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Amy N. Lester
The University of Montana

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NUMERICAL RESPONSE OF WOODPECKERS AND THEIR EFFECT ON MORTALITY OF MOUNTAIN PINE BEETLES IN LODGEPOLE PINE IN NORTHWESTERN MONTANA

By

Amy N. Lester

B.A., University of Rochester, 1973

B.S., University of Montana, 1977

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Master of Science

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Approved by:

B. Riley McClelland
Chairman, Board of Examiners

Dean, Graduate School

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Date

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Numerical Response of Woodpeckers and Their Effect on Mortality of Mountain Pine Beetles in Lodgepole Pine in Northwestern Montana

Director: B. Riley McClelland BRMc

Relationships between 5 woodpecker species and an epidemic population of mountain pine beetles (*Dendroctonus ponderosae*) were studied in lodgepole pine (*Pinus contorta v. latifolia*) forests of northwestern Montana from March 1978 through September 1979. Downy (*Picoides pubescens*), Hairy (*P. villosus*), Northern Three-toed (*P. tridactylus*), Black-backed Three-toed (*P. arcticus*), and Pileated (*Dryocopus pileatus*) Woodpeckers were observed nesting in the study area and feeding on the beetles. Maximum densities of feeding woodpeckers were 57.3 woodpeckers per 100 acres (40 ha) in the 1977-78 winter and 34.4 woodpeckers per 100 acres (40 ha) in the 1978 breeding season. The highest nesting density was 14.3 pairs per 100 acres (40 ha) in the 1979 breeding season. Northern Three-toed and Hairy Woodpeckers were the most abundant species in the study area, comprising 51-100% of the feeding woodpeckers censused per season and 76% of the nesting pairs located. Nine of 11 Northern Three-toed nests were in lodgepole pine snags. All had apparent heartwood decay at the nest holes. One of 8 Hairy nests was in a lodgepole snag; the remaining 7 nests were in quaking aspen (*Populus tremuloides*) or paper birch (*Betula papyrifera*). Evidence of heartwood decay was detected in all Hairy nest trees. The relative scarcity of nest sites for Hairy Woodpeckers probably prevented a large increase in their numbers in response to the beetle epidemic. Because of their ability to nest in lodgepole pine, the most common tree species in the study area, Northern Three-toed Woodpeckers responded numerically to the beetle epidemic. Territorial behavior and availability of suitable nest sites probably determined the maximum density of Northern Three-toed Woodpeckers in local areas. The beetle epidemic appeared to account for the high densities of woodpeckers in the infested area, but the epidemic was declining by the 1978-79 season. Feeding woodpeckers disturbed about 10% of the bark on lodgepole attacked in 1978 by beetles. This contributed to overall beetle mortality of 96-97%, but woodpecker feeding did not appear to exert a controlling effect on the epidemic beetle population. Severe winter and summer weather conditions probably were the most important factors in causing high beetle mortality.

ACKNOWLEDGEMENTS

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I would like to extend my sincerest personal thanks to Drs. Riley McClelland and Jim Lowe of the University of Montana School of Forestry, and Jerry DeSanto, Sub-district Ranger at the Polebridge Ranger Station, for sharing their expertise and experience and offering moral support and friendship throughout the duration of the project. All my committee members, Riley McClelland, Jim Lowe, and Dr. Dick Hutto of the Department of Zoology, deserve thanks for reviewing drafts of the manuscript and making suggestions for the final thesis.

Lastly, I want to acknowledge the support of my family and my friends in Missoula and Polebridge who have helped make this episode in my educational career an enjoyable and tremendously enlightening experience.

TABLE OF CONTENTS

APPENDIX

LIST OF TABLES

LIST OF FIGURES

CHAPTER I

INTRODUCTION

Since World War II, managers of forest lands have been under increasing pressure to produce commerical timber for the wood products industry. Forest harvesting often has resulted in loss or degradation of habitat for many animal species. Little attention has been given to the value of some of these species, particularly insectivorous birds, in the maintenance of a diverse ecosystem.

This report focuses on woodpeckers and their impact on a population of mountain pine beetles (*Dendroctonus ponderosae*), a major cause of tree mortality in the northern Rocky Mountains. The objectives of this research were to:

1. Determine densities of feeding woodpeckers in areas of epidemic and endemic populations of mountain pine beetles;
2. Determine densities of nesting pairs of woodpeckers in areas of epidemic and endemic mountain pine beetle populations;
3. Assess the impact of woodpeckers on the mortality of mountain pine beetles on the study sites; and
4. Characterize active woodpecker nest trees within the study area and make recommendations for forest management based on all relevant findings.

Mountain Pine Beetles

The mountain pine beetle is a native insect of the lodgepole pine (Pinus contorta v. latifolia) forests of the northern Rockies. The adult is dark brown to black, stout, cylindrical, and approximately 0.3 inches (8 mm) long (Amman 1977). It belongs to the group commonly known as bark beetles (Coleoptera; Scolytidae), and its primary hosts are lodgepole, ponderosa (Pinus ponderosa), and western white (Pinus montocola) pine.

In northwestern Montana, the beetle generally has a 1-year life cycle (Amman et al. 1977). Adults emerge from brood trees in mid- to late summer. Females fly to live trees and bore through the outer bark. A vigorous tree's response to this, or any, wound, is to produce a copious flow of pitch. This flow may prevent the female's entry into the tree. However, a less vigorous tree, or a tree sustaining an attack by many beetles, usually cannot prevent successful entries by some beetles. The pitch tubes that form around the beetles' entrance holes are a combination of pitch and boring frass, and are the first indications that a tree has been attacked.

As the female bores through the bark, she emits a sex attractant known as an aggregating pheromone (Pitman et al. 1968). In combination with terpenes of the tree, this pheromone attracts other beetles to the site (Vité and Pitman 1968). Mountain pine beetles are monogamous; each male locates a female's entry hole and follows her into the phloem tissue. The male emits an anti-aggregating pheromone that may signal to other males that a particular female has a mate. When the amount of anti-aggregating pheromone overcomes the aggregating pheromone, the attack on the tree stops (Rudinsky et al. 1974).

Copulation occurs, and the female beetle constructs a vertical egg gallery in the phloem. Eggs are laid in groups on alternate sides of each gallery. Eggs hatch in approximately 2 weeks, and the white, legless larvae feed horizontally on the cambium (Amman 1977). At the onset of cold weather, the larvae hibernate, although feeding may resume when the bark surface is sufficiently warmed by the sun. Normal feeding resumes in the spring, and the tree is usually girdled by the larvel galleries.

The fourth instar larvae construct chambers in which they pass the pupal stage. During late spring and early summer, the pupae metamorphose to adults. Callow adults appear yellow or red, and their exoskeletons are too soft for emergence and flight. These adults continue to feed on the phloem tissue until their exoskeletons harden and turn black. Then, the adults bore out through the bark and fly to live trees to initiate new attacks. Timing of the stages of development may vary within a population because adults may emerge and attack new trees from June through October if weather conditions are suitable.

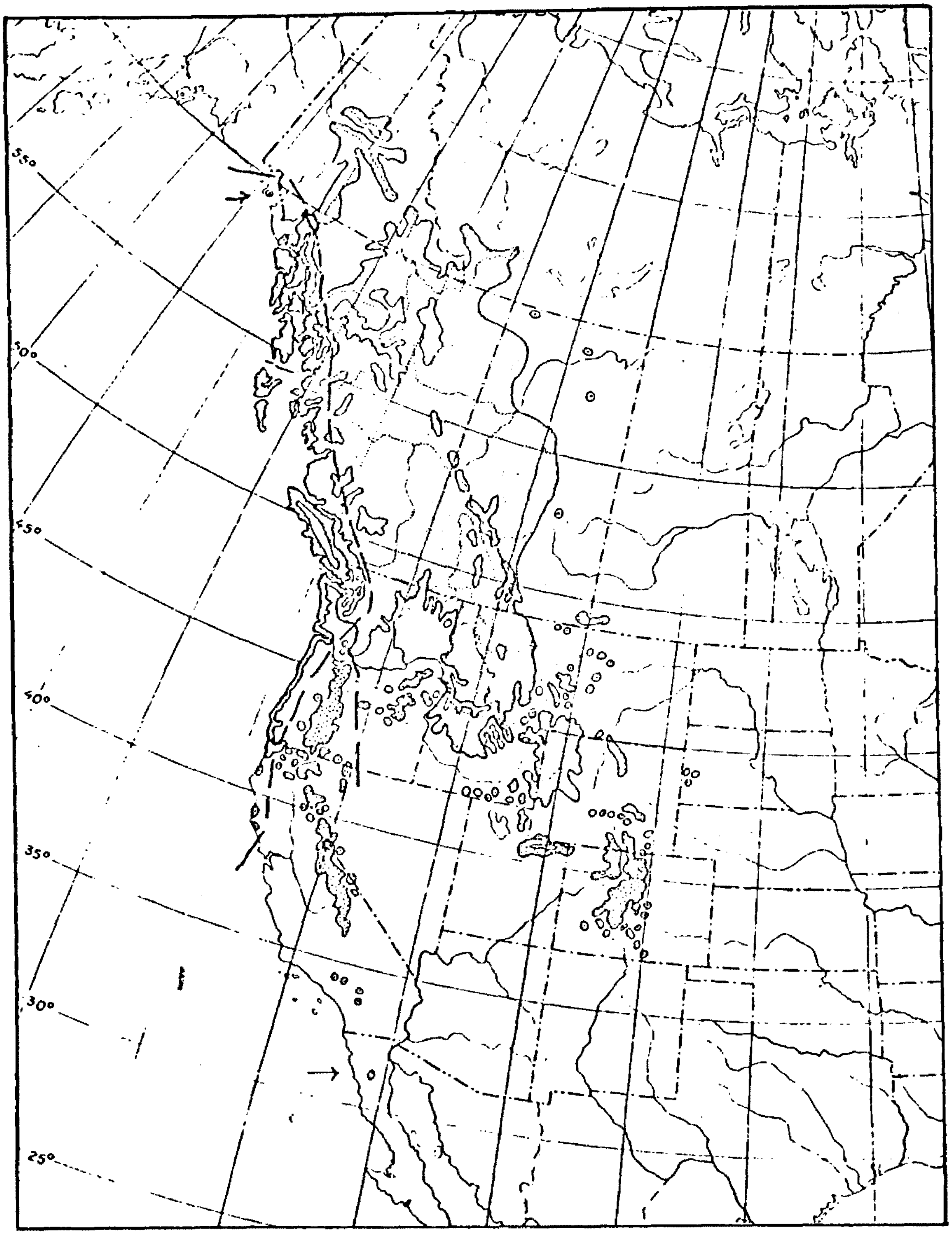
The mountain pine beetle has a symbiotic relationship with two blue-stain fungi, Ceratostomella montia and Europhium clavigerum, that are carried in the beetles' intestinal tracts (Whitney 1971). Spores are introduced into the host tree by the feeding adult beetles. The fungi proliferate in the vascular system of the tree and impede water conduction (Nelson 1934). The regulation of moisture conditions in trees during the larval stages appears to be the primary benefit to the beetles (Whitney 1971). In addition to the girdling action of the larvae, some investigators (Safranyik et al. 1974) consider the blue-stain fungi a primary cause of tree mortality.

