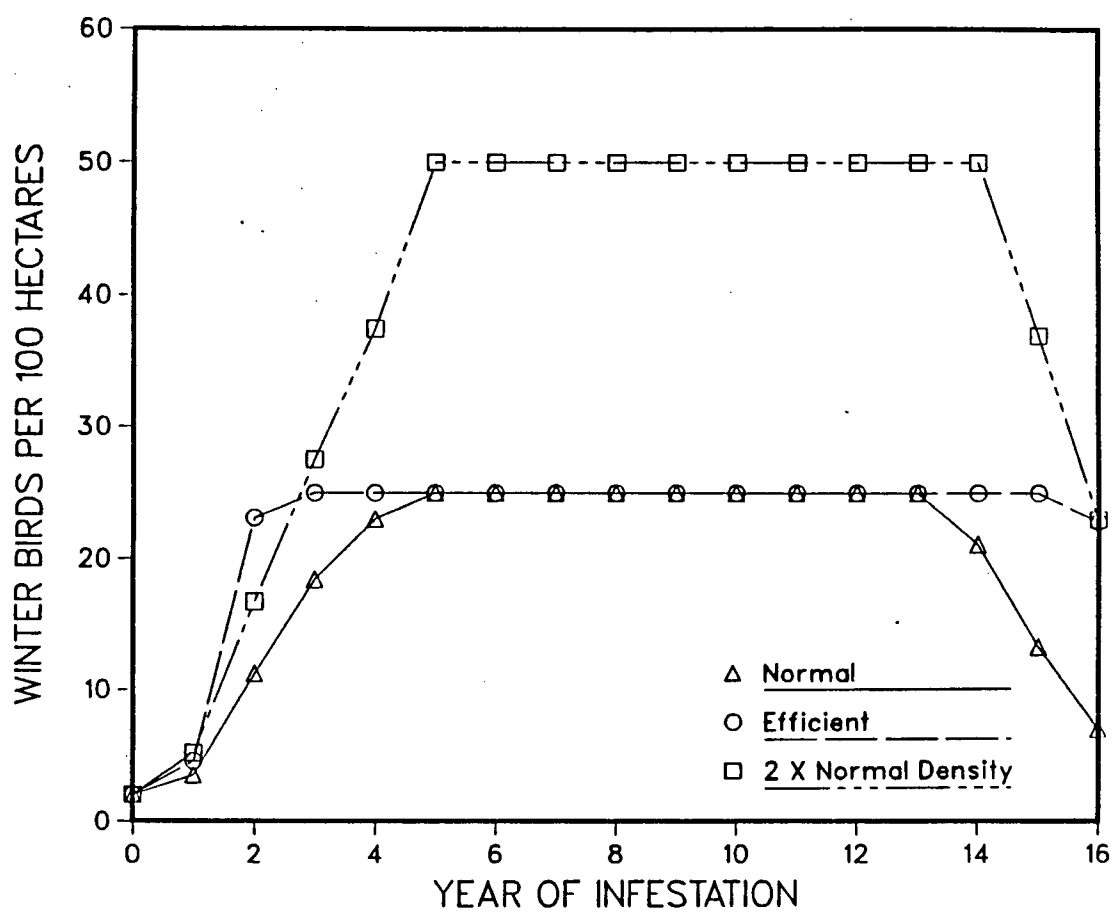


Figure 24: Yearly winter bird density in the control stand.

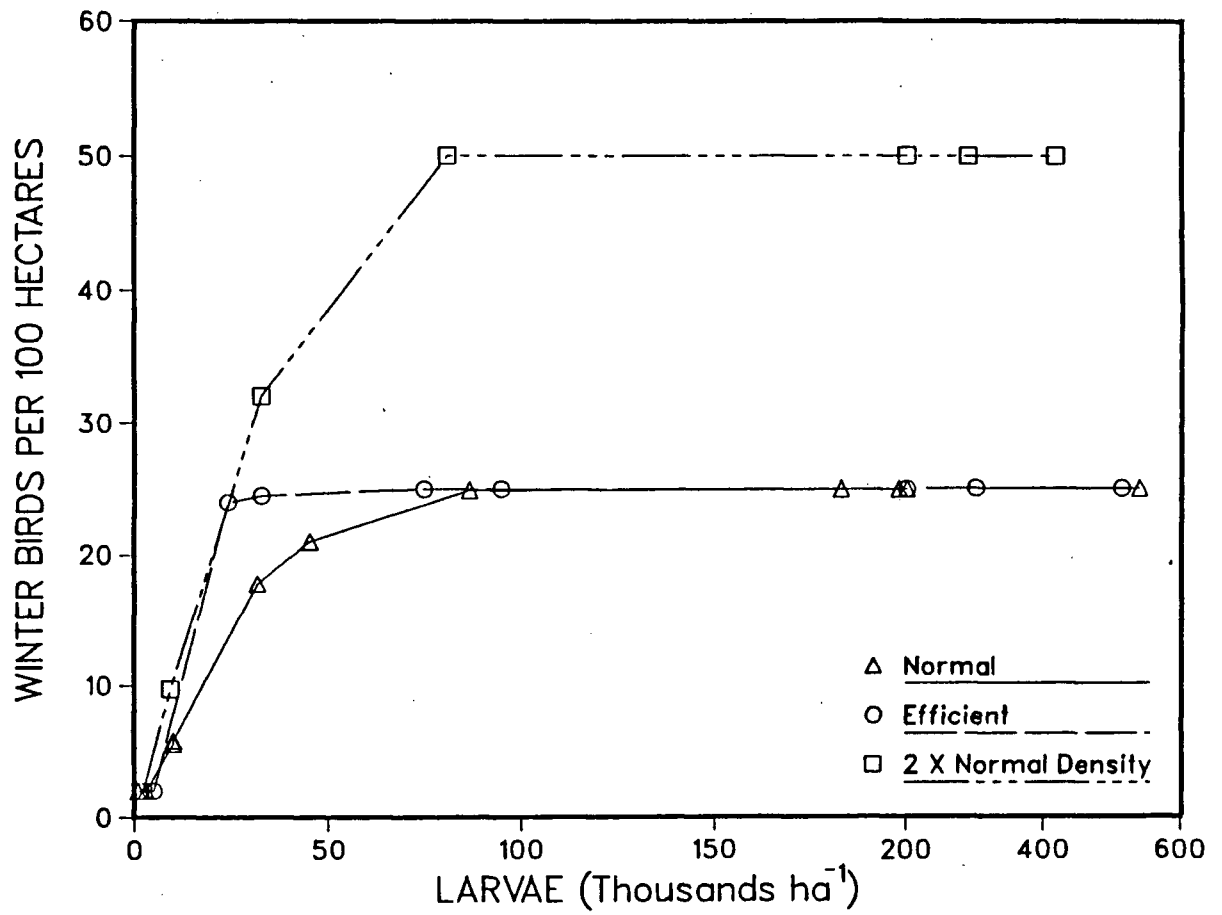


Figure 25: Winter bird density in the control stand relative to larval density.

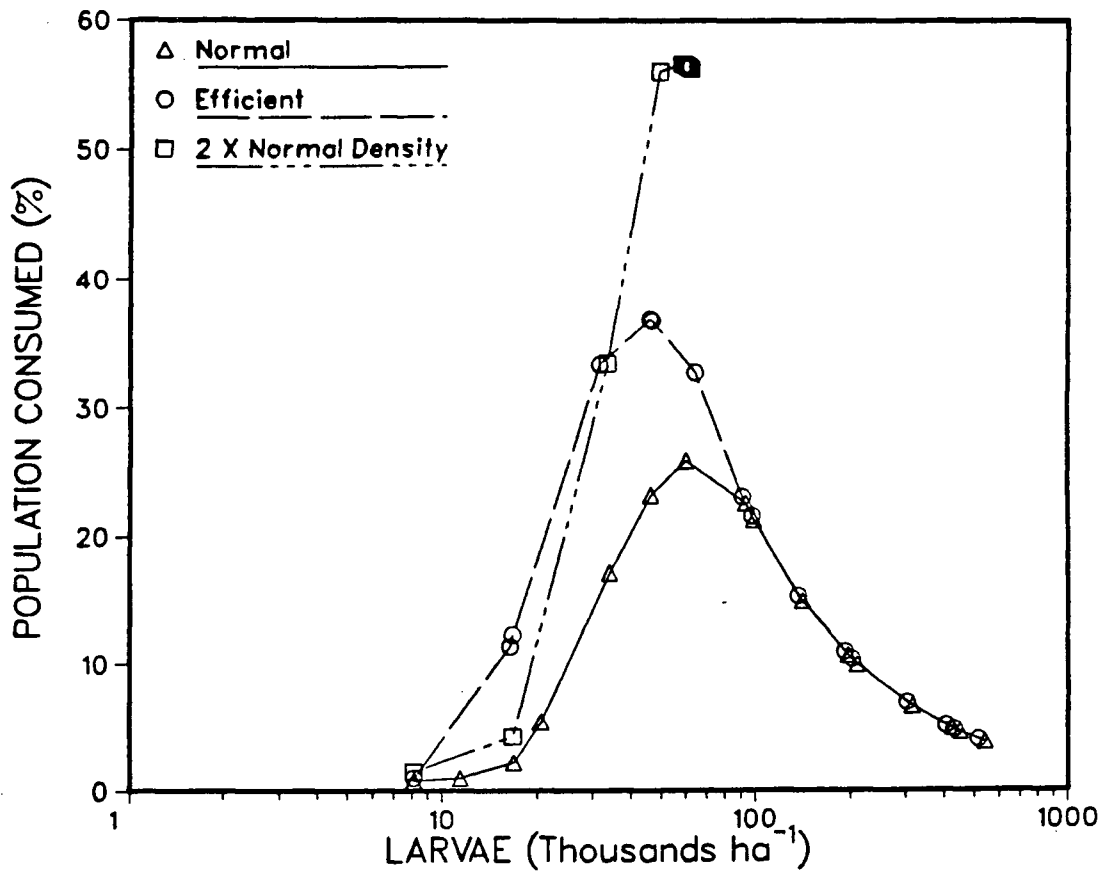


Figure 26: Percent of winter larval population consumed by woodpeckers in the control stand.

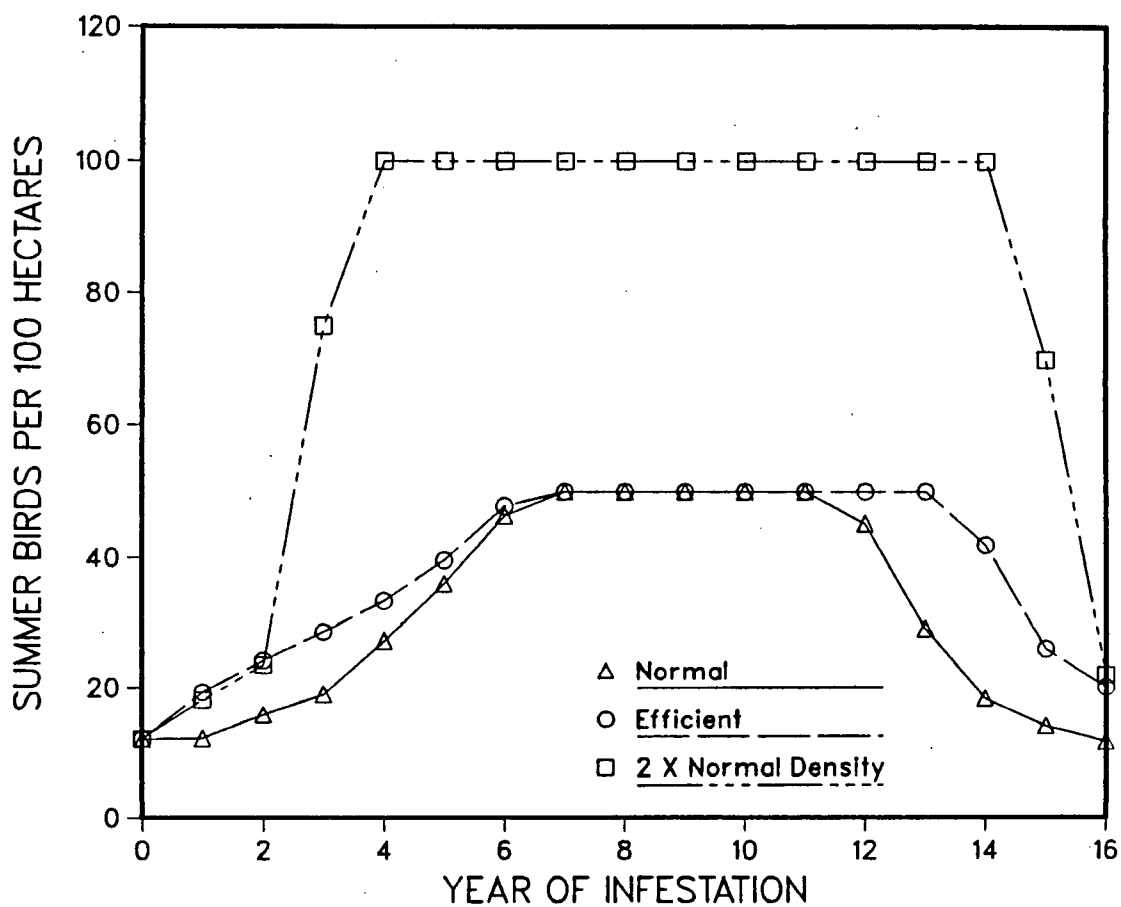


Figure 27: Total summer bird density in the control stand.

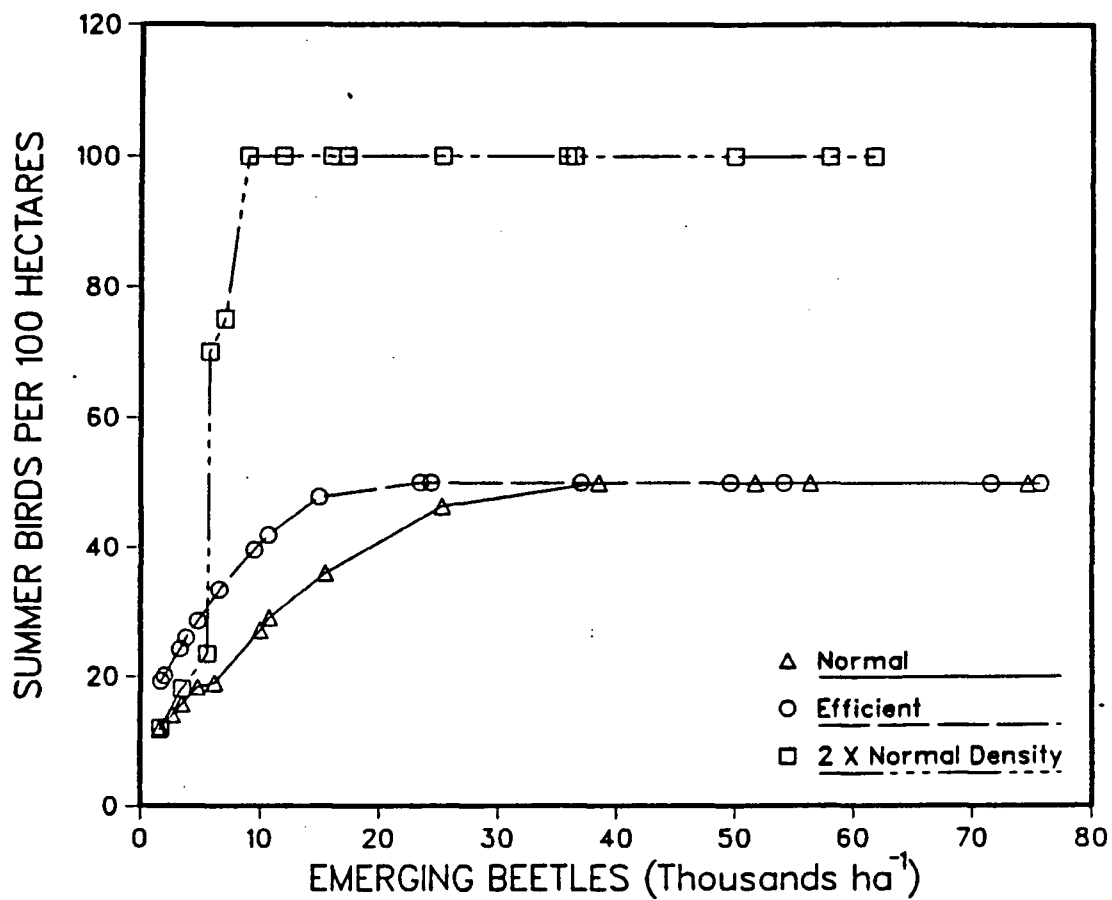


Figure 28: Total summer bird density in the control stand relative to adult density.