The foliage of an infested tree generally fades to yellow in the spring following the beetle attack. By summer, the needles are a bright red-orange. In subsequent years, the needles fade to gray or brown and fall from the limbs. Color and condition of foliage on standing dead trees may be used to estimate the year of beetle attack on those trees.

Lodgepole Pine

Lodgepole pine is one of the most widely distributed conifers in western North America, extending from the Yukon Territory to Baja California, and the Pacific coast to the Black Hills of South Dakota (Fig. 1, Little 1971). Lodgepole has low shade tolerance, but it possesses the ability to grow on almost any forest site. It grows best on moderately acid, sandy, or gravelly loams that are light, moist, and well-drained. It occurs from sea level to 11,500 feet (3450 m) and grows on all terrains and aspects (Kotok 1971). Lodgepole is found in 66% of the 70 recognized forest habitat types of northwest Washington, northern Idaho, Montana, and the Boise and Payette National Forests of southern Idaho. Lodgepole pine ranks third, after ponderosa pine and

Figure 1. Distribution of lodgepole pine (Little 1971).


55°
50°
45°
40°
35°
30°
25°

Douglas-fir, in abundance of commercial forest types in the Rocky Mountain states (Wellner 1975).

Four major successional stages for lodgepole pine are recognized by Pfister and Daubenmire (1975):

1. Minor seral. Lodgepole pine is a minor component of young, even-aged mixed species stands. It is replaced by shade-tolerant associates in 50-200 years; the more mesic the site, the sooner lodgepole is replaced;
2. Dominant seral. Lodgepole pine is the dominant cover type of even-aged stands with a vigorous understory of shade-tolerant species that replace lodgepole in 100-200 years;
3. Persistent. Lodgepole pine forms the dominant cover type of even-aged stands with little replacement by shade-tolerant species, and
4. Climax. Lodgepole pine is the only species capable of growing on particular sites and is self-perpetuating.

Beetles and Pine

Within a stand, adult beetles generally attack old (over 80 years), large diameter (over 10 inches {25 cm} dbh) lodgepole pines. Phloem thickness is positively correlated with diameter, and the phloem provides food for the developing larvae. The ratio of emerging adults to brood adults (that attacked and killed the tree) increases as phloem thickness increases. Therefore, within a tree, food is a major limiting factor and intraspecific competition is the most significant mortality factor for many mountain pine beetle populations (Amman 1977). However, at high elevations (over 8000 feet, 2400 m) or extreme northern latitudes, climate is the major limiting factor, and low temperature is the most significant mortality factor. The short growing season retards larval development and results in a 2-year life cycle. Brood mortality during 2 successive winters is high, and beetle populations rarely reach high densities (Amman 1973, Safranyik et al. 1974).

Vast, even-aged stands of lodgepole pine often result from large forest fires. In young trees, resistance to beetle attack may be low because of stand density and competition for limited nutrients and water (Safranyik et al. 1973). These trees are susceptible to mountain pine beetle attack. However, beetle reproduction is low in young trees with thin phloem; few, if any, larvae emerge as adults; and the beetle population remains low. As trees mature, lodgepole stands undergo natural thinning, and vigor of the surviving trees increases and peaks at about 60 years. Vigorous trees can usually resist attacks by small numbers of beetles. As trees grow older, resistance declines, and trees again become susceptible to a beetle attack. In older pines with thick phloem, brood survival is high, and the total beetle population increases rapidly. Beetles continue to attack the larger trees, and for several years the population continues to increase until epidemic levels are reached. When fewer large trees remain, the beetles are forced to attack smaller, younger pines in which reproductive success declines. Eventually, the epidemic population decreases to a normal, or endemic, level.

Woodpeckers

Woodpeckers (Piciformes: Picidae) are a unique group of birds classified as primary cavity-nesters. They require cavities for nest sites and usually excavate a new hole each spring. Most woodpeckers roost in cavities at night during all seasons. Many species are non-migratory, remaining in areas with adequate food sources year-round. Most woodpeckers feed primarily on insects, but tree sap and cambium tissue, fruits, berries, seeds, nuts, and grains are also eaten (Bent 1939, Lawrence 1966).

Woodpeckers have evolved several adaptations for their specialized nesting and feeding habits. The muscles of the thick skull act as a shock-absorbing mechanism, and sharp, chisel-like bills enable them to excavate nest and roost holes and drill for insects in live and dead wood. Their long, barbed or brush-tipped tongues assist in locating and withdrawing insects. Some woodpeckers have highly specialized feet that increase the efficiency of blow delivery while the birds cling vertically to the hole of a tree (Spring 1965), and their stiff, tapered tail feathers act as a prop in this position (Burt 1930).

In most woodpecker species, the sexes share parental duties

(Kilham 1962, Lawrence 1966, Kilham 1968). Both males and females excavate nest holes and incubate the eggs. No nest is built within the cavity. Both sexes brood and feed the nestlings, although the male usually remains on the nest through the night while the female roosts in another hole (Lawrence 1966, Kilham 1968). Both parents feed the fledglings for a period of 2 to 4 weeks after they leave the nest. Juveniles may disperse to unoccupied areas throughout the winter months, and dispersal probably is complete by the beginning of the breeding season. There is some evidence to indicate that woodpeckers form permanent pair bonds and remain faithful to the same nesting territory for several seasons (Lawrence 1966).

Woodpeckers and Beetles

An epidemic of Engelmann spruce beetles (*D. obesus*) in Colorado from 1939 to the 1950s triggered the first intensive research on bark beetle/bird relationships. Researchers observed that woodpeckers responded numerically and functionally to an increase in prey density. The numerical response consisted of an increase in numbers of birds inhabiting an area through immigration and/or increased nesting and reproductive success (Yeager 1955, Amman and Baldwin 1960, Baldwin 1968). Woodpecker densities in endemic beetle areas varied from 1 to 4 woodpeckers per 100 acres (40 ha) (Baldwin 1968, Koplin and Baldwin 1970). In epidemic beetle areas, 14 woodpeckers per 100 acres (40 ha) was typical, but densities as high as 30-45 woodpeckers per acre (0.4 ha) were found (Baldwin 1968). Koplin (1968) reported 70 birds per 100 acres (40 ha) in a beetle-infested burn in contrast to 3 woodpeckers per 100 acres (40 ha) in the adjacent forest.

In a forest with low spruce beetle populations, Baldwin (1968) reported 0.1 pairs of breeding woodpeckers per 100 acres (40 ha). In an epidemic beetle area, the breeding woodpecker density rose to 1.0 pair per 100 acres (40 ha).

The functional response consisted of an increase in the proportion of insects in the diets of individual birds in response to increased prey density. At endemic levels, the diets of Northern-Three-toed (Picoides tridactylus) and Hairy (P. villosus) Woodpeckers contained 7% and 2% spruce beetles respectively; in a low epidemic area, these figures rose to 28% and 14% (Baldwin 1968). In the winter, the lack of alternative prey increased the proportion of beetles in the diet. Spruce beetles represented 99% of the winter diets of Northern Three-toed, Hairy, and Downy (P. pubescens) Woodpeckers (Baldwin 1968).

Beetle mortality was caused directly by woodpecker feeding and indirectly by exposing the larvae to low temperatures, dessication, and insect predation and parasitism. Knight (1958) estimated that woodpeckers caused up to 98% mortality of spruce beetles when they disturbed more than 75% of the bark on an infested tree. By disturbing 26-74% of the bark, woodpeckers caused a 64% brood reduction. A lightly worked tree, with less than 26% of the bark disturbed, showed up to 45% brood mortality. Tunnock (1960) estimated that disturbance of 5% of the bark surface could cause up to a 50% reduction of mountain pine beetle broods. Total reduction of beetles varied with the densities of beetles and woodpeckers. Baldwin (1968) estimated that woodpeckers caused a 28% reduction of spruce beetles at densities of 400-1000 larvae per acre (endemic). At 160,000 larvae per acre (epidemic), woodpeckers caused 84% beetle mortality, and at 1,600,000 larvae per acre (pan-epidemic), woodpecker activity accounted for 53% beetle mortality. Hutchinson (1951) reported a 55% reduction of an epidemic spruce beetle population with 91-127 woodpeckers per 100 acres (40 ha). Koplin and Baldwin (1970) found that 1-4 woodpeckers per 100 acres (40 ha) caused a 20-29% reduction on an endemic beetle population.

CHAPTER II

STUDY AREA

The major study area was located in the northwest corner of Glacier National Park (GNP), Montana, between 48° and 49° north latitude (Fig. 2). The area is bounded on the west by the North Fork of the Flathead River; the Glacier View Ranger District of the Flathead National Forest (FNF), Montana state forest lands, and private holdings lie west of the River. Average annual precipitation at the Polebridge Ranger Station (RS) is 22 inches (55 cm). The average temperature in January is 21° F (-6.2° C) and 63° F (16.5° C) in July (Habeck 1970a).

The 1978-79 winter was unusually severe in the North Fork study area. A comparison of mean monthly high and low temperatures for November through March of 1976 through 1980 illustrates the abnormally low mean temperatures in December 1978 and January 1979 (Fig. 3). For 3 consecutive nights, temperatures dropped below -40° F (-40°C). The 1979 summer was hotter and received less precipitation than the summers of 1976-1978 (Fig. 4).

Lodgepole pine is the most common tree species in the valley. Other major species include ponderosa pine, Douglas-fir (*Pseudotsuga menziesii*), western larch (*Larix occidentalis*), Engelmann spruce (*Picea engelmannii*), white spruce (*P. glauca*), spruce hybrid (*P. engelmannii* X *P. glauca*), grand fir (*Abies grandis*), subalpine fir (*A. lasiocarpa*), quaking aspen (*Populus tremuloides*),

Figure 2. Map of the study area. Insets show location of Glacier National Park in Montana (1a), location of study area in Glacier National Park (1b), and location of study sites in the study area.

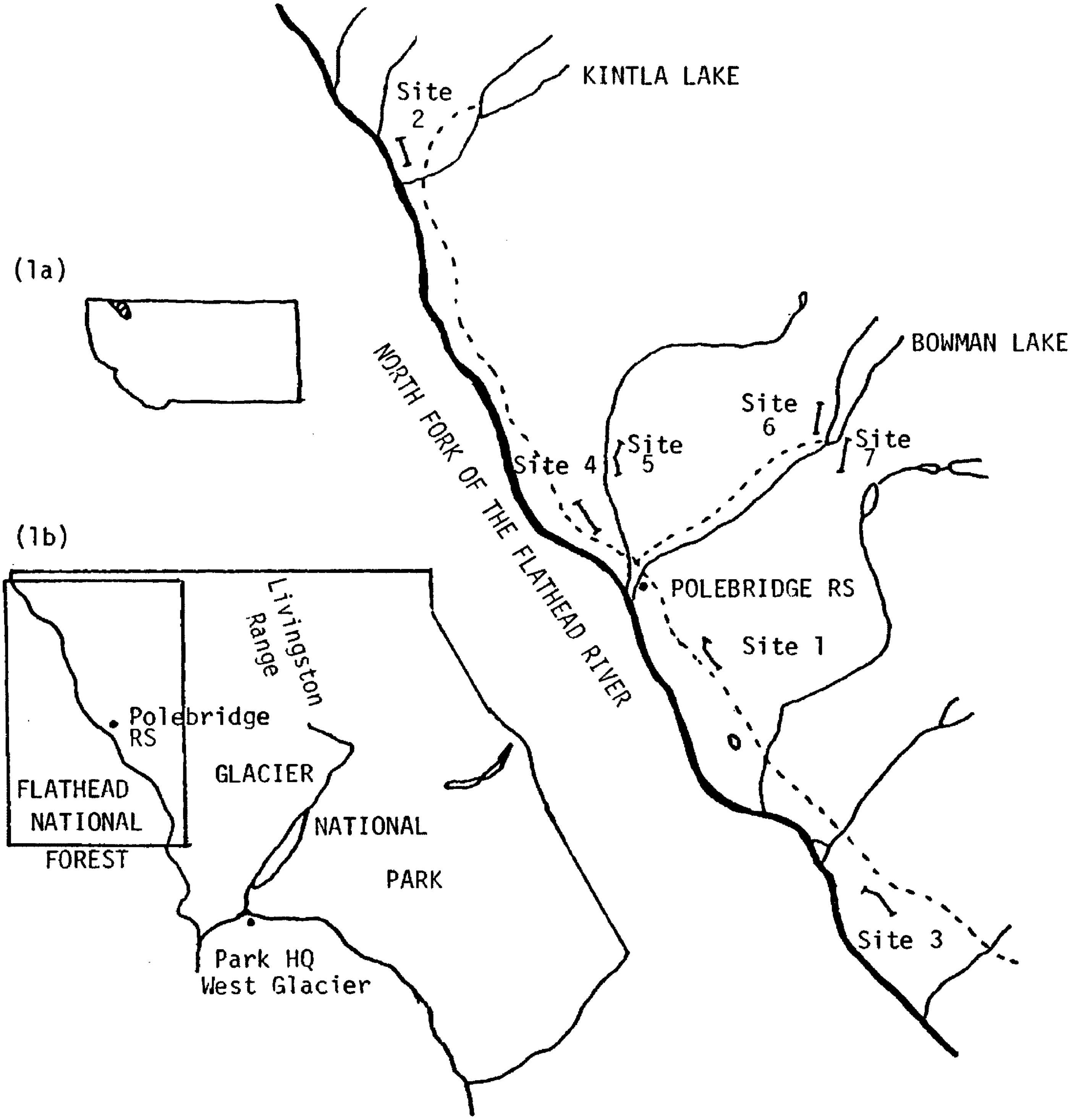

(1a)
(1b)
KINTLA LAKE
Site 2
BOWMAN LAKE
NORTH FORK OF THE FLATHEAD RIVER
Site 4
Site 5
Site 6
Site 7
POLEBRIDGE RS
Site 1
Site 3
Livingston Range
Polebridge RS
GLACIER
NATIONAL
PARK
FLATHEAD
NATIONAL
FOREST
Park HQ
West Glacier

Figure 3. Mean high and low temperatures, November through March, 1976 through 1980.

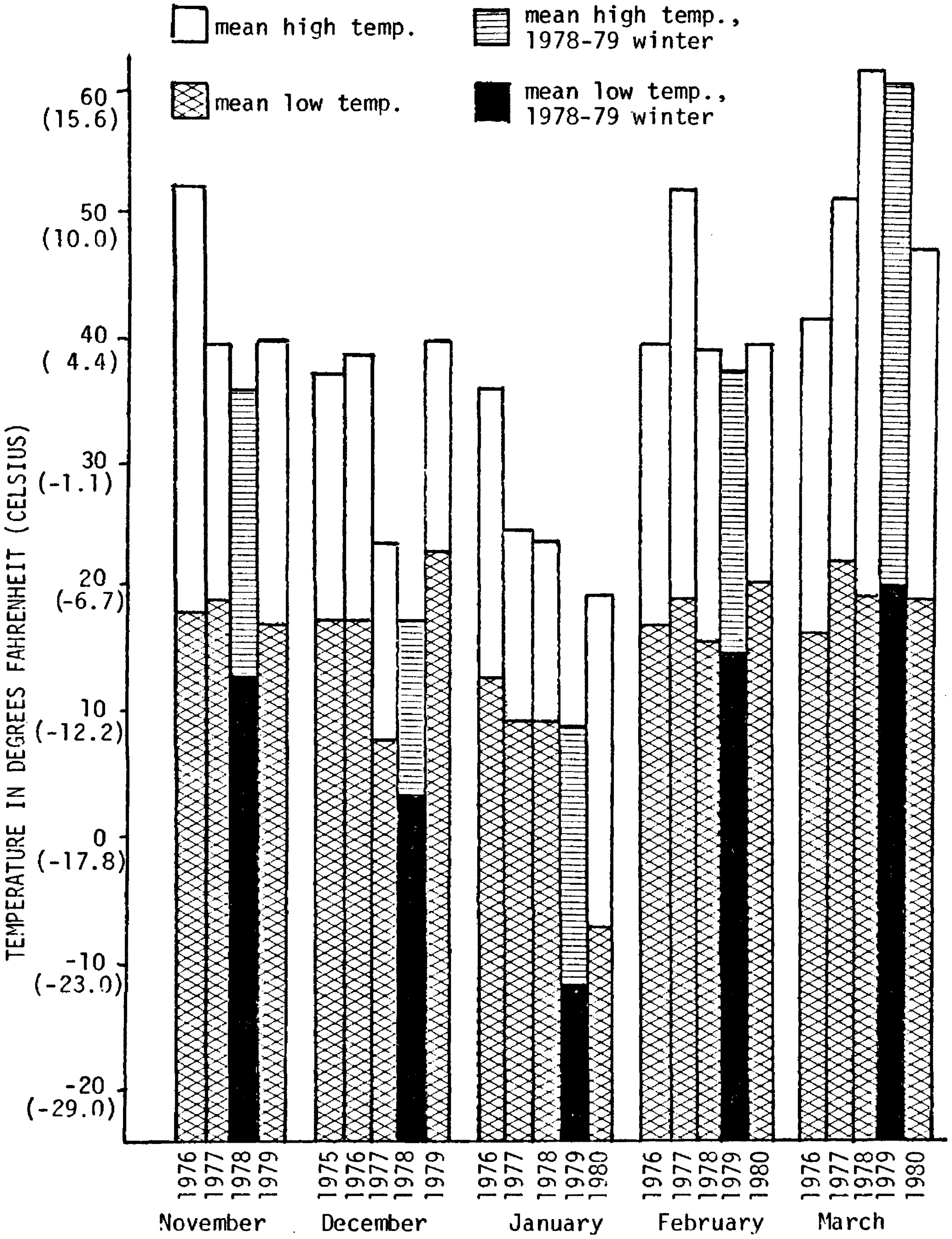
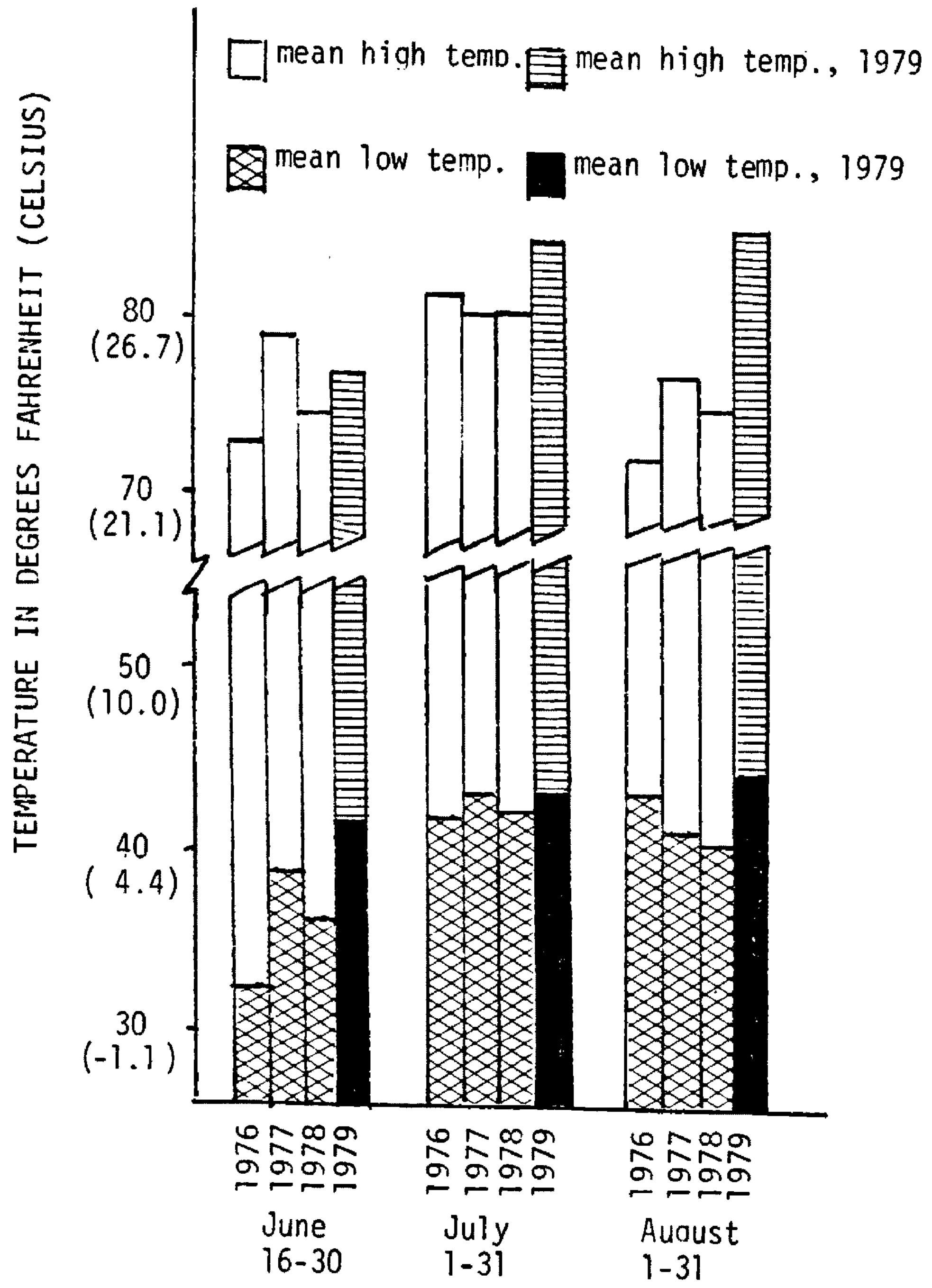
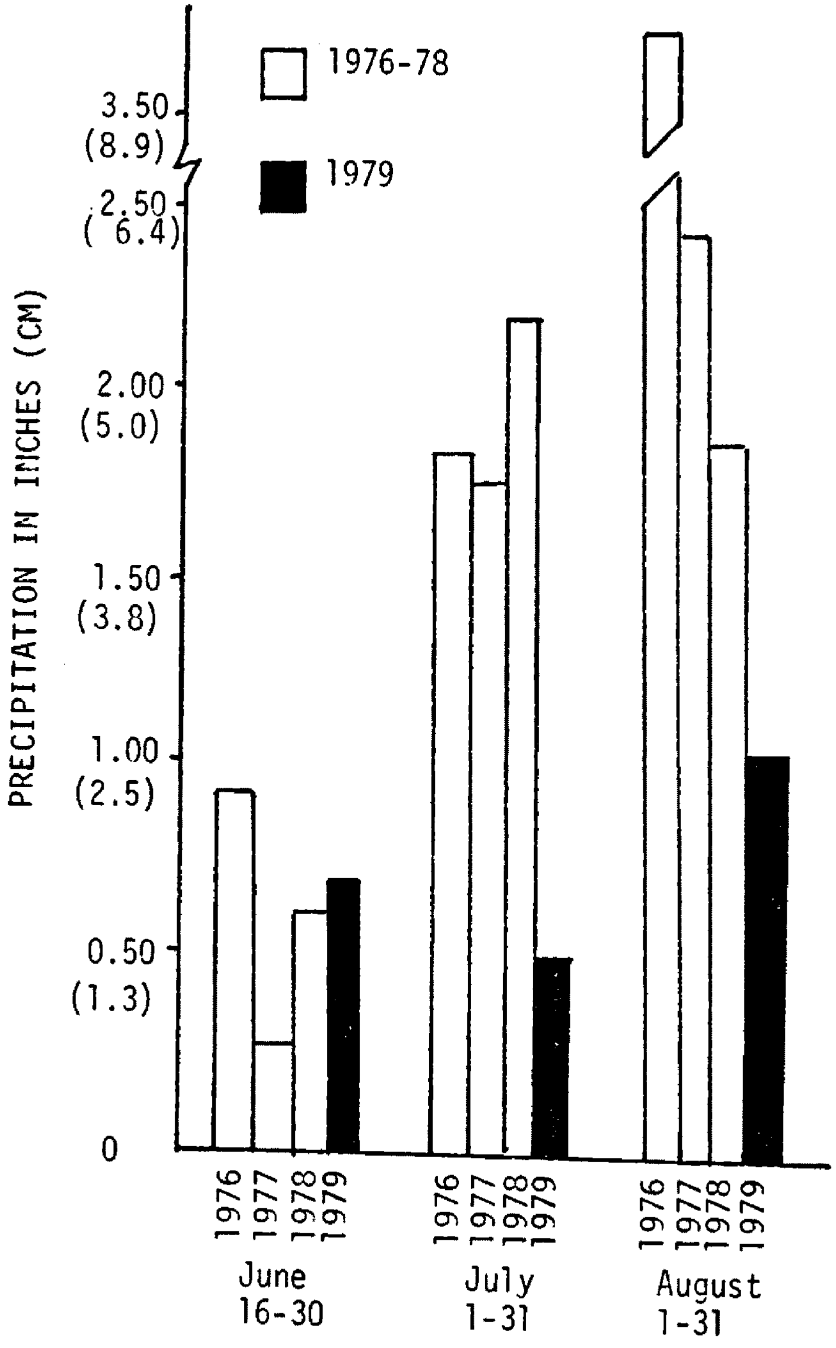