21-day flight period occurred at the same time. Unlike winter avian predation, the summer maximum percentage consumption, 0.9% of the emerging adult beetle population (Figure 29), occurred in the same year as the maximum numeric consumption. This was due to a combination of the slower growth of the emergent beetle population and slower bird responses.

For several reasons the percentage of the prey population consumed by summer birds was only about 3% of the winter prey consumption. First, bird energetic requirements are much lower in the summer (Koplin 1967, Kendeigh 1970). Second, the beetles are found on the exterior of the tree so the birds do not have to expend energy to remove the beetles from beneath the bark. Third, the adult beetles are larger than the larvae, and have a higher caloric value (Koplin 1967, Otvos 1969), so fewer insects are needed to satisfy bird caloric requirements. Finally, there is a greater abundance of alternate prey available during the summer. The percent of beetles in the birds' summer diets is smaller than during the winter, so fewer beetles are consumed.

Consumption of the summer adult beetle population was also 7% to 10% of that estimated by Stallcup (1963). There were several reasons for the differences in estimates. First, Stallcup made his calculations based on a bird

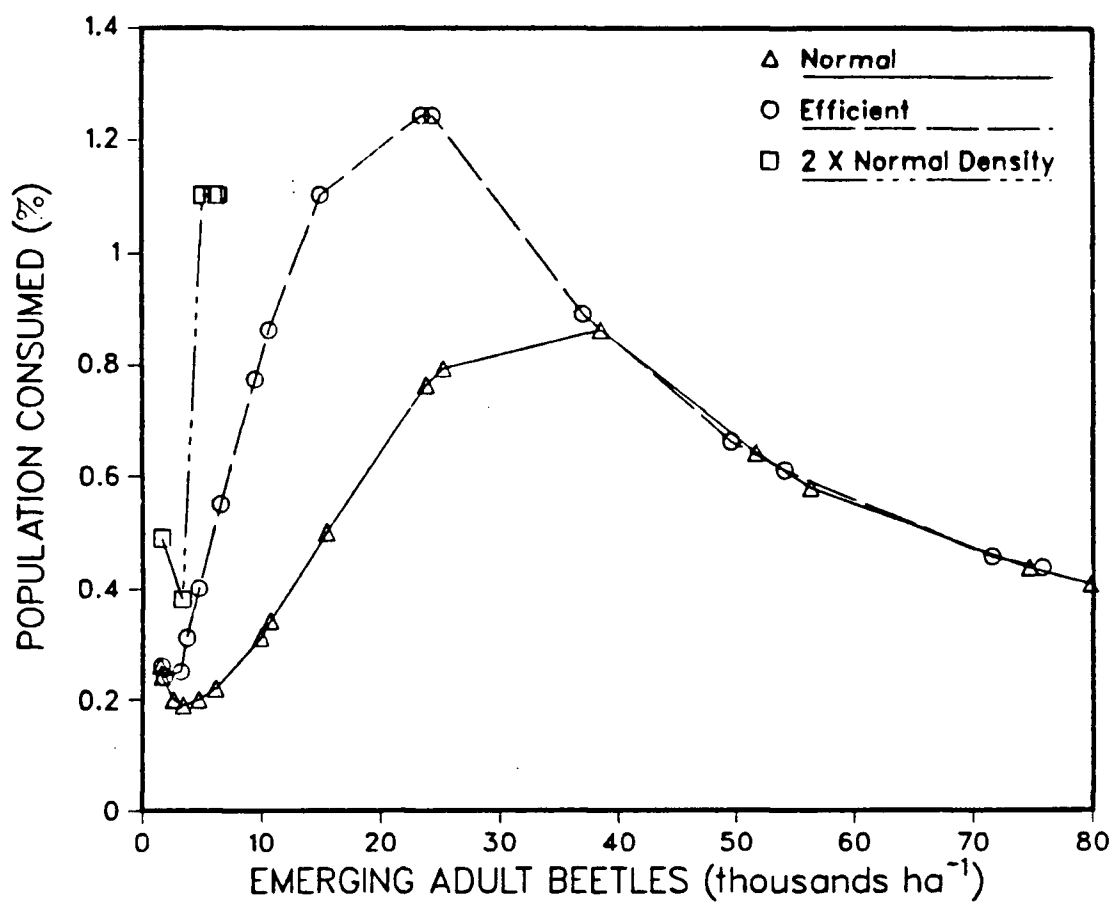


Figure 29: Percent of emerging adult population consumed by summer birds in the control stand.

population density of approximately 1.2 birds per hectare, whereas the model calculated a maximum of 0.5 birds per hectare. Second, Stallcup calculated consumption by assuming that each bird ate daily quantities of food equivalent to 25% of their body weight. The method for determination of daily consumption used in the model was described in section 4.5. The calculations made by Stallcup also assumed a longer flight period. Through these methods, Stallcup calculated the total mortality due to avian predation during the flight period to be 2730 beetles. The model calculated this total to be 329 beetles. These values were divided by beetle population density to determine the proportion consumed. In Stallcup's study, the estimated emerging beetle population density was 1306 beetles per hectare, whereas the model calculated a density of 39,464 beetles per hectare. The combination of greater total consumption and lower beetle density explains the difference in the estimates.

Despite the more detailed method for calculating the consumption of the prey, the values determined by the model for the percentage of the beetle population consumed may be an underestimates simply because the lack of basic data on bird densities limited the model to the simulation of only three summer bird species, the hairy woodpecker, brown creeper, and red-breasted nuthatch. The total bird density may actually be four to ten times greater (Stallcup 1963,

Taylor 1969, Roppe 1974, Hein 1980), so total consumption would be increased, as would the impact of summer predation.

An important consequence of the summer birds' slow functional and numerical responses is evident in Figure 29. The early expansion of the mountain pine beetle population beyond the endemic level, though slow, was still sufficiently rapid to exceed the birds' ability to respond. As a result, the percentage of the emerging beetle population consumed by birds initially decreased. Though total consumption by summer birds removes only a small percent of the beetle population, phenomenon such as the initial decrease in percentage consumption may assist the beetles in crossing the outbreak threshold theorized by Berryman (1978, 1981) and others.

5.2.2 SCENARIO 2: EFFICIENT PREDATORS

An increase in the efficiency of the avian predators had two major impacts on the mountain pine beetle population (Figure 20). First, population growth was reduced, delaying the peak population density by one year. Second, the peak density was 5% less than that of the control stand.

As a result of lower beetle density, the total stand and individual DBH class tree mortalities were also reduced (Figures 21, 22, and 23). The total stand mortality decreased from 17% to 16%, while mortality per each DBH

class ranged from 0.1% of the trees in the 15-cm class to 1.5% of the tree in the 40-cm class.

Greater predator efficiency resulted in more rapid achievement of peak winter woodpecker population density (Figures 24 and 25), and an increase in the winter consumption to 37% of the larval population (Figure 26). Additionally, peak winter consumption occurred a year earlier than with 'normal' predator responses, and at a lower larval population density of 45,813 larvae per hectare.

Changes in bird density and predation during the beetles' flight period exhibited a pattern similar to that of the winter birds (Figures 27-29). In this simulation a maximum consumption of 1% of the emerging adult beetle population was achieved at a beetle density of 23,508 beetles per hectare, compared to 38,464 when predator responses were less efficient. It was also evident from Figure 29 that the increased predator efficiency did not prevent the beetle population from growing at a rate beyond the summer birds' ability to respond.

5.2.3 SCENARIO 3: TWICE NORMAL PREDATOR DENSITY

In this scenario, the mountain pine beetle population never reached an epidemic level (Figure 20). Instead, it increased to 5,799 beetles per hectare, or roughly 7.7 times

greater than an endemic population density, by year seven, thereafter declining gradually. Even at year sixteen the population was still at a density of 5,576 beetles per hectare (7.4 times greater than an endemic population density).

Due to the low beetle density, the total stand and individual DBH class tree mortalities were very low and, after the initial insect population increase, remained fairly constant (Figures 21 and 22). Total stand tree mortality after sixteen years was only 4%. Final mortality per DBH class (Figure 23) ranged from 0.6% of the trees in the 15-cm class to 20% of the trees in the 40 cm-class. The reduced mortality rate of trees in the larger DBH classes was particularly important in that the presence of these larger trees enabled the beetle population to maintain itself in the face of heavy avian predation.

Winter woodpecker density reached a maximum of 37.5 birds per hectare at year four of the infestation when larvae were present at a density of 48,976 larvae per hectare (Figures 24 and 25). Winter consumption by woodpeckers peaked at 57% of the larval population in year five (Figure 26), three years prior to the peak larval density. Consumption remained at approximately this level during the remainder of the infestation, in response to nearly constant predator and prey population densities.

The summer bird densities and consumption followed much the same pattern as that exhibited during the winter (Figures 27, 28, and 29). However, peak consumption of 1% occurred in year three of the infestation. From that point on, consumption remained approximately constant. As total bird predation reached its maximum level in year five, while the pine beetle population continued to increase until year seven, declining thereafter, it is reasonable to assume that other mortality factors in combination with avian predation were responsible for keeping the insect population in check. The real value of the initially high bird densities may have been in sufficiently slowing beetle population growth to permit the combination of all factors to gain control over the insect population, and reverse its growth.

When considering the impacts of avian predation in this scenario one should recall that only bird densities were doubled. The proportion of the larvae or beetles in the birds' diets was the same as in the first (control) scenario. Also, bird densities were doubled at all beetle population densities, endemic as well as epidemic. Yet even with the doubling of predator densities it was the 'efficient' predators that exhibited a faster total response to changes in insect density.

In summary, the mountain pine beetle population reached its greatest peak density in Scenario 1 when the birds

exhibited normal functional and numerical responses. Approximately 17% of the trees in the stand were killed by the beetles. Consumption of the larvae during the winter accounted for 26% of the population, which compares favorably with Lester's (1980) estimate of 30%. Summer birds consumed an estimated 0.9% of the emerging beetle population. This value is much lower than that of Stallcup (1963) due to the differences in beetle and bird densities, and the methods used to calculate consumption. The value calculated by the model may be an underestimate due to the low number of bird species simulated.

Increases in predator efficiency (Scenario 2) resulted in greater winter and summer consumption, and earlier achievement of maximum consumption. This, in turn, helped delay the growth of the beetle population and reduce peak beetle density. However, tree mortality was only slightly reduced, and remained at about 16%. Doubling the predator densities (Scenario 3), prevented an outbreak of major proportions, leading instead to a long-term low-level infestation. The resulting total tree mortality and individual DBH class mortalities were greatly reduced. High woodpecker winter densities, combined with relatively low larval densities, resulted in a peak consumption of 57% of the larval population. Peak summer predation was also increased, and attained a maximum value of 1% of the

emerging beetle population. In none of three scenarios, however, did the beetle population fail to increase beyond its endemic level.

The first three scenarios illustrate the differences in impacts between increased predator efficiency and increased bird densities, particularly when insects are at endemic levels. The more efficient predators helped delay the infestation and reduce peak density, but only when bird densities were greater at all insect densities was a major infestation prevented. However, the bird densities simulated in Scenario 3 are probably higher than those which can be realistically maintained (Taylor 1969, Roppe 1974, Austin and Perry 1979). Researchers have indicated that the densities of some important mountain pine beetle consuming bird species may actually be increased by 25% through careful management practices (Austin and Perry 1979, Dickson *et al.* 1983, Scott and Oldenmyer 1983, Marcot 1983). Therefore, a scenario in which maximum summer bird densities were 1.25 times greater than 'normal' was simulated. The results of this scenario were very similar to those of the efficient predator scenario (#2). Through variations in simulation parameters it was found that increases in bird densities of between 150% and 175% were required before any major impacts on beetle population density were evident. However, reducing bird densities to 10% of 'normal' resulted

in beetle population growth to a maximum of 84,911 beetles per hectare, approximately 29% greater than the peak density in the first scenario. As a result more than 90 additional trees per hectare were killed; an increase in total stand tree mortality of more than 19%. Consumption of the winter larval population by woodpeckers reached only 3%, while adult beetle consumption in the summer never increased beyond 0.1%. The importance of beetle predation by forest birds was quite evident in this simulation.

Another significant difference between Scenarios 2 and 3 is that, although it is difficult, if not impossible, to manage stands to accelerate the bird functional responses, management practices can increase baseline bird densities. Studies like those of Dickson *et al.* (1983), Marcot (1983), and Scott and Oldenmyer (1983) indicated that even the drastic effects of clearcutting on population densities of some bird species can be reduced through careful planning and execution.

5.3 THE SENESCENT STAND

5.3.1 SCENARIO 4: NORMAL PREDATOR RESPONSES

The mountain pine beetle population achieved a peak autumn density of 438,420 beetles per hectare at year seven of a thirteen year infestation (Figure 30). This was the

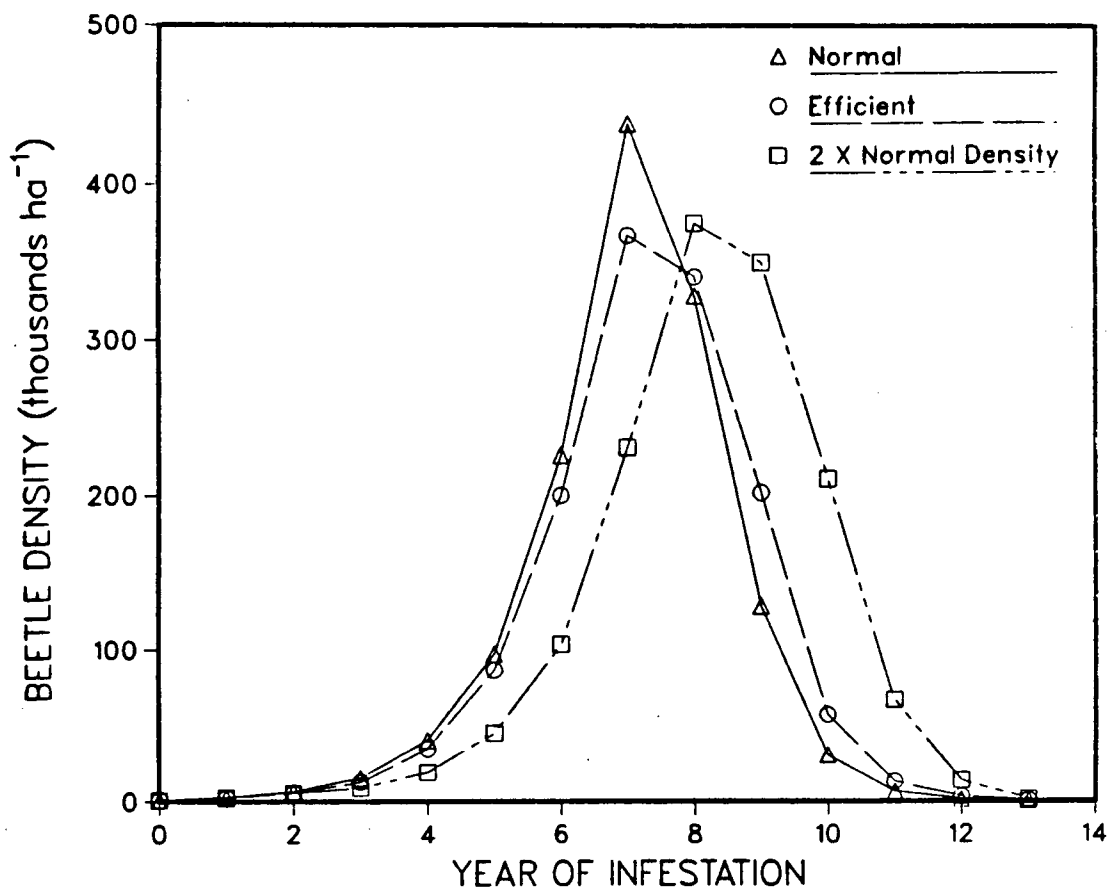


Figure 30: Yearly mountain pine beetle autumn density in the senescent stand.

greatest beetle population density achieved in any of the nine scenarios. The rapid expansion to a very high density was due mostly to the large number of trees in the 30, 35, and 40-cm DBH classes where beetle productivity is greatest.