mean high temp.
mean high temp., 1978-79 winter
mean low temp.
mean low temp., 1978-79 winter
TEMPERATURE IN DEGREES FAHRENHEIT (CELSIUS)
60 (15.6)
50 (10.0)
40 (4.4)
30 (-1.1)
20 (-6.7)
10 (-12.2)
0 (-17.8)
-10 (-23.0)
-20 (-29.0)
1976 1977 1978 1979
1975 1976 1977 1978 1979
1976 1977 1978 1979 1980
1976 1977 1978 1979 1980
1976 1977 1978 1979 1980
November
December
January
February
March

Figure 4. Mean high and low temperature (^{o}F), June through August, 1976-1979, and monthly precipitation, June through August, 1976-1979.


mean high temp.
mean high temp., 1979
mean low temp.
mean low temp., 1979
TEMPERATURE IN DEGREES FAHRENHEIT (CELSIUS)
80 (26.7)
70 (21.1)
50 (10.0)
40 (4.4)
30 (-1.1)
1976
1977
1978
1979
June 16-30
July 1-31
August 1-31


1976-78
1979
PRECIPITATION IN INCHES (CM)
3.50 (8.9)
2.50 (6.4)
2.00 (5.0)
1.50 (3.8)
1.00 (2.5)
0.50 (1.3)
0
1976
1977
1978
1979
June 16-30
July 1-31
August 1-31

and black cottonwood (P. trichocarpa) (Habeck 1970a). Evidence indicates widespread wildfires were common from 1880 to 1910 (Ayres 1900, Habeck 1970b). Major fires occurred in the valley in 1920, 1929, and 1967 (GNP records).

Researchers have recorded incipient local mountain pine beetle infestations in scattered locations within the Park since the 1950s (Tunnock 1960). The current widespread epidemic began in the early 1970s, and the number of trees killed and acres infested have increased annually (Table 1, McGregor et al. 1978).

Epicenters of infestation were noticed on Starvation and Quartz Ridges in the Park in 1970. By 1977, the infestation had developed east to treeline on the Livingston Range, north to the Canadian border, south to Park Headquarters in West Glacier, and west across the North Fork in several major drainages of the Glacier View Ranger District (McGregor et al. 1978). By the end of 1978, approximately 215,882 acres in the Park and 84,256 acres in the Glacier View Ranger District (FNF) were infested (10-20 dying trees per acre, 0.4 ha) by the beetles (McGregor, pers. comm.).

Salvage cutting of beetle-killed lodgepole is currently a widespread harvesting practice on the Glacier View Ranger District (FNF) and Montana state forest lands. The National Park Service views the beetle epidemic as a natural occurrence and has taken no action to interfere with the normal course of infestation.

Vegetative and topographical characteristics of the study site are summarized in Appendix A.

Table 1. Acres infested and number of infested trees per acre, GNP and Glacier View Ranger District, FNF. McGregor et al. 1978.

	Glacier National Park		Glacier View Ranger District	
Year	Acres (ha) infested	Trees/acre (ha)	Acres (ha) infested	Trees/acre (ha)
1972	1,189 (475.6)	4.9 (12.2)		
1973	3,600 (1,440.0)	10.8 (27.0)		
1974	4,630 (1,852.0)	32.9 (82.2)		
1975	13,354 (5,341.6)	19.3 (48.2)	80 (32.0)	6.1 (15.2)
1976	103,887 (41,554.8)	46.6 (116.5)	1,213 (485.2)	10.3 (25.2)
1977	142,871 (57,148.4)	76.7 (191.8)	27,610 (11,044.0)	55.7 (139.2)

CHAPTER III

METHODS

Several sampling schemes used in this study were developed in other studies and are based on English units of measurement. To avoid a loss of meaningfulness and to be consistent, all data in this report are presented in English units. The metric equivalents parenthetically follow the English units.

For the purposes of this thesis, the following terms and phrases need to be clearly defined.

Transect - a permanently marked line about 0.5 mile (800 m) long located in the study area.

Study site - a variable width strip with the long axis determined by a marked transect.

Stems (per acre) - all standing trees, live and dead.

Snag - a dead standing tree classified as either intact or broken.

Large snag - a snag greater than 9 inches (23 cm) diameter at breast height (dbh).

Old snag - a snag not killed by the current mountain pine beetle epidemic.

Woodpeckered tree - a tree showing evidence of bark disturbance by woodpeckers.

Woodpecker-related beetle mortality - mortality of mountain pine beetles caused directly by feeding woodpeckers (removal and/or ingestion of the beetle) and mortality of beetles in bark adjacent to areas that were affected by the woodpecker feeding.

Field research extended from mid-March 1978 through September 1979. Seven study sites were located in beetle-infested lodgepole pine stands in the Park. Sites were as similar as possible in stand age and density, and diameter and phloem thickness of individual trees. Elevation of sites ranged from 3600 feet (1080 m) to 5200 feet (1560 m). A 0.5-mile (800 m) transect was marked on each site for censusing woodpeckers and beetles, and sampling vegetation. A control study site in an area of endemic beetle population was located south of the Spotted Bear Ranger Station (RS) near the South Fork of the Flathead River on the Flathead National Forest. This site was at approximately 47°51' north latitude and 3950 feet (1185 m) above sea level.

Woodpecker Censusing

Feeding Woodpeckers

A modified version of a variable-width-strip method (Amman and Baldwin 1960) was used to census feeding woodpeckers. I walked each transect at approximately 2-week intervals. Birds were located by listening for their feeding sounds. Species, sex, perpendicular distance from and position along the transect were recorded for each bird. The audible range of feeding sounds varied for each woodpecker species. Densities were calculated separately for each species at the end of the field season. The area censused for each species was determined by the length of the transect and twice the greatest distance of that species from the transect. In some cases, particularly with the less common woodpeckers, the greatest distance from the transect that I ever observed a bird was 40 feet (12 m), although I could have heard that same bird if it had been farther from the transect. In order to avoid overestimations of these species' densities, the minimum strip width used for calculating a species' density was 400 feet (120 m). Censuses were classified as winter (September through April) or breeding season (May through August) based on the behavior of the feeding birds (flocking vs. territorial).

Nesting Woodpeckers

Active woodpecker nest sites were located by following sounds of excavating birds or vocalizations of nestlings, or by visual observation. Each nest tree was mapped relative to the transect and characterized by the following variables: species, diameter at breast height (dbh), tree height, orientation and height of the cavity, and basal area (square feet of trees per acre) of the surrounding forest. An increment borer was used to sample nest tree heartwood for the presence of decay. Cores were taken at breast height and immediately above and below the nest holes. Nest tree data were collected for all nests located in the study area, both on and off the study sites.

Vegetative Sampling

Five 0.1-acre (0.04 ha) circular plots were located on each transect at intervals of approximately 500 feet (150 m). James and Shugart (1970) recommended this method of quantitative habitat description as a standardized technique to permit comparisons of estimates of bird populations from differing habitats. In each plot, species, dbh, and condition (live, intact snag, or broken snag) of every tree 3 inches (7.6 cm) dbh or greater were recorded. Every lodgepole pine was designated as not attacked, attacked in 1978, attacked in 1977, or attacked in 1976 or earlier. Shrub stems (less than 3 inches, 7.6 cm, dbh) per acre, percent ground cover, and percent and height of canopy cover were estimated on each plot.

Beetle Sampling

Techniques for sampling the 1978 mountain pine beetle population were derived from a review of the beetle literature and presampling of the 1977 beetle brood in the study area. In April and May 1978, I removed a 12- by 12-inch (30.5 by 30.5 cm) square of bark at breast height in 36 2- by 2-inch (5 by 5 cm) samples from 35 trees to determine an adequate sample size for estimating the 1978-79 beetle population. Numbers of larvae, pupae, and adults, and numbers and total length of egg galleries were recorded for each sample. Analysis of variance indicated that a single 2- by 2-inch (5 by 5 cm) square was as accurate an estimator of beetle numbers as was a 12- by 12-inch (30.5 by 30.5 cm) square. Cole (1970) reported a 6- by 6-inch (15.3 by 15.3 cm) bark sample at breast height produced statistically reliable data on beetle densities and survival.

Some researchers have reported differential attack and emergence densities between north and south aspects of trees, but differences are not consistent (Reid 1963, Shepherd 1965, Rasmussen 1974). Significant and consistent differences in attack and emergence densities over the height of the tree have been widely reported (Rasmussen 1974, Berryman 1976). In this study, 3 trees were felled and 2 4- by 4-inch bark samples were collected from the north and south faces in each 5-foot (1.5 m) length to estimate the height distribution of the beetles. Approximately 85-90% of the beetles occurred in the lower 15 feet (4.6 m) of the bole. Rasmussen (1974) reported 93% of attacks between 4 feet (1.2 m) and 7.9 feet (2.4 m).

Sampling of the 1978 beetle brood began in August 1978, immediately following the flight of newly emerged adults, and continued for 1 year. Attacked trees were located randomly along each transect. Approximately every 2-4 weeks, 4- by 4-inch (10 by 10 cm) squares of bark were removed in 4 2- by 2-inch (5 by 5 cm) sections. Two samples were taken at breast height from each tree, one each from the north and south faces. Numbers of eggs, larvae, pupae, and adults, and numbers and total length of egg galleries were recorded for each sample. Entrance and exit holes were counted in 12- by 12-inch (30.5 by 30.5 cm) sections of bark at breast height on the north and south faces of all sampled trees.

Bark Disturbance by Woodpeckers

In September 1979, I sampled amount of bark disturbance on 11 woodpeckered trees on Sites 1, 2, and 3. Entrance and exit holes, and square inches of bark disturbed were counted in a 6- by 12-inch (15.3 by 30.5 cm) grid at 4 height intervals from 2 feet (0.6 m) to 15 feet (4.6 m) on the north and south faces of each tree. Diameters were taken at 2 feet (0.6 m), breast height, and 15 feet (4.6 m) to calculate bark surface area.

Calculations

The number of beetles were totaled in each 4- by 4-inch (10 by 10 cm) sample and multiplied by a factor of 9 to estimate densities per square foot (9.3 dm^2) at breast height. Over the height of a tree, beetle densities (expressed as a % of the density at breast height) were estimated per square foot (9.3 dm^2) in each 1-foot (30.5 cm) height interval from 2 feet (0.6 m) to 15 feet (4.6 m) on both north and south aspects. On the north face, the mean beetle density per square foot (9.3 dm^2) was estimated to be 64.5% of the density calculated at breast height; the same factor for the south face was estimated to be 77.3% of the beetle density calculated at breast height. Square feet of bark surface area between 2 feet (0.6 m) and 15 feet (4.6 m) were calculated for each diameter size class of tree. Beetle densities per tree were estimated by the following formula:

0.5 (ft^2 total bark surface) (.645) (beetles/ft^2
at breast height on north face)

+

0.5 (ft^2 total bark surface) (.773) (beetles/ft^2
at breast height on south face)

Densities per tree were multiplied by the number of successful brood trees, trees that produced 1979 adults, in each size class per acre and totaled to estimate beetle densities per acre on each site (Appendix C).

Statistical Analyses

Statistical differences in mean dbhs of trees on the sites, beetle densities on the north and south faces of trees, and mean dbhs of woodpeckered trees versus all 1978-attacked lodgepole were estimated by t-tests (Ott 1977). I calculated Pearson's correlations and performed step-wise multiple regressions for all woodpecker densities and the following variables: stems and basal area per acre; percent lodgepole pine; large, old snags per acre; large snags per acre; and numbers of trees attacked by beetles per acre per year. Calculated beetle densities were not used because they were estimated on only 3 sites.

CHAPTER IV

RESULTS

Vegetation

Lodgepole pine was the most common tree species on every site. Other species included Douglas-fir, spruce, larch, subalpine fir, ponderosa pine, aspen, and sitka alder (*Alnus sinuata*) (Appendix A). There were many vegetative differences between the sites (Table 2). Site 1 was the most diverse with 7 tree species and only 51.7% lodgepole pine. Site 4 had only 4 species and 85.4% lodgepole pine. Sites 2, 3, 5, and 8 had 5 tree species each and between 64.6 and 72.1% lodgepole pine. Stems and basal area per acre together indicate numbers and sizes of trees on each site. Site 4 had the fewest, but on the average, the largest trees. Site 8, the control site, had the most and smallest trees. Mean dbh varied from 6.1 inches (15.5 cm) on Site 8 to 12.0 inches (30.5 cm) on Site 4. From 47 to 84% of all standing trees were dead on the epidemic sites. Site 4 had more large, old snags per acre than any other site; Site 2 had no large, old snags.

Woodpecker Densities

I observed 5 species of woodpeckers nesting in the study area and feeding on mountain pine beetles: Downy, Hairy, Northern Three-toed, Black-backed Three-toed (*P. arcticus*), and Pileated (*Dryocopus pileatus*) Woodpeckers. Woodpecker densities were

Table 2. Vegetative characteristics of the study sites.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
No. of tree species	7	5	5	4	5	4	4	5
Percent LPP[1]	51.7	72.1	70.3	85.4	71.1	42.9	57.9	64.6
Basal area[2]	183.4 (42.0)	187.4 (43.0)	182.6 (41.9)	125.6 (28.9)	208.0 (47.7)	246.6 (56.5)	231.6 (53.1)	215.2 (49.3)
Stems/acre (ha)	294 (735)	480 (1200)	364 (910)	136 (340)	388 (970)	350 (875)	642 (1605)	786 (1965)
Live stems	138 (345)	174 (435)	122 (305)	22 (55)	128 (320)	184 (460)	252 (630)	670 (1675)
Intact snags (old)	36 (90)	54 (135)	44 (110)	34 (85)	42 (105)	30 (75)	156 (390)	102 (225)
Broken snags (old)	2 (5)	12 (30)	10 (25)	14 (35)	4 (10)	36 (90)	46 (115)	14 (35)
MPB snags[3] (LPP & PP)[4]	118 (295)	240 (600)	188 (470)	66 (165)	214 (535)	100 (250)	188 (470)	0 (0)
Mean dbh inches (cm)	9.3 (23.6)	7.5 (19.0)	8.4 (21.3)	12.0 (30.5)	8.8 (22.4)	9.6 (24.4)	7.1 (18.0)	6.1 (15.5)
Large old snags/acre (ha)	16 (40)	0 (0)	10 (25)	28 (70)	10 (25)	8 (20)	8 (20)	2 (5)
Large, MPB snags/acre (ha)	78 (195)	114 (285)	70 (175)	66 (165)	164 (410)	75 (188)	99 (248)	0 (0)
Total large snags/acre (ha)	94 (235)	114 (285)	80 (200)	94 (235)	174 (435)	83 (208)	107 (268	2 (5)

1. LPP = lodgepole pine
2. Basal area in ft^2/acre (m^2/ha)
3. MPB = beetle-killed snags
4. PP = ponderosa pine

consistently higher on Site 1 than on any other site (Table 3). No woodpeckers or woodpecker nests were found on Site 8. Sites 6 and 7 were not censused in winter because of difficulty of access. Sites 1 and 4 were the only sites that had active woodpecker nests in both 1978 and 1979.