Total stand and individual DBH class tree mortalities were also greatest in this scenario; approximately double those found in Scenario 1. Just over 1198 trees per hectare (64% of the original stand), were killed by the beetle (Figure 31). Final mortality in the 15-cm DBH class reached 5%, while 100% of the trees in the largest class (Figures 32 and 33) were killed by year nine.

Winter woodpeckers first reached their maximum density of 25 birds per hectare in year four, corresponding to a density of 197,882 larvae per hectare (Figures 34 and 35). The winter consumption by woodpeckers peaked at 24% of the winter larval population (Figure 36) in year three, five years prior to the maximum larval density. The peak consumption was slightly less than that recorded in Scenario 1, and also occurred a year earlier. This was probably due to the more rapid beetle population growth.

A similar pattern was evident for summer bird densities and adult beetle consumption (Figures 37, 38, and 39). The maximum consumption, 0.7% of the emerging adult population, was only 0.3% less than it was in Scenario 1, and as with winter consumption, the peak occurred earlier.

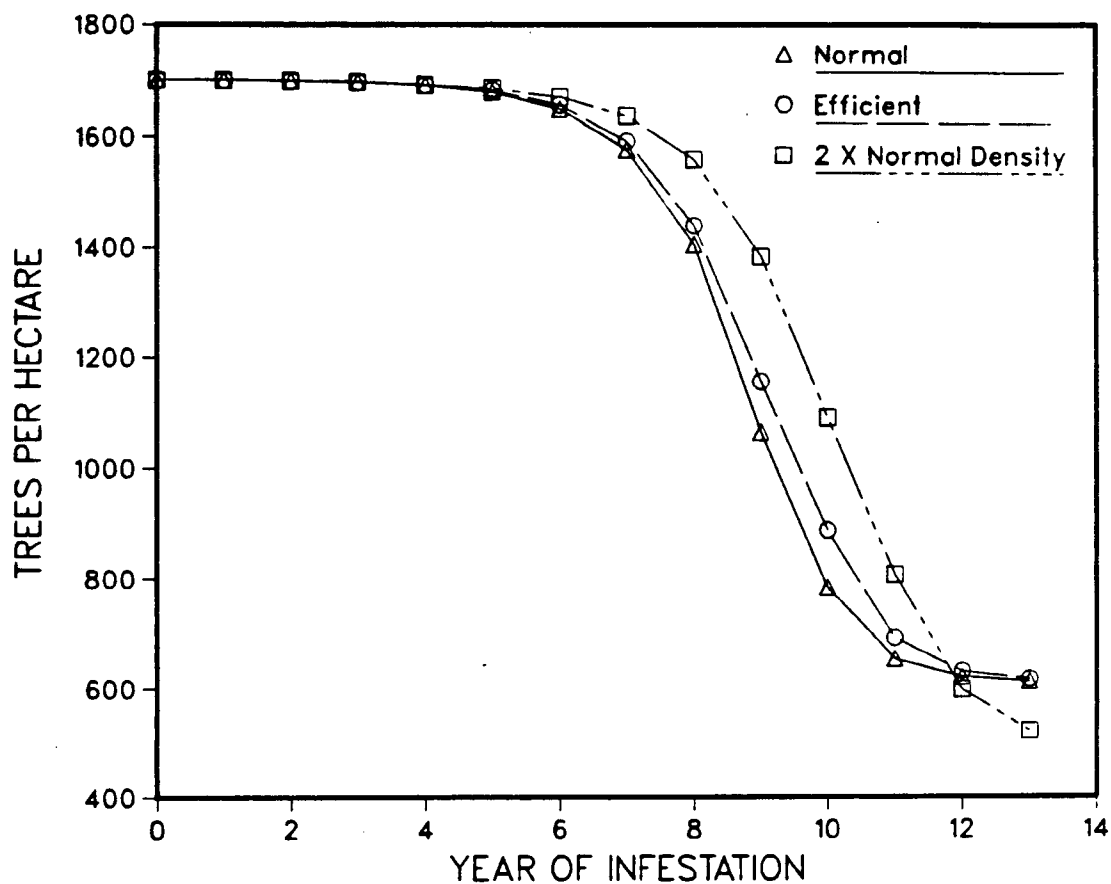


Figure 31: Yearly total stand density for the senescent stand.

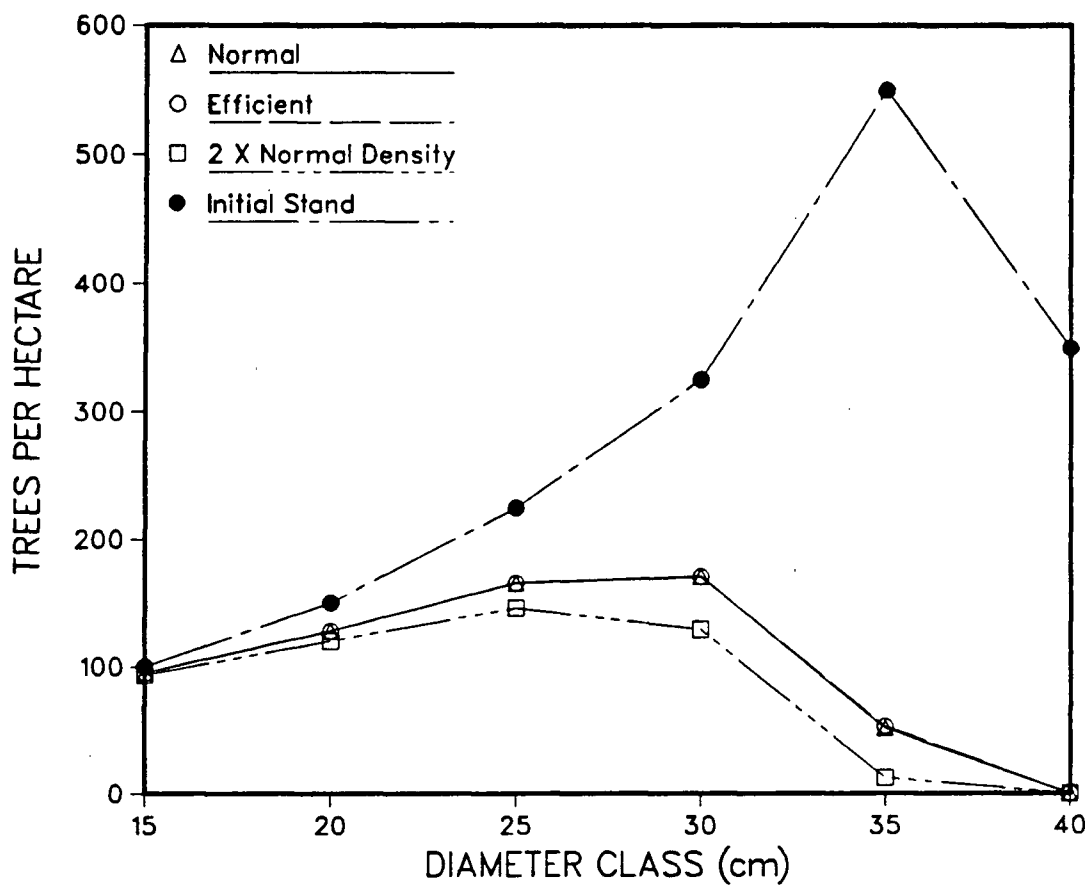


Figure 32: Initial and final stand structures for the senescent stand.

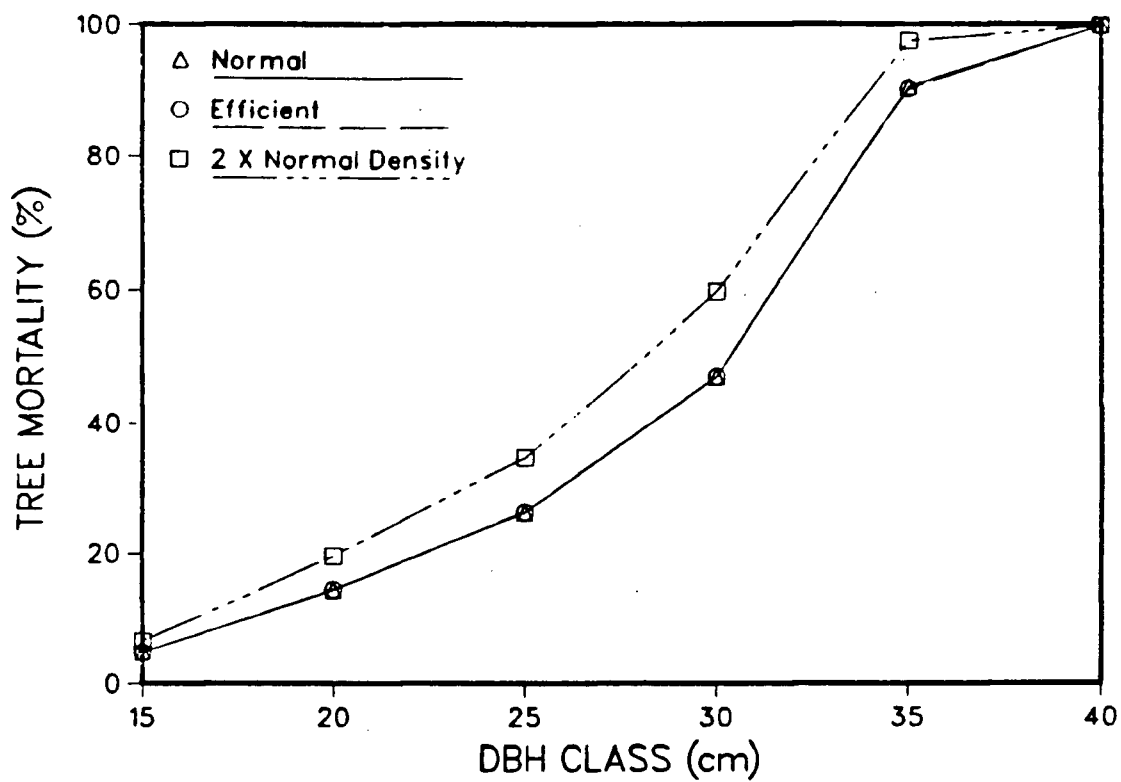


Figure 33: Total tree mortality for each diameter class in the senescent stand.

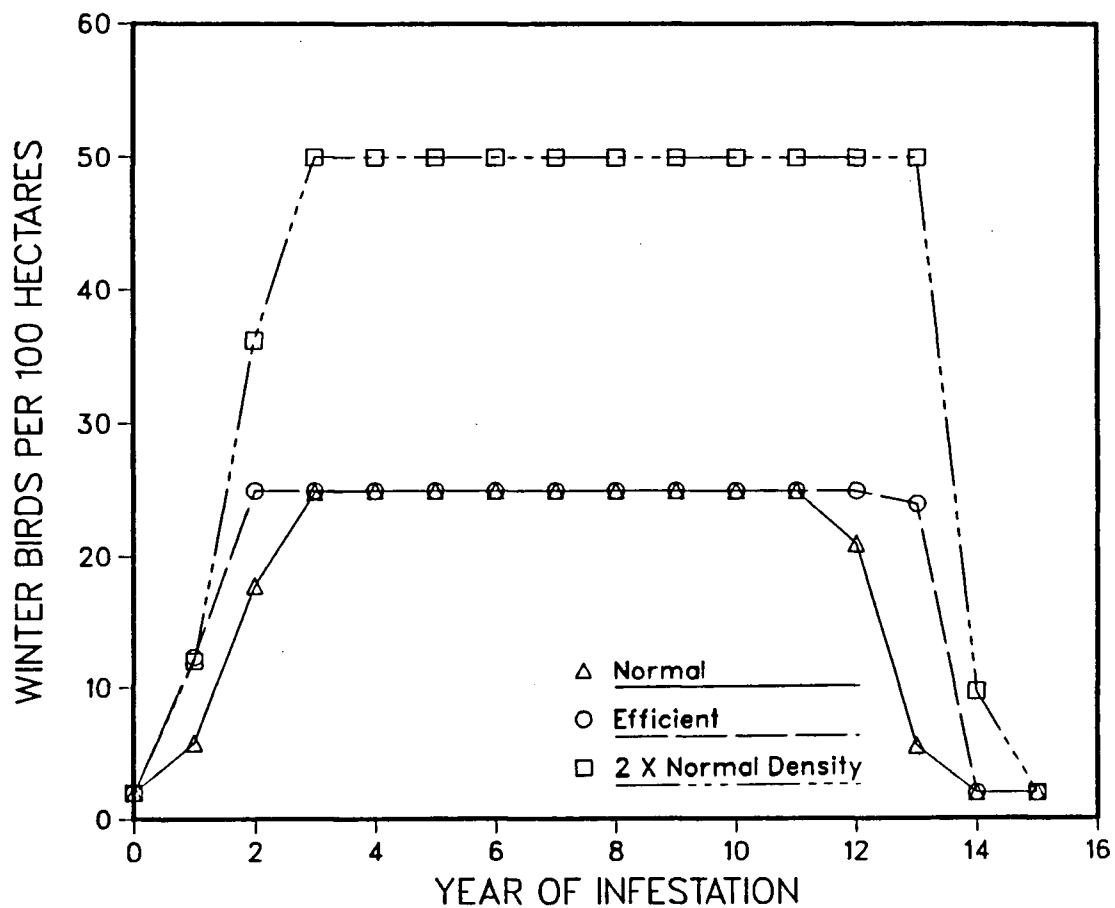


Figure 34: Yearly winter bird density in the senescent stand.

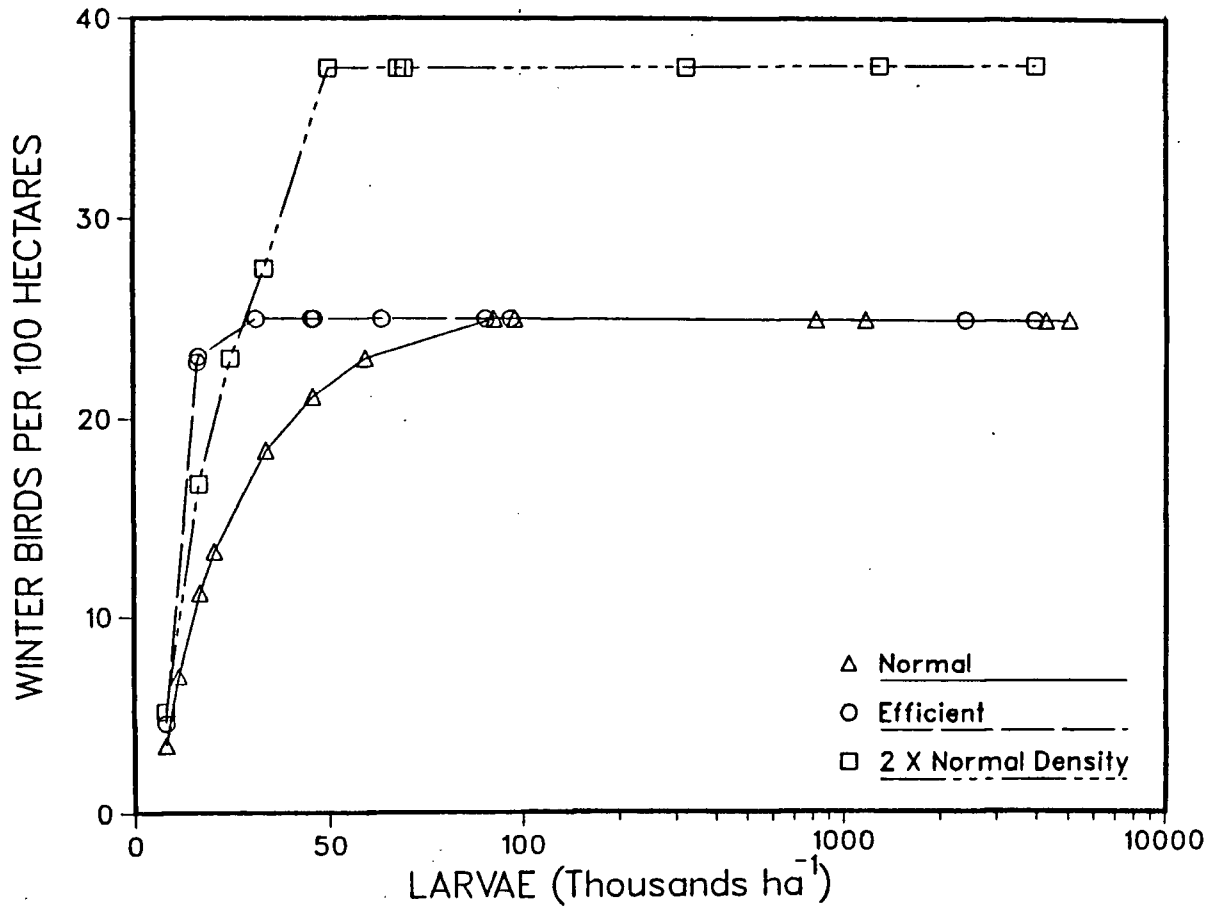


Figure 35: Winter bird density in the senescent stand relative to larval density.