Northern Three-toed and Hairy Woodpeckers were the most common species (Table 4). Together they represented 51-100% of the woodpeckers observed per season on all epidemic sites. They were the only species observed on Sites 6 and 7. Generally, Northern Three-toeds were more abundant and seen more frequently than Hairys on all epidemic sites.

Woodpecker Nests

I found 25 active woodpecker nests in 1978 and 1979 (Table 5). Fifteen nests were located on the study sites, and 10 additional nests were found near the sites. Seven of the 8 Hairy Woodpecker nests were located in live aspen and paper birch (*Betula papyrifera*); only 1 Hairy nest was found in beetle-killed lodgepole pine. In contrast, 9 of 11 Northern Three-toed nests and both Black-backed Three-toed nests were in dead lodgepole pine. The remaining 2 three-toed nests were in aspen and cottonwood.

One lodgepole and all aspen, birch, and cottonwood nest trees had conks. Core samples were taken from 10 lodgepole nest trees (8 beetle-killed and 2 old snags). All ten had advanced decay at the nest holes.

Table 3. Total woodpecker densities per 100 acres (40 ha).

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Winter 1977-78								
High	-	-	-	57.3	47.0	-	-	-
Low	-	-	-	35.8	6.2	-	-	-
Mean	-	-	-	47.2	28.7	-	-	-
Breeding season 1978								
High	21.0	17.4	-	24.5	34.4	17.5	13.3	0
Low	8.8	4.3	-	3.0	0	0	4.4	0
Mean	15.1	11.8	-	21.8	11.2	8.7	11.1	0
Nesting pairs*	10.7	0	-	7.6	4.8	0	4.5	0
Winter 1978-79								
High	22.3	4.3	30.7	26.4	12.5	-	-	0
Low	15.5	0	0	0	0	-	-	0
Mean	18.1	2.2	12.1	13.9	4.4	-	-	0
Breeding season 1979								
High	18.9	13.1	30.7	20.0	10.9	8.8	4.4	0
Low	6.7	0	0	4.0	0	0	0	0
Mean	14.0	7.4	11.0	10.2	3.3	3.1	2.5	0
Nesting pairs*	14.3	0	0	3.8	0	0	0	0

*Nesting pairs calculated from actual numbers of pairs nesting on the site, rather than from feeding birds.

Table 4. Hairy and Northern Three-toed Woodpecker densities and frequencies per 100 acres (40 ha).

	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		Site 7	
	$\bar{X}$	Freq.	$\bar{X}$	Freq.	$\bar{X}$	Freq.	$\bar{X}$	Freq.	$\bar{X}$	Freq.	$\bar{X}$	Freq.	$\bar{X}$	Freq.
Winter 1977-78														
Hairy	-	-	-	-	-	-	20.8	1.00	1.6	.33	-	-	-	-
Northern Three-toeds	-	-	-	-	-	-	15.2	1.00	14.6	1.00	-	-	-	-
Breeding season 1978														
Hairy	6.6	1.00	1.1	.25	-	-	5.3	.55	2.8	.40	1.1	.25	3.9	.75
Northern Three-toeds	1.1	.33	7.6	1.00	-	-	13.5	1.00	5.6	.90	6.9	.75	7.3	.75
Winter 1978-79														
Hairy	7.3	.67	0	0	5.5	.50	6.8	.71	1.9	.20	-	-	-	-
Northern Three-toeds	7.9	1.00	2.2	1.00	6.6	.50	5.2	.71	2.5	.60	-	-	-	-
Breeding season 1979														
Hairy	3.9	.55	1.6	.38	1.8	.30	4.9	.88	0.7	.19	0	0	1.1	.14
Northern Three-toeds	8.6	1.00	5.4	.75	8.8	.90	5.4	.88	2.7	.57	4.9	.43	4.4	.43

Table 5. Woodpecker nests.

Woodpecker species	Site	Year	Tree spp.	DBH inches (cm)	Condition[*]	Tree ht. ft (m)	Nest ht. ft (m)	Nest orient.	Basal area[1]	Evidence of decay[2]
Downy	1	78	Asp[3]	10.1 (25.7)	live	86 (26.2)	44 (13.4)	S 63° W	230 (52.8)	conk
Downy	1	79	Asp[3]	10.1 (25.7)	live	86 (26.2)	44 (13.4)	S 63° W	230 (52.8)	conk
Black-backed Three-toed	4	78	LPP	10.3 (26.2)	int. snag	72 (23.5)	22 (6.7)	N 20° E	135 (31.0)	+
Black-backed Three-toed	5	78	LPP	13.3 (33.8)	int. MPB	89 (27.1)	53 (16.2)	N 70° E	225 (51.8)	-
Pileated	1	78	Ctwd	19.1 (48.5)	int. snag	103 (31.4)	32 (9.6)	N 46° W	120 (27.6)	conk
Pileated	-	78	Lrch	35.2 (89.4)	live	115 (35.1)	37 (11.3)	N 28° W	165 (37.8)	-
Hairy	1	78	Asp	12.5 (31.8)	live	84 (25.6)	60 (18.3)	N 34° E	180 (41.3)	conk
Hairy	-	78	Brch[4]	10.4 (26.4)	live	30 (9.1)	15 (4.6)	S 34° W	140 (32.1)	conk
Hairy	-	78	Asp[5]	16.5 (41.9)	live	74 (22.6)	32 (9.8)	S 10° E	105 (24.1)	conk
Hairy	-	78	Asp	12.2 (31.0)	live	73 (22.3)	16 (4.9)	S 46° E	20 (4.6)	conk
Hairy	-	79	Asp[5]	16.5 (41.9)	live	74 (22.6)	22 (6.7)	S 20° E	105 (24.1)	conk
Hairy	-	79	Brch[4]	10.4 (26.4)	live	30 (9.1)	13 (4.0)	S 50° E	140 (32.1)	conk
Hairy	1	79	Asp	12.4 (31.5)	live	93 (28.3)	57 (17.4)	S 9° E	105 (24.1)	conk
Hairy	4	79	LPP	14.3 (36.3)	int. MPB	64 (19.5)	25 (7.6)	S 50° W	95 (21.8)	+
Northern Three-toed	4	78	LPP	17.2 (43.7)	int. snag	60 (18.3)	16 (4.9)	N 53° W	170 (39.0)	+
Northern Three-toed	7	78	LPP	9.9 (25.1)	bkn. snag	17 (5.2)	13 (4.0)	N 10° E	40 (9.2)	-
Northern Three-toed	4	78	LPP	12.8 (32.5)	int. MPB	82 (25.0)	7 (2.1)	S 57° W	145 (33.3)	+
Northern Three-toed	4	78	LPP	16.6 (42.1)	int. MPB	87 (26.5)	21 (6.4)	N 70° W	105 (42.1)	+
Northern Three-toed	-	78	LPP	11.1 (28.2)	int. MPB	92 (28.0)	15 (4.6)	N 88° E	105 (24.1)	+
Northern Three-toed	4	79	LPP	13.9 (35.3)	int. MPB	104 (31.7)	27 (8.2)	S 76° W	185 (42.4)	+
Northern Three-toed	1	79	LPP	9.8 (24.9)	int. MPB	75 (22.9)	23 (7.0)	S 32° W	180 (41.3)	conk +
Northern Three-toed	1	79	LPP	14.0 (35.6)	int. MPB	92 (28.0)	32 (9.8)	S 78° W	220 (50.4)	+
Northern Three-toed	-	79	LPP	11.1 (28.2)	int. MPB	77 (23.5)	13 (4.0)	S 54° W	170 (39.0)	+
Northern Three-toed	-	79	Ctwd	11.9 (30.2)	int. snag	48 (14.6)	16 (4.9)	N 36° E	115 (26.4)	conk
Northern Three-toed	-	79	Asp	8.6 (21.8)	live	60 (18.3)	9 (2.7)	N 56° E	150 (34.4)	conk

[*] int. snag = intact snag; MPB = beetle-killed snag; bkn. snag = broken snag

1. Basal area measured in ft^2/acre (m^2/ha)

2. "+" = core sample showing heartwood decay

3, 4, 5. Same nest trees

In 1978, on Sites 1, 4, and 5, I found nests of Yellow-bellied Sapsuckers (*Sphyrapicus varius*) and Common Flickers (*Coleaptes auratus*). These species were not observed feeding on mountain pine beetles, but their presence may have affected other woodpecker species; they may have occupied the only suitable nest trees in the area. The pairs of sapsuckers nested in live aspen on Sites 1 and 5. A pair of flickers nested in a broken lodgepole snag on Site 4.

Beetle Densities and Mortality

I sampled beetle densities and bark disturbance by woodpeckers on Sites 1, 2, and 3. On Sites 4-8 there were too few trees attacked by mountain pine beetles in 1978 to allow sampling of the beetle brood throughout the year.

Beetles had been present on most epidemic sites since 1976, but the numbers and sizes of trees killed each year varied from site to site (Table 6). There were no significant differences in brood densities between the north and south aspects of attacked trees. Beetle densities at breast height on the north face exceeded densities on the south face in 60% of the samples. But, densities on south faces were higher just above and below breast height than at breast height. Brood densities on the north face rarely exceeded the density at breast height (Appendix C).

Approximately 85% of the beetle population occurred from 2 feet (0.6 m) to 15 feet (4.6 m) above the ground. Generally, the larger diameter trees had more beetles. Numbers of beetles

Table 6. Numbers of lodgepole pine attacked by mountain pine beetles per acre (ha), and sizes of lodgepole pine attacked by mountain pine beetles in inches (cm) dbh.