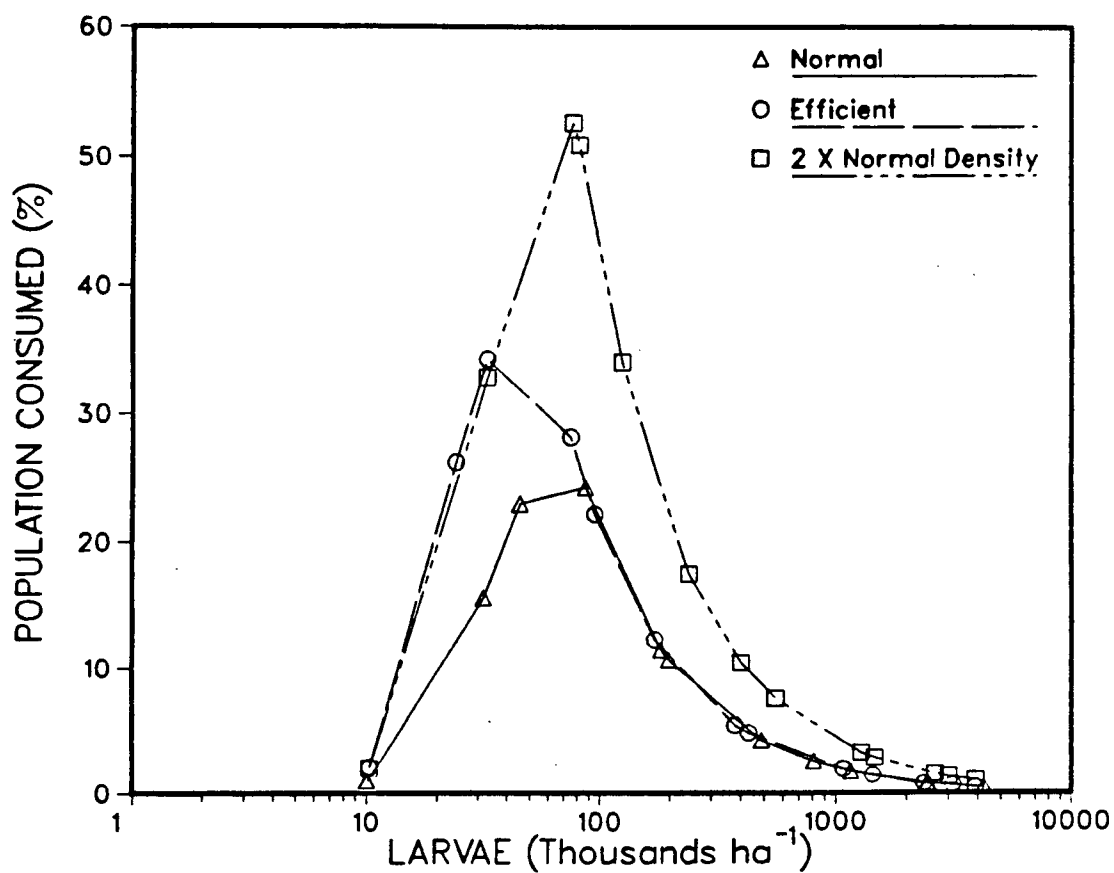


Figure 36: Percent of winter larval population consumed by woodpeckers in the senescent stand.

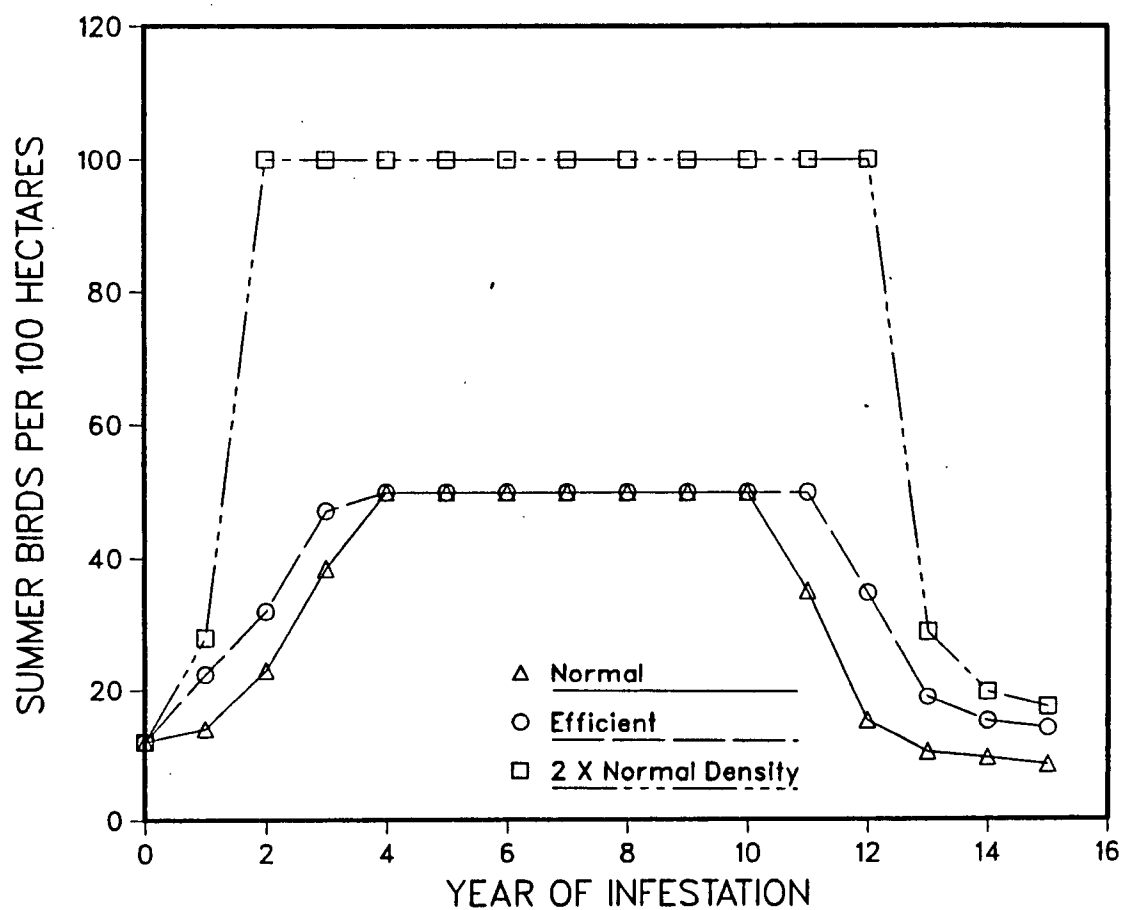


Figure 37: Total summer bird density in the senescent stand.

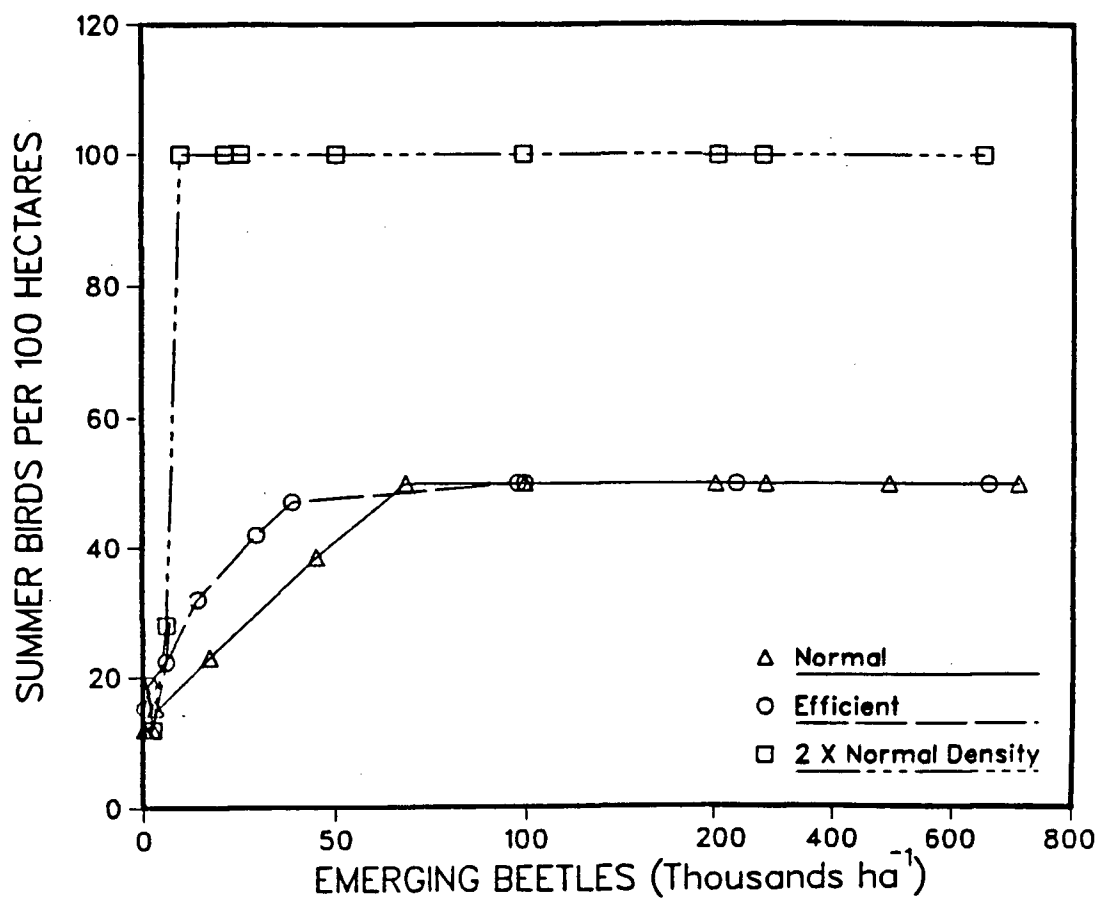


Figure 38: Total summer bird density in the senescent stand relative to adult density.

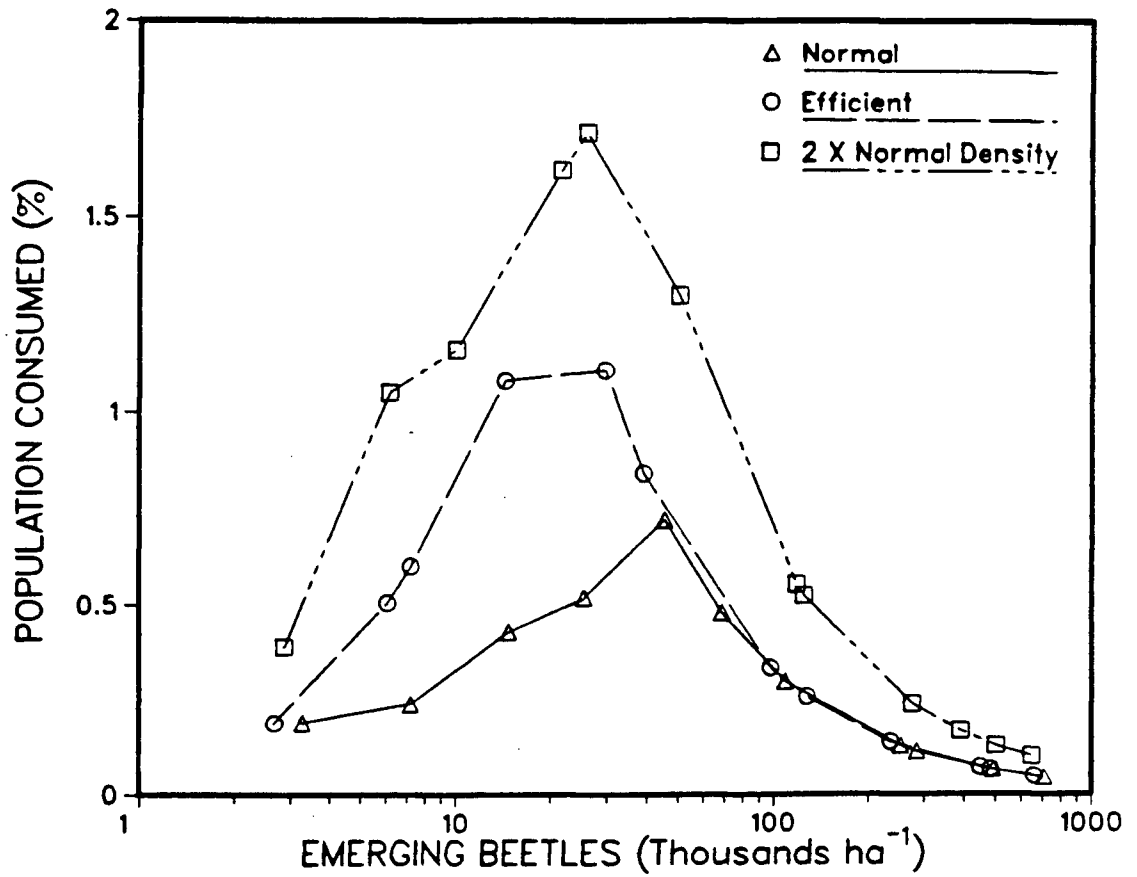


Figure 39: Percent of emerging adult population consumed by summer birds in the senescent stand.

5.3.2 SCENARIO 5: EFFICIENT PREDATORS

As in Scenario 2, an increase in predator efficiency increased winter and summer predation, depressed beetle population growth, and aided in reducing the peak beetle population density (Figure 30). However, the achievement of the peak density was not delayed as it was in Scenario 2. Due to the large food supply, beetle population growth in this stand was too rapid for the birds to suppress for long, despite the earlier functional and numerical responses of the birds.

Although maximum mountain pine beetle density was reduced 16% from that of the previous scenario, the total tree mortality for Scenario 5 (Figure 31) was approximately equal to the total tree mortality of scenario 4. This was most likely due to the beetle population in Scenario 5 remaining at greater densities in years ten to thirteen of the infestation. During those final four years the beetles killed approximately 100 more trees per hectare, resulting in the near-equal total mortalities. Compared to Scenario 4, the individual DBH class mortalities in Scenario 5 (Figures 32 and 33) were reduced in all but the 40-cm class where, once again, all trees were killed by year nine.

The maximum winter bird density of 25 birds per hectare occurred at a density of 32,835 larvae per hectare in year 2 (Figures 34 and 35). Winter consumption by woodpeckers, 34%

of the larval population, was slightly less than that recorded in Scenario 2, and also occurred two years earlier (Figure 36). Both the reduction in and earlier occurrence of peak winter consumption was due, for the most part, to the rapid expansion of the beetle population. Summer bird densities and predation followed a similar pattern (Figures 37 and 38), with a maximum consumption of 1% of the emerging population corresponding to a beetle density of roughly 7,226 beetle per hectare (Figure 39).

5.3.3 SCENARIO 6: TWICE NORMAL PREDATOR DENSITY

The results of Scenario 6 were very different than those of Scenario 3. The extensive food source in the senescent stand, represented by the trees in the large DBH classes, permitted the beetle population to expand rapidly. Though growth was depressed and the peak density was delayed by a year, the doubling of predator densities could not prevent the epidemic from occurring (Figure 30). Surprisingly, the maximum autumn density in this scenario (375,065 beetles per hectare) was actually 2% greater than that of Scenario 5. As a result 111 more trees per hectare were killed (Figure 31), increasing total stand mortality to 70%. Tree mortality in the individual DBH classes ranged from 7% of the trees in the 15-cm class to 98% of the trees in the 35-cm class (Figures 32 and 33). Once again, all

trees in the 40-cm class were killed, though this did not occur until year ten of the infestation.

Woodpeckers first reached their maximum density of 50 individuals per hectare in year three when larvae were present at a density of 76,136 larvae per hectare (Figures 34 and 35). The peak winter consumption by woodpeckers accounted for 58% of the larval population in year three of the infestation. This value was slightly lower than that of Scenario 3, however, it occurred two years earlier. Again, the summer bird densities and predation exhibited a typical pattern (Figures 37, 38, and 39). The birds consumed a maximum of 2% of the emerging beetle population. This value is the greatest consumption by summer birds in any of the nine scenarios.

In summary, the great number of trees in the large DBH classes provided the beetles with an abundant food source. As a result, the beetle population rapidly attained a high density. Total stand mortality in Scenario 4 was more than three times greater than in the control scenario (#1). Peak winter and summer predation by birds was reduced, and also occurred earlier in response to the rapid beetle growth.

Increasing the efficiency of the birds had little impact on the beetle population. Peak density was slightly reduced but it was not delayed as in Scenario 2. Total stand mortality was practically unchanged from Scenario 4.

Doubling the bird densities (Scenario 6) did not prevent the outbreak, as in Scenario 3. Beetle population growth was simply too rapid for the birds to have such an effect. The total stand mortality of 70% was the highest recorded for any of the nine scenarios. This was due to the beetle population remaining at a high density for a longer period of time, and killing more trees in the smaller diameter classes. Winter predation by birds accounted for 53% of the larval population, while the summer consumption (2% of the emerging beetle population) was the highest recorded in any of the nine scenarios.

This second set of scenarios illustrates the ability of the mountain pine beetle to take advantage of a large food source, as is currently evident in the Chilcotin Plateau area in B.C. In cases such as this, birds may reduce the peak beetle population density slightly, but it is very unlikely that any natural or enhanced bird population would be able to prevent the outbreak.

5.4 THE THINNED STAND

The role of avian predators in the following scenarios was greatly reduced for three reasons. First, the major reduction in the number of trees in the four largest DBH classes greatly reduced total beetle population productivity. Second, all of the bird species used in the

simulations are negatively affected by major thinning operations. Therefore, their initial and peak densities (Appendix 5) were much reduced. Finally, the mountain pine beetle population never increased beyond the original endemic density, so bird densities and the percentage of larvae or beetles in their diets did not increase beyond the original levels. In other words, the numerical and functional responses did not occur. Due to the absence of these responses, the normal and efficient predator scenarios are the same, and are discussed as one.

5.4.1 SCENARIOS 7 AND 8: NORMAL AND EFFICIENT PREDATORS

In these two scenarios the mountain pine beetle population immediately declined from its endemic level. By year ten there were only 54 beetles per hectare (Figure 40), a decrease of 93%. In the first year of the scenarios, only 743 beetles survived to emerge in the summer, and the flight-period mortality had not yet been applied.

The total stand tree mortality was only 1.0% at the end of ten years (Figure 41). Though large diameter trees represented only a minor proportion of the stand (Figure 42), the beetles were still attracted to them. Individual DBH class mortality ranged from 15% of the trees in the 40-cm class to only 1% in the 15-cm class (Figure 43).

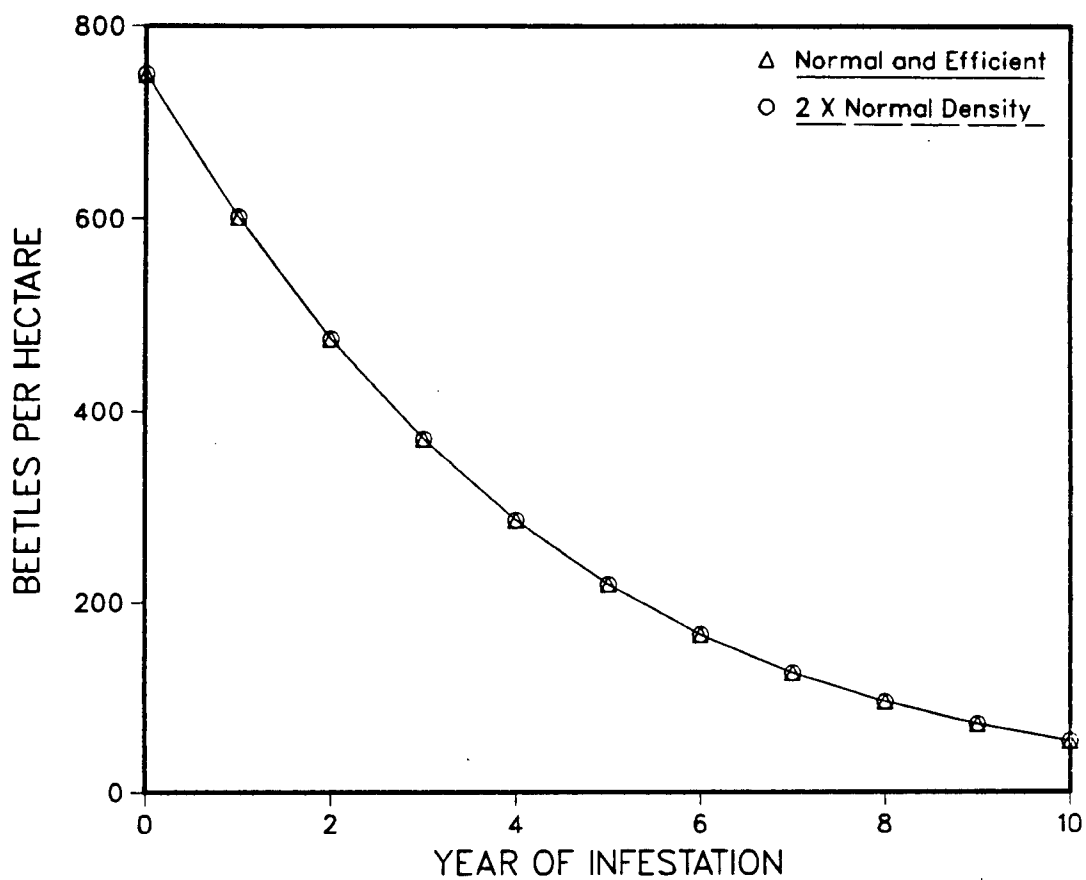


Figure 40: Yearly mountain beetle autumn density in the thinned stand.

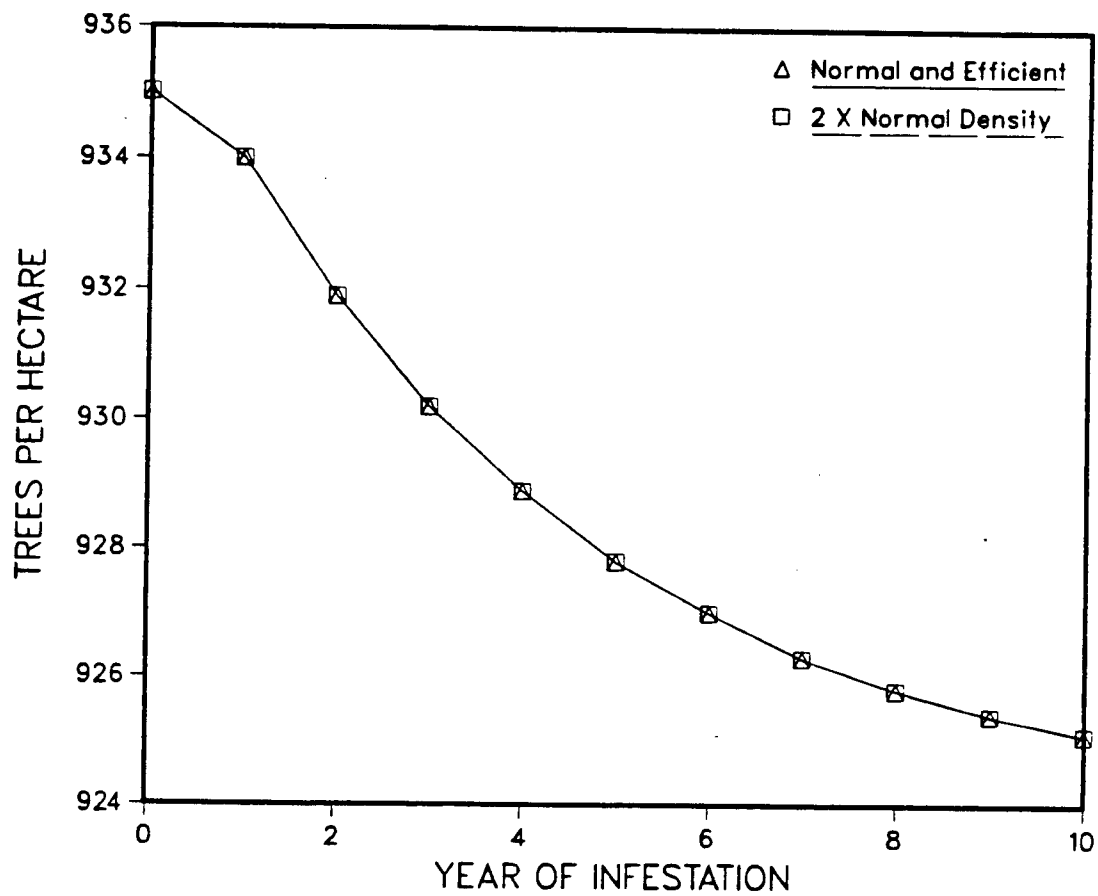


Figure 41: Yearly total stand density for the the thinned stand.

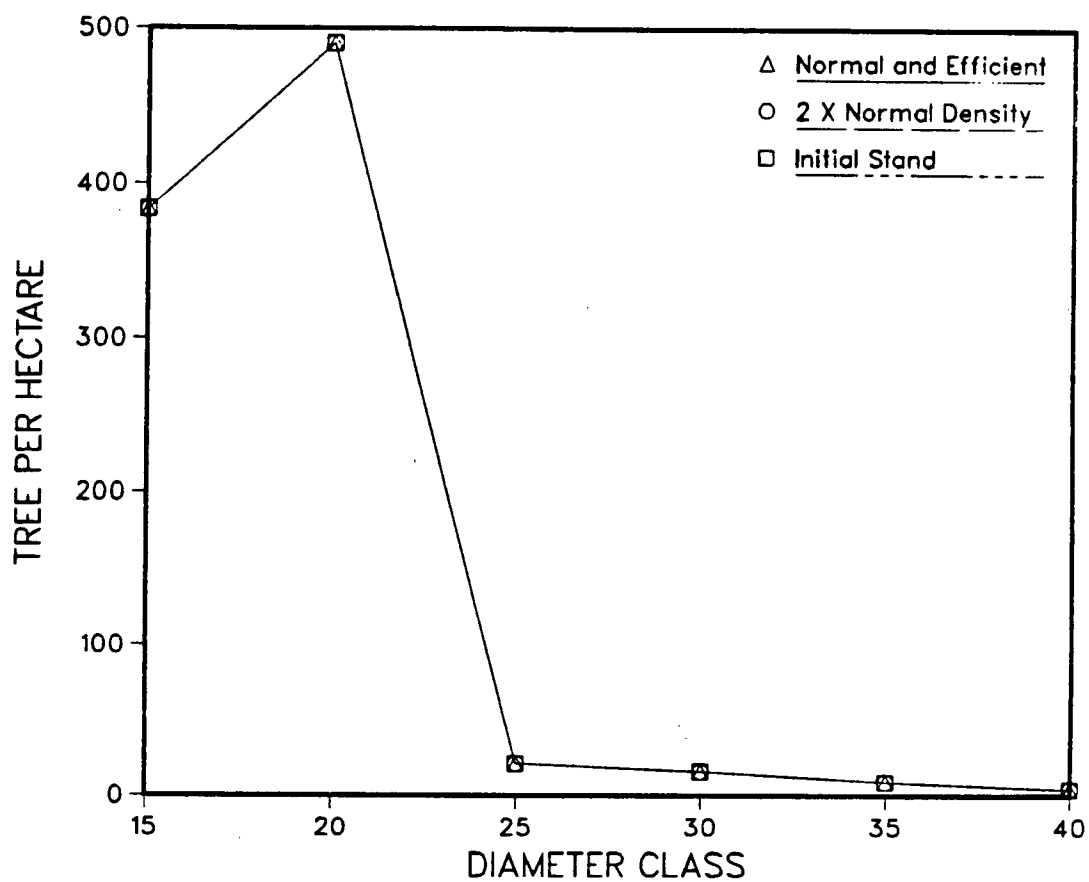


Figure 42: Initial and final stand structures for the the thinned stand.

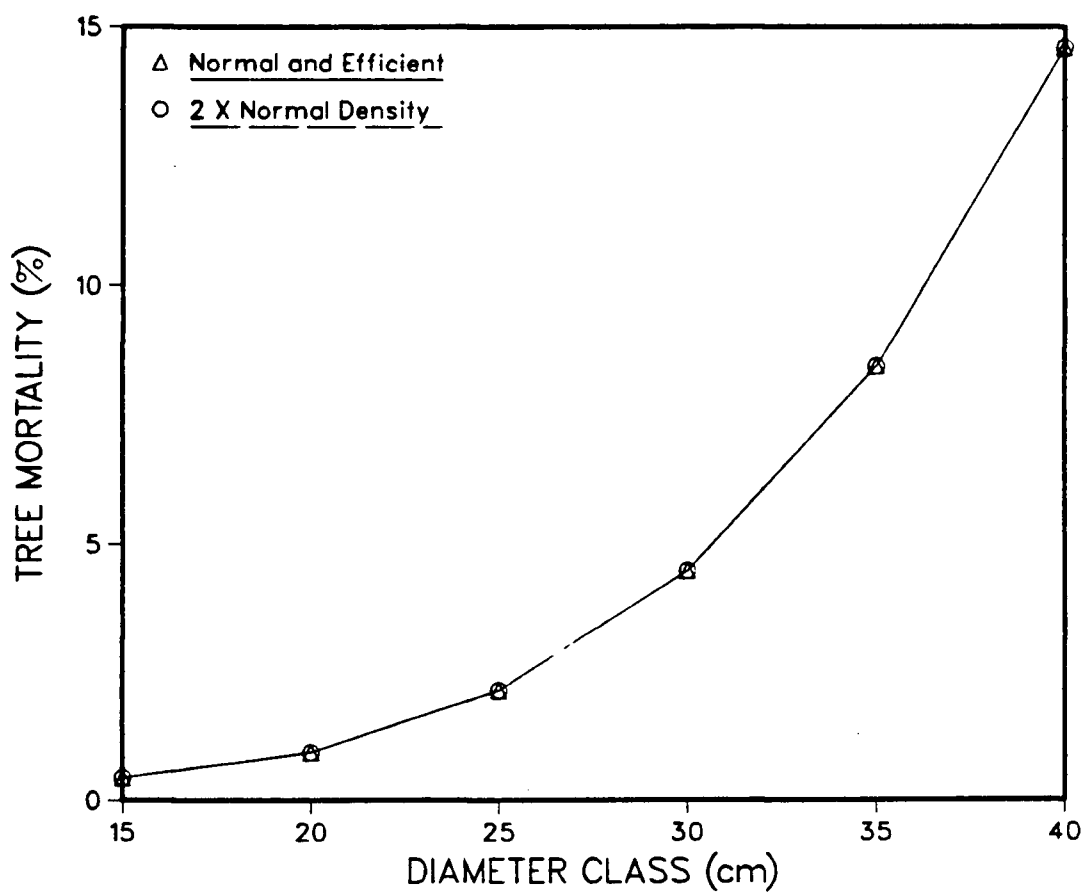


Figure 43: Total tree mortality for each diameter in the thinned stand.