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
LPP attacked by MPB in:								
1976 or earlier	12 (30)	36 (90)	0 (0)	32 (80)	42 (105)	10 (25)	10 (25)	0 (0)
1977	58 (145)	76 (192)	4 (10)	24 (60)	156 (390)	87 (218)	138 (345)	0 (0)
1978	42 (105)	116 (290)	100 (250)	10 (25)	8 (20)	3 (8)	28 (70)	2 (5)
1979 (as of 9/30)	4 (10)	12 (30)	80 (200)	0 (0)	6 (15)	0 (0)	10 (25)	0 (0)
LPP not attacked by MPB	4 (10)	46 (115)	38 (95)	6 (15)	22 (55)	17 (42)	20 (50)	402 (1005)
Old LPP snags/acre (ha)	32 (80)	6 (15)	34 (85)	44 (110)	42 (105)	34 (85)	164 (410)	104 (260)
Mean dbh of LPP attacked by MPB in:								
1976 or earlier	13.3 (33.8)	12.3 (31.2)	- -	15.3 (38.9)	12.2 (31.0)	10.6 (26.9)	10.2 (25.9)	- -
1977	10.5 (26.7)	9.9 (25.1)	12.9 (32.8)	13.6 (34.5)	10.2 (25.9)	9.8 (24.9)	9.9 (25.1)	- -
1978	9.6 (24.4)	8.2 (20.8)	9.7 (24.6)	10.7 (27.2)	8.1 (20.6)	6.5 (16.5)	7.3 (18.5)	10.3 (26.2)
1979 (as of 9/30)	8.8 (22.4)	9.6 (24.4)	8.9 (22.6)	- -	7.6 (19.3)	- -	6.6 (16.8)	- -
Mean dbh of LPP not attacked	5.8 (14.7)	5.4 (13.7)	6.4 (16.3)	8.9 (22.6)	7.4 (18.8)	6.6 (16.8)	6.5 (16.5)	7.1 (18.0)

per tree in December 1978 ranged from 3055 in 6-7 inch (15.2 - 17.8 cm) diameter trees to 20,128 in 14-15 inch (35.6 - 38.1 cm) diameter trees. By July 1979, numbers of beetles per tree in these size classes had declined to 80 and 756, respectively. Beetle survival was greatest in trees in the 10-11 inch (25.5 - 27.9 cm) diameter size class, which had 6318 beetles per tree in December 1978 and 557 beetles per tree in July 1980 (8.8% survival rate).

Actual initial beetle densities were greater than the highest estimates indicated. Highest beetle counts occurred in early to mid-December, after most eggs had hatched and larvae had grown to a size easily visible. Cole (1975) estimated that mortality of about 7% of the brood occurred prior to this stage. Percent mortality figures in Table 7 are derived from an adjusted initial beetle density based on a fall mortality figure of 7%. Adjusted initial densities are minimum estimates because only successful brood trees were used to calculate beetle densities. There were many trees that at some time in the 1978-79 season contained immature stages of beetles, but did not produce 1979 adults.

Initial beetle densities were greatest on Site 3. The average diameter of 1978-attacked trees on Site 3 was larger than on Sites 1 and 2, and Site 3 had a greater number of successful brood trees than either Site 1 or 2 (Table 8). Percent mortality through March ranged from 78 to 83% on the 3 sites. Only 3-4% of the 1978 brood survived to adulthood.

Table 7. Mountain pine beetle densities and mortality.

	Site 1			Site 2			Site 3		
		Probability			Probability			Probability	
	Beetles per acre (ha)	Life	Death	Beetles per acre (ha)	Life	Death	Beetles per acre (ha)	Life	Death
Adjusted initial density*	216,000 (540,000)			241,000 (602,500)			484,000 (1,210,000)		
December 1978	201,000 (502,000)	.93	.07	224,000 (560,000)	.93	.07	450,000 (1,125,000)	.93	.07
March 1979	48,000 (120,000)	.22	.78	40,500 (101,250)	.17	.83	104,000 (260,000)	.21	.79
May 1979	23,500 (58,750)	.11	.89	26,000 (65,000)	.11	.89	46,500 (116,000)	.10	.90
June 1979	17,500 (43,750)	.08	.92	16,000 (40,000)	.07	.93	36,000 (90,000)	.07	.93
July 1979	8,900 (22,250)	.04	.96	7,200 (18,000)	.03	.97	19,500 (48,750)	.04	.96

*Based on 7% fall mortality.

Table 8. Numbers of 1978-attacked lodgepole pine, mean dbh of 1978 attacked lodgepole pine, and numbers of successful 1978 brood trees.

	Site 1	Site 2	Site 3
No. LPP attacked/ acre (ha)	42 (105)	116 (290)	100 (250)
Mean dbh inches (cm)	9.6 (24.4)	8.2 (20.8)	9.7 (24.6)
No. successful 1978 brood trees/acre (ha)	32 (80)	44 (110)	62 (155)

Statistical Analyses

The results of the regression and correlation analyses were inconclusive. Variables, such as basal area, that did not change from year to year, had a strong positive correlation with woodpecker densities in one season and a negative correlation with woodpecker densities in the next season. The amount of woodpecker food, represented by numbers of trees attacked by beetles, never had a significant correlation with woodpecker densities. In most cases, the number of large snags per acre was strongly negatively correlated with woodpecker densities, or had no significant correlation at all. I believe the lack of consistent correlations and predictors of woodpecker densities reflects the short time period represented by the data and the small sample size. Data were not available for several study sites during several seasons; thus, some analyses were based on as few as 4 samples. Regression analyses may be helpful in measuring and predicting trends in woodpecker densities in relation to vegetation and food abundance. However, in order to predict a trend, data must be collected before the phenomenon begins and throughout its duration. My 1.5-year field season was not intended to fulfill this requirement.

Impact of Woodpeckers on Beetle Mortality

The results of sampling woodpeckered trees were pooled for Sites 1, 2, and 3. The mean dbh of woodpeckered trees was 9.8 inches (24.9 cm) and there was no significant difference in bark disturbance between the north and south faces of the trees

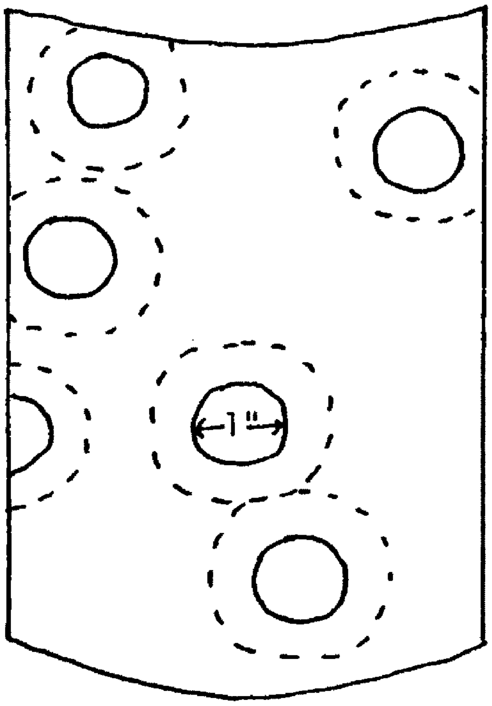
(Appendix E). Approximately 10% of the bark on all 1978-attacked lodgepole that showed evidence of woodpecker feeding was disturbed (Appendix D). Knight (1958) and Tunnock (1960) estimated percent reductions in bark beetle broods resulting from bark disturbance by woodpeckers. Based on their estimates, woodpecker disturbance of 10% of the bark surface could cause a 17-100% reduction in the beetle brood. In order to make a more specific estimate of woodpecker-related beetle mortality, additional observations must be made.

Most of the bark removal I observed occurred in patches of about 1 square inch (6.5 cm^2) or less, scattered over the bole. Because of exposure of the phloem, beetles under bark immediately adjacent to disturbed areas were more likely to be exposed to dessication and lethal temperatures than beetles in undisturbed areas. I believe a conservative estimate of this zone of influence was 0.5 inches (1.27 cm). Bark in this zone usually had separated from the wood of the tree because of drying and shrinking of the phloem. Thus, the total bark area affected by woodpecker activity exceeded the 10% of the bark surface that was actually disturbed. And, the total area affected on a given tree was greater if the disturbed areas were small and scattered than if they represented a few large patches (Fig. 5).

Thus, an estimate of woodpecker-related mortality could range from a minimum of 10% to 39% or even higher, since small scattered areas of disturbance have a greater affect than fewer,

Figure 5. Pattern of bark disturbance and affect on beetle mortality.

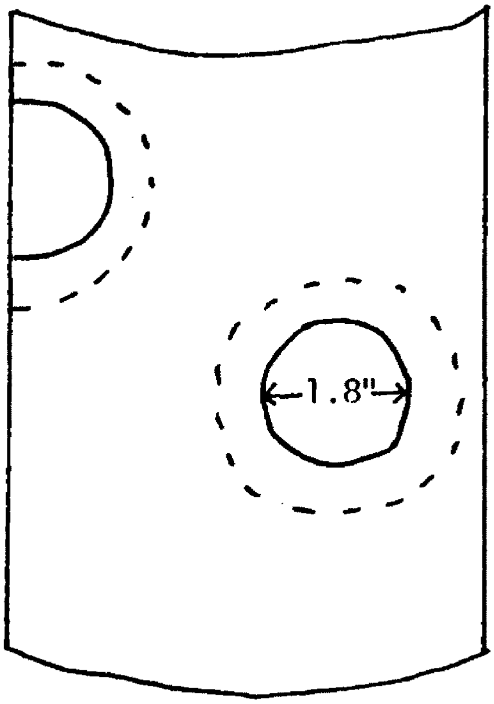
(5a) 10% of bark surface disturbed in 10 approximately circular patches 1.0 inches (2.54 cm) in diameter



- Each patch = 0.79 square inches (5.1 cm^2).
- Total area disturbed = 7.9 square inches (51.0 cm^2).
- Total bark surface area = 79 square inches (510 cm^2).
- Area disturbed = 10% of total surface area.

- Zone of influence = 0.5 inches (1.27 cm).
- Area affected per patch = 3.1 square inches (20.3 cm^2).
- Total area affected = 31.0 square inches (203 cm^2)
- Area affected = 39% of total surface area.

(5b) 10% of bark surface disturbed in 3 approximately circular patches 1.8 inches (4.6 cm) in diameter.



- Each patch = 2.6 square inches (16.7 cm^2).
- Total area disturbed = 7.9 square inches (51.0 cm^2).
- Total bark surface area = 79 square inches (510 cm^2).
- Area disturbed = 10% of total surface area.

- Zone of influence = 0.5 inches (1.27 cm).
- Area affected per patch = 6.2 square inches (40.0 cm^2).
- Total area affected = 18.5 square inches (120 cm^2).
- Area affected = 23.5% of total surface area.

large disturbed patches. Possibly, some of the smallest disturbed areas did not cause any beetle mortality, directly or indirectly; the woodpeckers may have done some unsuccessful bark-flaking in an area without beetles. Even if this occurred in 50% of the foraging attempts, woodpecker-related beetle mortality would probably be much greater than the figure based on actual bark disturbance.