Changes in the percentage of the beetle population consumed by winter and summer avian predators were due mainly to the changes in the density of the beetle population itself. For the most part, the actual number of larvae or adult beetles consumed by the birds remained constant. However, the proportion consumed increased simply because the insect population decreased. When the larval or adult beetle densities became too low, the proportion of the insects in the birds' diets dropped to zero, and the corresponding proportion of the insect population consumed fell to zero as well. The maximum consumption of the winter larval population was 0.3% (Figure 44), while maximum summer consumption was 0.1% of the emerging adult population (Figure 45).

5.4.2 SCENARIO 9: TWICE NORMAL PREDATOR DENSITY

The mountain pine beetle population decreased more rapidly in this scenario than in the previous two scenarios (Figure 40). By the end of the ten year simulation, there were only 53 beetles per hectare, 2% less than in Scenarios 7 and 8.

This population reduction did not have a major impact on total stand tree mortality. After ten years it was virtually equal to that of the previous two scenarios, having been reduced by only 0.004% (Figure 41). The

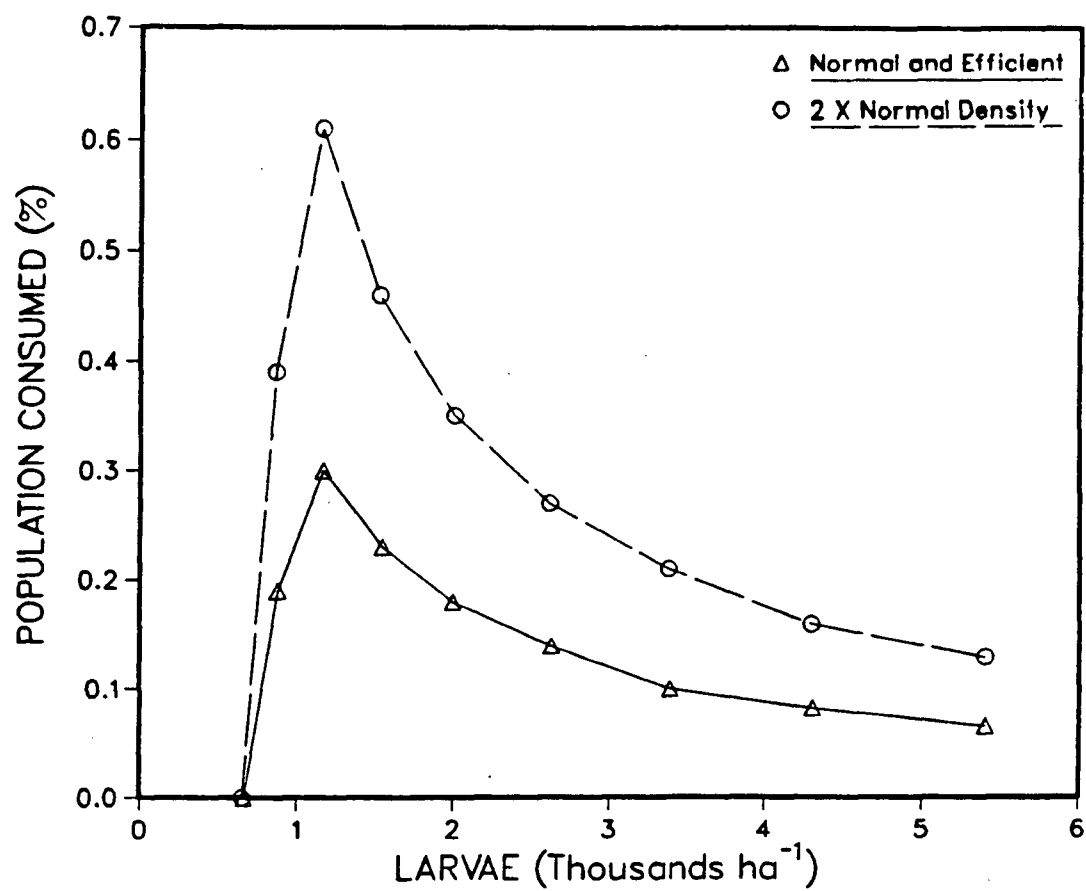


Figure 44: Percent of winter larval population consumed by woodpeckers in the thinned stand.

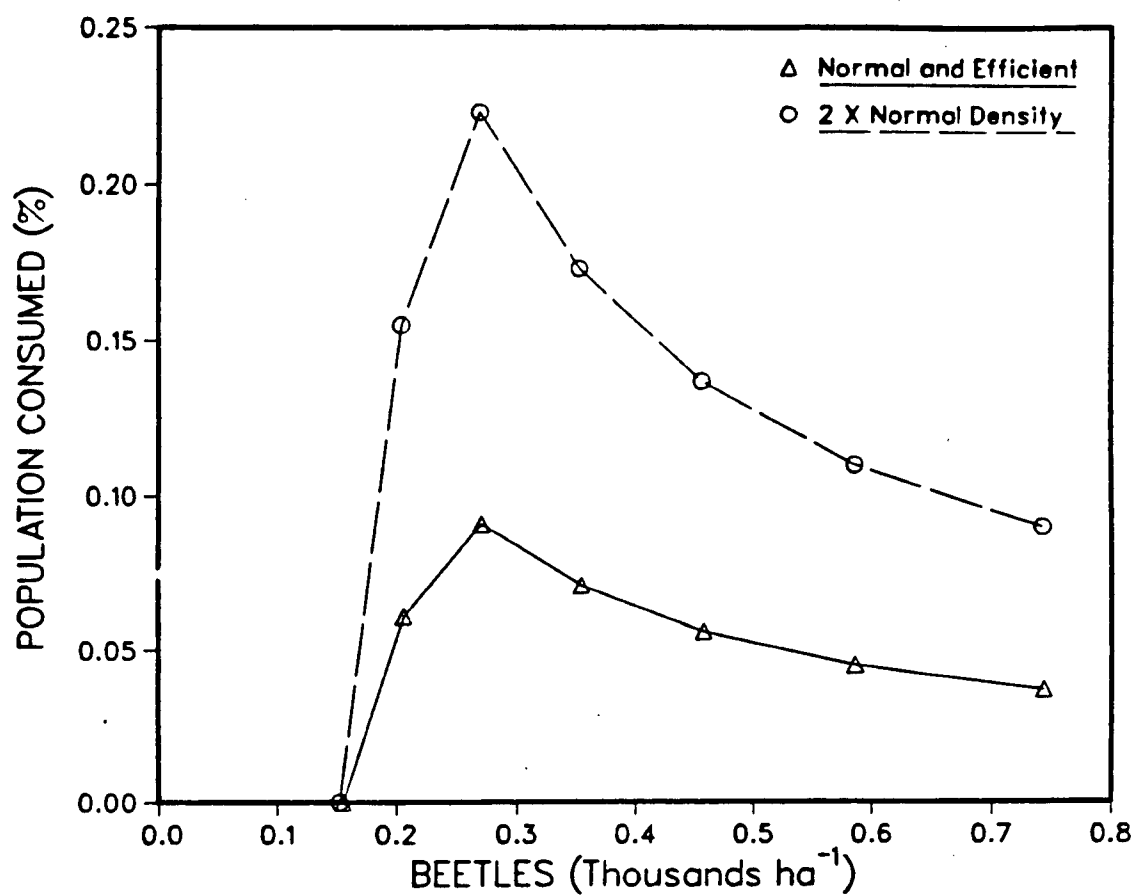


Figure 45: Percent of emerging adult population consumed by summer birds in the thinned stand.

corresponding individual DBH class mortalities (Figure 42) were reduced to an even lesser degree.

Consumption of the larval population by woodpeckers was about double that of Scenarios 7 and 8. Practically all changes in the proportion of the population consumed were due to changes in the larval population density. Maximum winter consumption by birds represented 0.6% of the larval population (Figure 44).

Summer avian predation exhibited a nearly identical pattern (Figure 45). Predation in this scenario, however, was 2.3 times that of Scenarios 7 and 8, due to the cumulative effect of simulating three species instead of one. Total summer consumption was a maximum of 0.2% of the emerging adult beetle population.

To summarize, in Scenarios 7 through 9 the small supply of good quality food had a far more significant impact on beetle dynamics than did avian predation. In all three scenarios the beetle population immediately declined from its original endemic level. Total stand and individual DBH-class tree mortalities were all expectedly low. The maximum total stand mortality was 1.0%. Maximum individual DBH class mortality was 15% of the trees in the 40-cm class of Scenarios 7 and 8.

As a result of the immediate decline in beetle population density, avian functional and numerical responses

did not occur. Changes in the proportion of the insect population consumed by birds were due mostly to the decreases in insect population density. At extremely low beetle densities the consumption dropped to zero when the proportion of larvae or beetles in the birds' diets became zero. Changes in predator efficiency had no effect on consumption because the functional and numerical responses did not occur. Doubling the bird densities essentially doubled the proportion of the beetle population consumed as a result of the dynamics described above. Maximum winter consumption was 0.6% of the larval population, while maximum summer consumption was 0.2% of the emerging adult beetle population.

The third set of scenarios indicated that preventive management can have a major impact on beetle dynamics. The beetle population declined due to an inadequate food source. Bird densities were reduced, and functional and numerical responses did not occur. However, the proportion of the insect population consumed by birds still increased. The pattern of total consumption was the same as that described by Holling (1959), but as the result of a totally different process. These final three scenarios illustrated a management practice which reduces stand susceptibility to the mountain pine beetle, while simultaneously increasing the avian impact on the insect.

5.5 SENSITIVITY ANALYSIS AND MODEL LIMITATIONS

Each yearly iteration of the mountain pine beetle simulation model required the calculation of more than 70 parameters for each of six tree DBH classes. The values for many of these parameters were derived from publications that represented summaries of many other studies. In other cases, the simulation values were the best estimates of factors that have proven extremely difficult to accurately measure in the field. Arbitrarily chosen values based on related studies were used in a few cases when no other information was available. Because of these drawbacks and gaps in data, it proved impossible to place meaningful confidence intervals on the model results.

In an attempt to examine model accuracy and sensitivity seven variables were altered by +20%, and the impact on simulation results recorded. The magnitude of the impact was assessed by monitoring the amount of change in two output variables; mountain pine beetle autumn density, and total tree mortality in an intermediate (25 cm) DBH class.

Alteration of three variables, the proportion of the adult beetle population dispersing out of the stand, and the caloric value of one adult beetle and one larva, changed the beetle autumn density less than 10%. This alteration in beetle density resulted in an increase/decrease in tree mortality of slightly less than 1%. The proportion of

beetles leaving the stand was one of the variables about which practically no information is available, though field investigations are in progress. The caloric values of different beetle life stages were not difficult to determine, and currently do not present a problem.

Two additional variables, the proportion of the adult beetle population killed during the flight/attack period by causes other than avian predators, and total beetle attack density, altered beetle density by 9% to 11% and 14% to 17%, respectively. This resulted in changes in tree mortality slightly more than 1%. Like the proportion of the beetle population dispersing from the stand, the proportion killed during the flight period by causes other than birds is not well known because it is so difficult to measure. Attack density is simply beyond generalization because a particular density will have a different effect on each individual tree, depending on the tree's history and current state of vigour.

The final three variables, phloem thickness, number of eggs laid per female, and proportion of females in the attacking population, had the greatest impact, altering beetle population density by a maximum of 144%, 90%, and 57%, respectively. These large increases, however, only increased tree mortality by, at most, 18%. These last three variables, particularly phloem thickness and the number of

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eggs laid per female, were closely linked. Trees with thicker phloem produced females capable of laying more eggs. The proportion of females may be related to the others in that it varies over the duration of the outbreak, depending on tree DBH. The cause or causes of this variation are not well understood at this time.

The computer model developed for this study functions accurately under the conditions set forth in this report. However, caution should be used when interpreting the model results. The model, as a highly simplified representation of the real bird insect forest system cannot simulate all key relationships. For instance, the assumption was made that the simulated stand was static. Although infestations of up to sixteen years were simulated the trees in the stands did not age. Natural mortality of trees did not occur, and new, young trees did not 'grow into' the smallest DBH class.

A second, perhaps more important, characteristic of the model is that it simulates temporal but not spatial relationships. The mountain pine beetle infestations develop in and spread through a 20 hectare stand in time only. Therefore, effects such as the outward spreading of an infestation from an initially localized population cannot be simulated. It is hoped that continued investigations of bird insect interactions will make inclusion of these spatial inter-relationships possible.

6. CONCLUSIONS

The value of non-game bird predation of the mountain pine beetle was evident in the large numbers of insects that the birds consumed, and in the proportion of the population destroyed directly through consumption and indirectly through the effects of bark removal. During the winter, one bird alone could consume more than 86,000 larvae, accounting for up to 10% of the local larval population. The total impact on the insect population depended on the speed with which the bird community responded to changes in insect density, and on the endemic and maximum bird densities.

When functional and numerical responses occurred rapidly the initial expansion of the beetle population was suppressed, and peak beetle population density was reduced. Initial bird densities and maximum density achieved during numerical response appeared to be more important than speed of response in the suppression of beetle population growth. It was only when bird densities were initially high that there was an immediate increase in the proportion of the beetle population consumed.

The results of this model gave no indication that bird predation alone was sufficient to prevent a major pine beetle outbreak in a susceptible stand, even when initial bird densities were high or the birds' responses rapid. In

stands where the diameter distribution was such that beetle productivity was optimized even unrealistically high bird densities could not prevent the outbreak from occurring.

Major epidemics did not occur in stands where preventive silvicultural methods were used. In these stands the beetle populations never increased beyond the endemic level, so avian functional and numerical responses did not occur. The proportion of the beetle population consumed by birds increased, however, because the number of insects consumed remained constant while insect population density declined.

A combination of preventive thinning and intelligent non-game bird habitat management designed to increase bird densities would have the greatest impact on local beetle populations. The thinning would effectively remove the beetles' food supply, while proper bird habitat management would reduce the more drastic impacts of the cut. The birds would be present to feed on beetles moving into the thinned stand and, more importantly, would probably feed on beetles moving into the adjacent unthinned stands as well.

6.1 RESEARCH NEEDS

During the construction of the simulation model it became apparent that most of the gaps in the current knowledge of bird-mountain pine beetle interactions concern

the birds, not the insects. Considering the amount and distribution of lodgepole pine in British Columbia, and the extent of mountain pine beetle infestations, the lack of basic data concerning birds in provincial lodgepole pine stands is dismaying. Most of the bird density figures used in the simulation model had to be derived from data collected in Arizona, Colorado, and Wyoming. Though not a Biogeoclimatic Unit in B.C., extensive, pure stands of lodgepole pine certainly represent a distinct forest type with their own particular avifauna. There is a need for the collection of basic data on winter, breeding, and post-breeding bird densities in provincial lodgepole pine stands. Stratification by successional stage or age class, as in the research conducted by Lofroth and Wetmore (1985), is strongly recommended. Stratification by stand density and/or elevation are other possibilities.

More detailed investigations of bird-mountain pine beetle dynamics should focus on bird responses, both functional and numerical, to insect density changes, and bird responses to lodgepole pine management practices. The research conducted by Lester (1980) provides a basic example for the investigation of avian numerical responses to a mountain pine beetle infestation. Ideally, both summer and winter bird censuses should be conducted in stands of comparable age and density where the mountain pine beetle is

existing at endemic, epidemic, and post-epidemic levels. Additionally, it should be possible to select a stand where the beetle is at an endemic level, and also in the path of the infestation front, so as to conduct sequential censuses as the infestation moves through the stand. Such monitoring of bird densities in stands of different insect densities or sequentially in one stand as densities change, or both, should aid in determining the type of numerical response that the birds exhibit.

Similarly, it should be possible to distinguish the type of functional response that the birds exhibit by recording changes in diets at different levels of insect density. This information would be more difficult to collect because destructive sampling would almost certainly be necessary, though the use of emetics (*i.e.* Zach and Falls 1976) may offer an alternative.

Information relating bird densities to provincial lodgepole pine management practices would be very valuable, provided that data were collected both before and after the practice in question was applied. As with the basic bird densities, the bird responses to the thinning simulated with this model were based on data from the western United States. Decisions on the management of non-game birds in British Columbia would undoubtedly be more accurate if provincial data were available.

Lastly, more detailed information concerning woodpecker winter feeding methods and strategies is needed. The birds have a well developed ability to accurately locate insects beneath tree bark, possibly through auditory cues (Bent 1939, Otvos 1970). It also appears that they can assess stand insect densities as well. Theoretically, there exists some insect tree density at which the energetic costs of searching the tree and removing its bark outweigh the caloric value of the larvae in the tree. Similarly, there is some beetle stand density at which the energetic costs of remaining in a stand with a low insect density outweigh the costs and risks of moving to a new stand.

Measurements of the amount of bark removed from a tree during the winter in relation to measurements of the initial autumn larval density may help in understanding the woodpeckers' criteria for feeding tree selection. In a similar manner, it may be possible to relate measurements of overall stand beetle density to woodpecker use of the stand. If so, a pattern similar to one of the forms of functional responses may be observed. This information would help increase the accuracy of future models on the impacts of birds on the mountain pine beetle, and other bark beetles as well.

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APPENDIX 1

COMMON AND SCIENTIFIC NAMES

Fungi

Blue stain fungi *Ceratocystis montia* Rumbold
Blue stain fungi *Euophium clavigerum* Robinson and Davidson

Trees

Lodgepole pine *Pinus contorta* Douglas var. *latifolia*
Engelmann

Insects

Mountain pine beetle *Dendroctonus ponderosae* Hopkins

Birds

Common nighthawk	<i>Chordeiles minor</i> Forster
Pileated woodpecker	<i>Dryocopus pileatus</i> Linnaeus
Hairy woodpecker	<i>Picoides villosus</i> Linnaeus
Downy woodpecker	<i>Picoides pubescens</i> Linnaeus
Black-backed woodpecker	<i>Picoides arcticus</i> Swainson
Three-toed woodpecker	<i>Picoides tridactylus</i> Linnaeus
Western wood pewee	<i>Contopus sordidulus</i> Sclater
Olive-sided flycatcher	<i>Contopus borealis</i> Swainson
Clark's nutcracker	<i>Nucifraga columbiana</i> Wilson
Mountain chickadee	<i>Parus gambeli</i> Ridgway
White-breasted nuthatch	<i>Sitta carolinensis</i> Latham
Red-breasted nuthatch	<i>Sitta canadensis</i> Linnaeus

APPENDIX 1 continued

Pygmy nuthatch

Sitta pygmaea Vigors

Brown creeper

Certhia americana Linnaeus

American robin

Turdus migratorius Linnaeus

Townsend's solitaire

Myadestes townsendii Audubon

. Mountain bluebird

Sialia currucoides Bechstein

Yellow-rumped warbler

Dendroica coronata Linnaeus

APPENDIX 2

KEY REFERENCES USED IN MODEL CONSTRUCTION

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Bull 1983
- 2 : Beaver 1967, Amman 1973, Schmidt and Frye 1977, Lester
1980
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- 4 : Amman 1972b, Cole and Amman 1980
- 5 : Rust 1929 and 1930, Salt 1957, Stallcup 1963, Taylor
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and Perry 1979, Hein 1980
- 6 : Reid 1962a, Rasmussen 1974, Peterman 1974, Hynum 1978
- 7 : Hopping and Beall 1948, Shepherd 1966, Cole and Amman
1969, Safranyik *et al* 1974
- 8 : Rasmussen 1974, Klein *et al* 1978, Cole and Amman 1980,
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- 9 : Reid 1962b, Cole and Amman 1969, Safranyik *et. al.* 1975,
Raffa and Berryman 1983
- 10: Cole *et. al.* 1976, Amman and Cole 1983
- 11: Reid 1962b, Peterman 1974, Safranyik *et al* 1974
- 12: Reid 1963, Reid and Gates 1970, Amman and Cole 1983

- 13: Reid 1963, Amman 1973, Cole 1974, Cole *et al* 1976, Cole 1981, Amman and Cole 1983
- 14: Safranyik *el al* 1974, Amman and Cole 1983, Safranyik 1985 personal communication
- 15: Safranyik *el al* 1974, Klein *et al* 1978, Safranyik 1985 personal communication
- 16: Cole *el al* 1976, Cole 1978, Cole and Amman 1980
- 17: Reid 1963, Shepherd 1965, Cole and Amman 1969, Peterman 1974, Safranyik *el al* 1974, Klein *et al* 1978, Raffa and Berryman 1983, Berryman *et al* 1985, Schmitz 1985 personal communication, Safranyik 1985 personal communication
- 18: Koplin 1967, Otvos 1969, Otvos 1984 personal communication
- 19: Salt 1957, Stallcup 1963, Koplin 1969, Otvos 1969, Bock and Lynch 1970,
- 20: Massey and Wygant 1954, Koplin 1967, Otvos 1969, Otvos 1984 personal communication
- 21: Pynnonen 1939, Koplin 1967, Otvos 1969, Otvos 1984 personal communication
- 22: Salt 1957, Stallcup 1963, Koplin 1969, Otvos 1969, Bock and Lynch 1970
- 23: King and Farner 1961, Lasiewski and Dawson 1967, Koplin 1967, Kendeigh 1969 and 1970

24: Rust 1929 and 1930, Stallcup 1963

25: Stallcup 1963, Koplin 1967, Moeck 1984 personal
communication, Otvos 1984 personal communication

APPENDIX 3

BASIC MOUNTAIN PINE BEETLE SIMULATION MODEL

```

1      SUBROUTINE UMODEL(ITIME)
2      $CONTINUE WITH MC1 RETURN
3      TREES=0.
4      TTRHA=0.
5      ATTR=0.
6      ALLBET=0.
7      ALLATT=0.
8      TEGS=0.
9      TTEGS=0.
10     TSLRV=0.
11     TTSLRV=0.
12     WSLRVT=0.
13     TWLRV=0.
14     WLRT=0.
15     TCATS=0.
16     TBETS=0.
17     ALLEM=0.
18     AVDBH=0.
19     DM2=0.
20     ACATS=0.
21     DO 10 I=1,6
22     C   Total number of trees per hectare
23         TTRHA=TTRHA+TRHA(I)
24     C   Total number of trees in each DBH class
25         TOTTR(I)=TRHA(I)*STAR
26     10  TREES=TREES+TOTTR(I)
27         DO 15 I=1,6
28     C   Average diameter of stand
29         DM1(I)=TRHA(I)*DIAM(I)
30     15  DM2=DM2+DM1(I)
31         AVDBH=DM2/TTRHA
32
33         DO 20 I=1,6
34     C   Proportion of total trees represented by each DBH class
35     20  PROST(I)=TOTTR(I)/TREES
36         DO 30 I=1,6
37     C   Relative 'attractiveness' of trees in each DBH class in the stand
38         TRELAT(I)=RELAT(I)/0.95
39     C   Total 'attractiveness' of trees in each DBH class in the stand
40         TOTAT(I)=TRELAT(I)*PROST(I)
41         IF(TOTAT(I).EQ.0)PROBET(I)=0
42     C   Sum of 'attractiveness' for all DBH classes
43     30  ATTR=ATTR+TOTAT(I)
44

```

```

45 C Total number of mountain pine beetles in the stand
46 ALLBET=PBPOP*STAR
47 PFR=PBPOP/1000
48
49
50 DO 40 I=1,6
51 C Percentage of MPB population per DBH class
52 PROBET(I)=TOTAT(I)/ATTR
53 C Total number of MPB per DBH class in the stand
54 TOTBET(I)=PROBET(I)*ALLBET
55 C Percentage of MPB population that is female
56 PROFEM(I)=0.6919-(0.0035*DIAM(I))
57 C Total number of attacking MPB per DBH class in the stand
58 TOTAT(I)=TOTBET(I)*PROFEM(I)
59 C Total number of attacks in the stand
60
61 C Attacked surface area (square meters) per tree for each DBH class
62 ASRF(I)=-3.78+(0.3221*DIAM(I))
63 AMOD=TH(PFR,1.0,10.0,1.0,1.1)
64 ATSA(I)=ASRF(I)*AMOD
65 C Mountain pine beetle attack density
66 ATDN=52.33+(7.56*PFR)
67 IF(PFR.GE.3.0)ATDN=75.0
68 ATMD=TH(PFR,1.0,10.0,1.0,1.1)
69 ATDEN=ATDN*ATMD
70 C Total number of attacks per tree
71 TATT(I)=ATSA(I)*ATDEN
72
73 C Total number of trees killed for each DBH class
74 TREKIL(I)=TOTAT(I)/TATT(I)
75 C Number of trees killed per hectare for each DBH class
76 TREKHA(I)=TREKIL(I)/STAR
77
78 C Phloem thickness for trees in each DBH class
79 PHTH(I)=0.3072+(0.0523*DIAM(I))
80 C Number of eggs per female
81 EGFM(I)=62.878-(37.027*PHTH(I))+(15.529*(PHTH(I)**2))
82 C Percent of females mated
83 FMTR(I)=0.95*TATT(I)
84 C Number of eggs per tree
85 EGTR(I)=FMTR(I)*EGFM(I)
86 C Number of eggs per hectare
87 EGHA(I)=EGTR(I)*TREKHA(I)
88 TEGS=TEGS+EGHA(I)
89 C Percentage of eggs that hatch
90 EGGA=TH(AVDDBH,23.5,24.5,0.90,0.98)

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```

91      GMD(I)=0.92+(0.002*DIAM(I))
92      EGHCH(I)=GMD(I)*EGGA
93      C   Number of small larvae per tree
94      SLRV(I)=EGTR(I)*EGHCH(I)
95      SLRVH(I)=SLRV(I)*TREKHA(I)
96
97      C   Autumn mortality
98      AMRT(I)=0.30052+(0.02031*DIAM(I))-(0.0005035*(DIAM(I)**2))
99      DMOD=DSP(AVDBH,23.5,24.0,1.2,1.0)
100     AUTMRT(I)=AMRT(I)*DMOD
101     WWSLRV(I)=SLRV(I)*(1.0-AUTMRT(I))
102     TRMRT(I)=(TRH(I)-TRHA(I))/TRH(I)
103
104     C   Initial winter mortality
105     WNMRT(I)=0.30052+(0.02031*DIAM(I))-(0.0005035*(DIAM(I)**2))
106     WMOD=DSP(PFR,10.0,20.0,1.0,1.2)
107     WINMRT(I)=WNMRT(I)*WMOD
108     WWSLRV(I)=WWSLRV(I)*(1.0-WINMRT(I))
109     WWSLRVH(I)=WWSLRV(I)*TREKHA(I)
110     C   Total number of larvae alive per hectare (woodpecker food source)
111     40 WSLRVT=WWSLRVH(I)
112     C
113     WS=WWSLRVT*0.3333
114     C   Number of woodpeckers per 100 hectares for the winter
115     WPHHA=-38.953+(2.6661*WS)-(0.027628*WS**2)
116     IF(WS.LT.20.0)WPHHA=2.0
117     IF(WS.GT.45.0)WPHHA=25.0
118     C   Number of woodpeckers per hectare for the winter
119     WPHA=WPHHA/100.0
120     C   Number of woodpeckers in the stand for the winter
121     C   Kcals required per gram of woodpecker weight
122     WKGD=0.64-(0.008*TEMP)
123     C   Kcals required per woodpecker per day
124     WPKD=WKGD*WPWT
125     C   Proportion of MPB larvae in woodpeckers' diets
126     DIET=4.6734-(0.49062*WS)+(0.01608*WS**2)-(0.0001558*WS**3)
127     IF(WS.GT.45.0)DIET=0.95
128     IF(WS.LT.25.0)DIET=0.02
129     C   Number of larvae required per woodpecker per day
130     CATWPD=(WPKD*DIET)/CALRV
131     CATWPW=CATWPD*WINTER
132     C   Number of larvae required per hectare per day by woodpeckers
133     CATWWH=WPHA*CATWPW
134     WNM=CATWWH/WSLRVT
135

```

```

136 C Percentage of larvae available per tree
137 UNVL=UNV/AMOD
138 AVL=TH(WS,25.0,50.0,0.20,0.80)
139 SVD=1.0-(AVL+UNVL)
140 DO 50 I=1,6
141 C Number of larvae per tree available to woodpeckers
142 AVAIL(I)=AVL*WSLRV(I)
143 AVLHA(I)=AVAIL(I)*TREKHA(I)
144 C Number of larvae per tree protected by snow
145 UNVAL(I)=UNVL*WSLRV(I)
146 UNVLH(I)=UNVAL(I)*TREKHA(I)
147 C Number of larvae per tree unavailable to woodpeckers
148 SAVED(I)=SVD*WSLRV(I)
149 50 SVDH(I)=SAVED(I)*TREKHA(I)
150
151 DO 60 I=1,6
152 DSTWPF(I)=WSLRVH(I)/WSLRVT
153 C Larvae consumed per hectare during winter for each DBH class
154 CCWPH(I)=CATWWH*DSTWPF(I)
155 C Number of 'woodpeckered' trees per hectare in each DBH class
156 WPTRHA(I)=CCWPH(I)/AVAIL(I)
157 IF(WPTRHA(I).GT.TREKHA(I))WPTRHA(I)=TREKHA(I)
158 IF(WPTRHA(I).GT.TREKHA(I))UWPTHA(I)=0
159 IF(WPTRHA(I).LE.0.)WPTRHA(I)=0.
160 C Number of 'non-woodpeckered' trees per hectare in each DBH class
161 UWPTHA(I)=TREKHA(I)-WPTRHA(I)
162 IF(UWPTHA(I).LE.0.)UWPTHA(I)=0.
163
164 C Larval mortality due to cold for each DBH class
165 CLD(I)=0.30052+(0.02031*DIAM(I))-(0.0005035*(DIAM(I)**2))
166 CMOD=DSP(PFR,10.0,50.0,1.0,1.1)
167 COLD(I)=CLD(I)*CMOD
168 C Larval mortality due to dessication for each DBH class
169 DSC(I)=0.44-(0.006*DIAM(I))
170 DSCMD=DSP(PFR,10.0,50.0,1.0,1.2)
171 DESC(I)=DSC(I)*DSCMD
172 C Number of larvae per 'woodpeckered' tree dying during the winter
173 DWTRS(I)=AVAIL(I)+(DESC(I)*UNVAL(I))+((CLD(I)*SAVED(I))
174 C Number of larvae per 'non-woodpeckered' tree dying during the winter
175 DNWTRS(I)=(DESC(I)*UNVAL(I))+((COLD(I)+DESC(I))*(SAVED(I)
176 1 +AVAIL(I)))
177 C Number of larvae that survived winter per 'woodpeckered' tree
178 CWTAW(I)=WSLRV(I)-DWTRS(I)
179 IF(CWTAW(I).LT.0)CWTAW(I)=0
180 C Number of larvae that survived winter per 'non-woodpeckered' tree

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```

181      CNWTAW(I)=WSLRV(I)-DNWTRS(I)
182      CAWTAW(I)=WPTRHA(I)*CWTAW(I)
183      CANWTW(I)=UWPTH(A(I)*CNWTAW(I)
184      TCATAW(I)=CAWTAW(I)+CANWTW(I)
185      C    Total number of larvae alive at end of winter
186      ACATS=ACATS+TCATAW(I)
187
188      C    Spring mortality
189      SPMR(I)=0.30052+(0.02031*DIAM(I))-(0.0005035*(DIAM(I)**2))
190      SPMOD=DSP(AVDBH,23.5,24.0,1.3,1.0)
191      SPMRT(I)=SPMR(I)*SPMOD
192      SSWT(I)=CWTAW(I)*(1.0-(SPMRT(I)*DSCMOD))
193      SSNWT(I)=CNWTAW(I)*(1.0-SPMRT(I))
194
195      C    Early summer mortality
196      ESMR(I)=0.84-(0.016*DIAM(I))
197      SMMOD=DSP(AVDBH,23.5,24.0,1.3,1.0)
198      ESMRT(I)=ESMR(I)*SMMOD
199
200      C    Number of MPB adults emerging per 'woodpeckered' tree
201      TBEWTR(I)=SSWT(I)*(1.0-ESMRT(I)*DSCMOD)
202      TBEWH(I)=TBEWTR(I)*WPTRHA(I)
203      WEAR(I)=TBEWTR(I)/TATT(I)
204      C    Number of MPB adults emerging per 'non-woodpeckered' tree
205      TBENWT(I)=SSNWT(I)*(1.0-ESMRT(I))
206      TBENH(I)=TBENWT(I)*UWPTH(A(I)
207      WEARN(I)=TBENWT(I)/TATT(I)
208      C    Total number of MPB adults emerging from each DBH class
209      TBETEM(I)=TBEWH(I)+TBENH(I)
210      IF(TBETEM(I).LT.0)TBETEM(I)=0
211      TBETS=TBETS+TBETEM(I)
212      C    Total number of MPB adults emerging in the stand
213      60    ALLEM=TBETS*STAR
214
215      DO 70 I=1,6
216      70    TRHA(I)=(TOTTR(I)-TREKIL(I))/STAR
217
218      TB=TBETS/10000.0
219      C    Summer bird species densities per 100 hectares
220      HAWPN=0.54972+(2.4594*TB)-(0.32531*TB**2)
221      IF(TB.GT.3.0)HAWPN=5.0
222      BRCRN=3.4162+(8.8138*TB)-(1.1294*TB**2)
223      IF(TB.GT.3.0)BRCRN=20.0
224      RBNHN=4.3156+(11.099*TB)-(1.4358*TB**2)
225      IF(TB.GT.3.0)RBNHN=25.0

```

```

226
227 C Percentage of MPB adults in summer birds' diets
228 HAWPD=0.010919-(.005405*TB)+(0.08968*TB**2)-(0.013995*TB**3)
229 IF(TB.GT.3.0)HAWPD=0.50
230 BRCRD=0.017419-(0.004630*TB)+(0.051552*TB**2)-(0.0079595*TB**3)
231 IF(TB.GT.3.0)BRCRD=0.30
232 RBNHD=0.015068-(0.0058746*TB)+(0.03099*TB**2)-(0.0050352*TB**3)
233 IF(TB.GT.3.0)RBNHD=0.20
234
235 C Kcals required per bird species per day
236 CALHW=0.5404*(HAWPW**0.7545)*1.5
237 CALBC=1.5720*(BRCRW**0.6210)*1.5
238 CALRB=1.5720*(RBNHW**0.6210)*1.5
239
240 C Total number of MPB adults consumed per bird species
241 TPBHW=((CALHW*HAWPD)/CALAD)*DAYAV*(HAWPN/100.0)
242 HWA=TPBHW/TBETS
243 TPBBC=((CALBC*BRCRD)/CALAD)*DAYAV*(BRCRN/100.0)
244 BRA=TPBBC/TBETS
245 TPBRB=((CALRB*RBNHD)/CALAD)*DAYAV*(RBNHN/100.0)
246 RBA=TPBRB/TBETS
247
248 C Total number of MPB adults consumed by all bird species
249 BBIF=TPBHW+TPBBC+TPBRB
250 BBA=BBIF/TBETS
251 C Total number of MPB adults killed 'in flight' by other causes
252 BOIF=ALLEM*OIFMRT
253 C Total number of MPB adults killed 'in flight' by all causes
254 BKIF=BBIF+BOIF
255 PBHA=(ALLEM-BKIF)/STAR
256
257 C Proportion of MPB adults dispersing from the stand
258 DISP=DSP(AVDBH,23.5,24.0,0.40,0.01)
259 ALDISP=PBHA*DISP
260 C New mountain pine beetle population
261 PBPOP=(PBHA-ALDISP)
262 C Ratio of increase: population t/population t-1
263 ROI=PBPOP/BLAST
264 BLAST=PBPOP
265 RETURN

```



```
266      END
267      SUBROUTINE UINIT
268      CALL CMREAD('MC1 ')
269      RETURN
270      END
271      FUNCTION TH(X,X1,X2,Y1,Y2)
272      TH=Y1
273      IF(X.LT.X1)RETURN
274      TH=Y2
275      IF(X.GE.X2)RETURN
276      TH=(Y1-Y2)/(X1-X2)*(X-X2)+Y2
277      RETURN
278      END
```

APPENDIX 4

GLOSSARY OF SIMULATION MODEL VARIABLES

ACATS: Total number of larvae that survived the winter
 ALDSP: Total number of beetles dispersing out of the stand
 ALLBET: Total number of beetles in the stand in early autumn
 ALLEM: Total number of emerging beetles in the stand in
 early summer
 AMOD: Attack modifier (based on beetle population density)
 AMRT: Initial autumn mortality
 ASRF: Initial attacked surface area (m^2) per tree
 ATDEN: Final beetle attack density (attacks/ m^2)
 ATDN: Initial attack density (attacks/ m^2)
 ATMD: Attack modifier (based on beetle population density)
 ATSA: Final attacked surface (m^2) area per tree
 ATTR: Sum 'attractiveness' of the stand
 AVAIL: Number of larvae per tree available to winter
 woodpeckers
 AVDBH: Average DBH of the stand
 AVL: percent of beetle brood per tree available to winter
 woodpeckers
 AVLHA: Number of larvae per hectare available to winter
 woodpeckers
 AUTMRT: Total autumn mortality (percent) of larval
 population killed per tree)

 BBA: Percent of emerging adult beetle population killed
 during flight period by all birds
 BBIF: Number of emerging adult beetles killed during flight
 period by all birds
 BKIF: Total number of emerging adult beetles killed during
 flight period by all causes
 BLAST: Mountain pine beetle population at time $t-1$
 BOIF: Number of emerging adult beetles killed during flight
 period by causes other than birds

BRA: percent of emerging adult beetle population consumed by all brown creepers

BRCRD: percent of brown creepers' diet represented by adult mountain pine beetles

BRCRN: Number of brown creepers per 100.0 hectares during the summer

BRCRW: Weight in grams of one brown creeper

CALAD: Value in Kilocalories of one adult mountain pine beetle

CALBR: Number of Kilocalories per day required by one brown creeper

CALHW: Number of Kilocalories per day required by one hairy woodpecker

CALRB: Number of Kilocalories per day required by one red-breasted nuthatch

CALRV: Value in Kilocalories of one mountain pine beetle larva

CANWTW: Number of larvae in all non-woodpeckered trees alive at the end of winter

CATWPD: Number of larvae consumed by one woodpecker in one day

CATWPW: Number of larvae consumed by one woodpecker during the winter

CATWWH: Number of larvae consumed per hectare during the winter by all woodpeckers

CAWTAW: Number of larvae in all woodpeckered trees alive at the end of the winter

CCWPH: Number of larvae consumed per hectare during the winter by all woodpeckers for each tree diameter class

CLD: Initial larval mortality due to cold temperatures

CMOD: Modifier for mortality due to cold temperatures (based on population density)

CNWTAW: Number of larvae per non-woodpeckered tree alive at the end of winter

COLD: Final mortality due to cold temperatures (percent of larval population killed per tree)

CWTAW: Number of larvae per woodpeckered tree alive at the end of winter

DAYAV: Number of days in adult beetle flight/attack period

DESC: Final mortality due to desiccation (percent of larval population killed per tree)

DIAM: Mean diameter (cm at DBH) of the diameter classes

DIET: percent of winter woodpeckers' diet represented by mountain pine beetle larvae

DISP: percent of beetle population dispersing out of the stand

DMOD: DM1: Sum of tree diameters per hectare for each diameter class

DM2: Sum of tree diameters per hectare for all diameter classes

DNWTRS: Number of larvae dying during the winter per non-woodpeckered tree

DSC: Initial mortality due to desiccation

DSCMD: Modifier for mortality due to desiccation (based on population density)

DSCMOD: Spring and early summer desiccation modifier (based on larval population density)

DSTWPF: Distribution of woodpecker feeding

DWTRS: Number of larvae dying during the winter per woodpeckered tree

EGFM: Number of eggs per female beetle

EGGA: Initial percentage of eggs that hatch

EGHA: Number of eggs per hectare in each diameter class
EGHCH: Final percentage of eggs that hatch
EGTR: Number of eggs laid per tree in each diameter class
ESMR: Initial early summer mortality per diameter class
ESMRT: Final early summer mortality per diameter class
FMTR: Number of female beetles per tree

GMD: Egg hatch modifier

HAWPD: percent of hairy woodpeckers diet represented by
adult mountain pine beetles
HAWPN: Number of hairy woodpeckers per 100.0 hectares during
the summer
HAWPW: Weight in grams of one hairy woodpecker
HWA: percent of emerging adult beetle population consumed by
all hairy woodpeckers

OIFMRT: percent of emerging adult population killed during
flight period by causes other than birds

PBHA: Number of beetles per hectare remaining in the stand
after dispersal
PBPOP: Number of beetles per hectare in early autumn
PFR: PBPOP/1000.0
PHTH: Tree phloem thickness (mm)
PROBET: percent of beetle population 'assigned' to each
diameter class
PROFEM: percent of beetle population that is female
PROST: percent of trees in the stand represented by each
diameter class

RBA: percent of emerging adult beetle population consumed by
all red-breasted nuthatches

RBNHD: percent of red-breasted nuthatches' diet represented by adult mountain pine beetles

RBNHN: Number of read-breasted nuthatches per 100.0 hectares during the summer

RBNHW: Weight in grams of one red-breasted nuthatch

RELAT: 'Initial attractiveness' of trees in each diameter class

ROI: Ratio of beetle population at time t to population at time $t-1$

SAVED: Final number of larvae per tree unavailable to woodpeckers but not protected by snow

SLRV: Initial number of larvae per tree alive at the beginning of autumn

SLRVH: Initial number of larvae per hectare alive at the beginning of autumn

SMMOD: Modifier for early summer mortality (based on larval population density)

SPMOD: Modifier for spring mortality (based on population density)

SPMR: Initial spring mortality (percent of larval population killed per tree)

SPMRT: Final spring mortality (percent of larval population killed per tree)

SSNWT: Number of larvae per non-woodpeckered tree alive at the end of spring

SSWT: Number of larvae per woodpeckered tree alive at the end of spring

STAR: Stand area (hectares)

SVD: Initial number of larvae per tree unavailable to woodpeckers but not protected by snow

SVDH: Final number of larvae per tree unavailable to woodpeckers but not protected by snow

TATT: Total number of attacks per tree

TB: TBETS/10,000.0

TBENH: Number of beetles per hectare emerging from non-woodpeckered trees

TBENWT: Total number of beetles emerging from non-woodpeckered trees

TBETEM: Total number of beetles emerging from the early summer per diameter class

TBETS: Total number of beetles emerging in the early summer

TBEWH: Number of beetles per hectare emerging from woodpeckered trees

TBEWTR: Total number of beetles per hectare emerging from woodpeckered trees

TCATAW: Total number of larvae alive at the end of winter

TEGS: Total number of eggs hatching per hectare

TEMP: Mean winter temperature (°C)

TOTAT: 'Total attractiveness' of trees in each diameter class

TOTBET: Total number of beetles 'assigned' to each diameter class

TOTTAT: Total number of attacks per diameter class

TOTTR: Total number of trees in each diameter class

TPBBR: Total number of adult beetles consumed per hectare in summer by brown creepers

TPBHW: Total number of adult beetles consumed per hectare in summer by hairy woodpeckers

TPBRB: Total number of adult beetles consumed per hectare in summer by red-breasted nuthatches

TREES: Total number of trees (>12.7 cm DBH) in the stand

TREKHA: Number of trees killed per hectare per year in each diameter class

TREKIL: Number of trees killed per year in each diameter class

TRELAT: 'Relative attractiveness' of trees in each diameter class

TRH: Number of trees per hectare in each diameter class

TRHA: Number of trees per hectare in each diameter class

TRMRT: Cumulative tree mortality for each diameter class

TTRHA: Total number of trees per hectare

UNAVAL: Number of larvae per tree protected by snow

UNV: Initial percent of beetle brood per tree protected by snow

UNVL: Final percent of beetle brood per tree protected by snow

UNVLH: Number of larvae per hectare protected by snow

UWPTHA: Number of non-woodpeckered trees per hectare

WEAR: Ratio of emerging beetles to attacking beetles for woodpeckered trees

WEARN: Ratio of emerging beetles to attacking beetles for non-woodpeckered trees

WINMRT: Final general winter mortality (percent of larval population killed per tree)

WINTER: Number of days in woodpecker winter feeding period

WKGD: Energy requirement (Kilocalories per gram body weight) for winter woodpeckers

WMOD: Modifier for general winter mortality (based on population density)

WNW: percent of larval population consumed by all woodpeckers during the winter

WNMRT: Initial general winter mortality (percent of larval population killed per tree)

WPKD: Woodpecker energetic requirement in kilocalories per day

WPHA: Number of woodpeckers per hectare

WPHHA: Number of woodpeckers per 100.0 hectares

WPSTD: Number of woodpeckers in the stand

WPTRHA: Number of woodpeckered trees per hectare in each diameter class

WPWT: Mean winter woodpecker weight (grams)

WS: (WSLRVT)**0.33333

WSLRB: Number of larvae per tree alive after general winter mortality

WSLRVH: Number of larvae per hectare alive after general winter mortality

WSLRVT: Total number of larvae per hectare alive after general winter mortality

WWSLRV: Number of larvae per tree alive at the beginning of winter

APPENDIX 5

INITIAL VALUES OF SELECTED MODEL PARAMETERS

11. INITIAL VALUES OF SELECTED MODEL PARAMETERS

Stand area: 20 hectares

Initial mountain pine beetle density: 750 beetles per hectare

Initial winter woodpecker density

(Control and Senescent stands): 2 individuals per 100 hectares

(Thinned stand): 0.2 individuals per 100 hectares

Initial summer hairy woodpecker density

(Control and Senescent stands): 1 individual per 100 hectares

(Thinned stand): 0.1 individual per hectare

Initial summer brown creeper density

(Control and Senescent stands): 4 individuals per 100 hectares

(Thinned stand): 0.4 individual per hectare

Initial summer red-breasted nuthatch density

(Control and Senescent stands): 5 individuals per 100 hectares

(Thinned stand): 0.5 individual per hectare

Maximum summer hairy woodpecker density

(Control and Senescent stands): 5 individuals per 100 hectares

(Thinned stand): 0.5 individuals per 100 hectares

Maximum summer brown creeper density

(Control and Senescent stands): 20 individuals per 100 hectares

(Thinned stand): 2 individual per hectare

Maximum summer red-breasted nuthatch density

(Control and Senescent stands): 25 individuals per 100 hectares

(Thinned stand): 2.5 individual per hectare

Caloric value of one mountain pine beetle larva: 0.062 kilocalories

Caloric value of one mountain pine beetle adult: 0.098 kilocalories

Initial rate of mountain pine beetle emigration: 1%

Maximum rate of mountain pine beetle emigration: 40%

Initial Control stand structure (trees per hectare)

in the 15, 25, 30, 35, and 40-cm DBH classes:

385 495 440 330 205 90

Initial Senescent stand structure (trees per hectare)

in the 15, 25, 30, 35, and 40-cm DBH classes:

100 150 225 325 550 350

Initial Thinned stand structure (trees per hectare)

in the 15, 25, 30, 35, and 40-cm DBH classes:

385 495 22 17 10 5