Woodpeckers may have fed more heavily in areas with greater beetle densities, and ignored areas with low densities. About 50% of the bark samples on woodpeckered trees showed no bark disturbance. In these undisturbed areas, there were averages of about 5 entrance holes and 5 exit holes per square foot (9.3 dm^2) of bark, indicating that for every pair of attacking adults, only 1 offspring emerged. However, Reid (1963) and Amman (1969) reported that when pupal cells coalesce during feeding of callow adults, all new adults may leave through a common exit hole. In my samples, most pupal cells appeared to be separate. And, of the 5 exit holes per square foot (9.3 dm^2) an average of 2 were made from pupal cells; the remaining 3 exit holes were made from egg galleries. Amman (1975) reported a 33% rate of abandonment of galleries by unfertilized females. He classified an additional 10% of galleries as potential cases for abandonment. Very few, if any, beetle offspring were associated with these galleries. It is possible that the undisturbed bark areas of a woodpeckered tree represented areas of relatively low beetle densities within that tree. If this is true, the 10% of the bark that was disturbed represents a much larger percentage of the beetle brood within that tree.

Within a stand, woodpeckered trees may have had greater beetle densities than beetle-attacked trees without evidence of woodpecker feeding. Beetle densities are usually greater in larger trees (Amman 1969), and the mean dbh of woodpeckered trees was 9.8 inches (24.9 cm) in contrast to a mean dbh of 9.1 inches (22.9 cm) of 1978-attacked trees. This difference was significant at the 0.5 level (Appendix E). There was a mean of 9 entrance holes per square foot (9.3 cm^2) of bark at breast height on trees that had no evidence of woodpecker feeding at the time they were sampled (trees sampled to estimate beetle densities). On woodpeckered trees, the mean number of entrance holes per square foot (9.3 cm^2) of bark at breast height was six. However, some of the breast height samples on woodpeckered trees had to be moved horizontally or vertically to exclude disturbed areas where entrance and exit holes could not be counted. This may have resulted in sampling an area of low beetle density, and the figures may not be comparable to the figures obtained from trees without bark disturbance.

Based on mortality resulting from the zone of influence surrounding bark disturbed or removed by woodpeckers, and the possibility that woodpeckers do not feed randomly on beetle-infested trees, I beleive about 30% mortality of the beetle brood may be related to woodpecker activity.

CHAPTER V

DISCUSSION

Results of my woodpecker censuses illustrate variability in woodpecker densities, but I obtained much higher densities in the epidemic beetle study area than in the endemic beetle study area. High and mean woodpecker densities on several epidemic sites were equal to or greater than figures reported by other researchers in bark beetle infestations (Yeager 1955, Otvos 1965, Baldwin 1968, Koplin 1969). Although I found no consistent predictors of woodpecker densities, I do not believe this indicates a lack of real correlations between woodpecker densities and the independent variables. More research for a longer duration may produce statistically reliable predictors of woodpecker densities in areas of insect epidemics. However, based on my data and results of other researchers, I believe several valid observations may be made.

Mountain Pine Beetle Densities

Woodpecker Food

Although many lodgepole were attacked by mountain pine beetles in 1978, and almost all attacked trees were killed, my estimates of the 1978 beetle population were not particularly high for an epidemic infestation. I believe the infestation in the study area was in a decline by the 1978-79 season. The beetles had infested the area for at least 2 years prior to 1978. They had already eliminated most of the large lodgepole in which reproduction was most successful. The weather was relatively mild in 1975, 1976, and 1977, which contributed to the success of the beetles in those years. An average of 60% of all the lodgepole on all the epidemic sites were attacked and killed before 1978. The fewer remaining live lodgepole, and the smaller diameters of those trees, 8.6 inches (21.8 cm) in 1978 vs. 11.0 inches (27.9 cm) in 1977, resulted in a reduction in the 1978 beetle brood over those of previous years.

Stages of the infestation varied from site to site. In some cases, conditions on the site, estimated from beetle and vegetation samples, accurately represented the surrounding forest. For example, on Sites 6 and 7 only 8-11% of all lodgepole were alive by mid-1979, and the average size of those trees was 6.5-6.6 inches (16.5-16.8 cm) dbh. Similar conditions prevailed in the surrounding lodgepole forest; I found no adjacent areas with significantly more 1978-attacked or unattacked lodgepole. There were also few unattacked and 1978-attacked lodgepole in areas adjacent to Site 5. Site 3 was located in an area heavily attacked by beetles in 1978, but there were many lodgepole attacked in 1979, as well as unattacked lodgepole, on the site itself as well as in the surrounding forest. However, other sites were adjacent to areas with very different characteristics. There were stands of unattacked, small (6 inches, 15.2 cm) dbh lodgepole next to Sites 1 and 4, although vegetative sampling showed those conditions did not occur on the sites themselves. Site 2 was more isolated from the adjacent forest than any other site. It was bounded on 2 sides by the North Fork and on the other 2 sides by a steep bluff. There were fewer live lodgepole above the bluff than on Site 2 itself, and although lodgepole stands west of the North Fork (on the Flathead National Forest) were similar to those on the site, they were logged heavily in 1978 and 1979. Areas adjacent to study sites often provided foraging sites for woodpeckers seen on the sites.

Within sites, beetle densities varied seasonally. Although very high densities may have occurred in the fall, larvae were probably quite small and may not have been as attractive to woodpeckers as were the larger larval instars that occurred at lower densities later in the winter. As a woodpecker food source, beetles were generally at their lowest numbers from early summer, after heavy natural mortality reduced the population, through early fall, when adults and eggs represented most of the population.

Vegetation

Woodpecker Nest Sites

Numbers of snags per acre could indicate the availability of suitable nest trees. Characteristics of snags used by cavity-nesting birds have been described in western larch and Douglas-fir forests in northwestern Montana (McClelland and Frissell 1975), and in ponderosa pine in Arizona (Scott 1978). Lodgepole snags were not a significant component of the forest in either study, and very little use of lodgepole was reported. Scott et al. (1978) studied use of snags by cavity-nesting birds in a subalpine zone in Colorado. Although spruce snags showed the greatest use, 20 nest holes were found in lodgepole snags. Nine of the 20 holes were in broken-top snags over 11 inches (27.9 cm) dbh.

The smallest tree I found with a woodpecker nest was 8.6 inches (21.8 cm) dbh; the other 24 nests were in trees over 9.8 inches (24.9 cm) dbh. Therefore, I felt that most trees less than 9 inches (22.9 cm) dbh could not be considered as suitable potential nest sites. Broken-top snags 9 inches (22.9 cm) dbh or larger were rare on all sites. None of the beetle-killed lodgepole sampled appeared to have broken tops. Potential nest trees (total large snags per acre) increased every year as the beetles killed more and more pines.

The importance of aspen to nesting woodpeckers in the northern Rockies was reported by McClelland (1977) and became apparent in my study. Vegetative sampling on the transects often missed aspen groves that were, in fact, present on the study sites. Site 1 had a large aspen grove, and there were smaller, younger groves located on Sites 2, 3, and 5. There were very few aspen on or in areas adjacent to Sites 4, 6, 7, and 8.

The role of site conditions in influencing woodpecker densities was not clear. A wet site, such as Site 4, may have created conditions more favorable to the development of root and/or heart rot decay in live and dead trees (Lawrence 1966). McClelland

(1977) discussed the importance of heartwood decay to woodpeckers in selection of a nest site. Rotten wood is easier to excavate than sound wood. Some species, such as aspen, birch, and western larch, are very susceptible to heart rot fungi and often develop decay as live trees. Conks that grow on the boles of these species indicate the presence of heart rot. Lodgepole pine less than 100 years old is not highly susceptible to heart rot decay, and conks rarely are found on lodgepole, even when the tree has advanced heartwood decay (Loman and Paul 1963).

Woodpecker Densities

Variability in Censusing

Within sites, woodpecker densities varied greatly with season, weather conditions, and time of day. In the winter, or non-breeding season, woodpeckers usually fed in mixed-species flocks of up to 10 birds. Periodically, I encountered 2 or more flocks on a census and a high calculated density of woodpeckers resulted. I was just as likely to miss the flocks altogether and obtain a very low woodpecker density. Because of their flocking behavior, the birds were never evenly distributed throughout the infested area, and I did not attempt to determine the size of a flock's foraging area. Mean density figures probably did not accurately represent winter woodpecker populations on any particular sites or throughout the infested area as a whole.

During the breeding season, the advent of nest site selection and territorial behavior caused lower densities than winter densities. Adults tended to forage relatively close to their nest tree, and the general distribution of feeding birds on a given site was probably determined by the location of active nest trees on that site. This caused less variation among censuses on a given site, and a mean breeding season density probably more accurately represented the woodpecker population on that site than did the mean winter density.

Time of day and weather conditions combined to affect my behavior as well as the woodpeckers'. Any conditions that created noise, such as wind, rain, or sleet, impaired my ability to hear woodpeckers, and I tried to avoid censusing under those conditions. On a winter day with little or no precipitation, woodpecker feeding generally started between 0900 and 0930. Feeding started earlier in the morning in the summer, but rarely before 0730. Morning feeding usually persisted for several hours, and I found this was the best time for censusing. During the winter there did not appear to be a strict daily feeding pattern; I often heard woodpeckers feeding throughout the day. During the summer, there was generally a mid-day break in feeding, especially if it were a hot, sunny day. Afternoon feeding bouts were less intense than morning feeding during all seasons. When adults were feeding nestlings, there were few prolonged breaks in foraging and feeding activity.

All these factors introduced considerable variation into my estimates of densities of feeding woodpeckers. The figures I obtained may be used to make general comparisons between sites on the study area. They also indicate the relatively high densities of woodpeckers that occurred in the epidemic beetle study area compared to the endemic beetle area. However, I believe caution should be used in comparing my figures, on an absolute basis, with woodpecker densities reported by other researchers in different geographical areas and habitat types.

Woodpecker Densities on the Study Sites

Woodpecker densities throughout the study area were probably influenced by the same variables affecting densities on individual study sites. Assessing the most important factors on each site helps to determine the relative importance of the individual variables. Sites are discussed in order of increasing woodpecker densities.

Site 8 (Endemic beetle population)

Site 8 had almost no mountain pine beetles, only 2 large snags per acre, and no woodpeckers were feeding there during any of my censuses. I occasionally heard birds drumming near the study site, and I believe woodpeckers did use the area for feeding, but at such low densities that almost continuous observation would be required to accurately establish woodpecker densities in the area. The forest on Site 8 was very similar to much of the North Fork study area except in age, as indicated by the high numbers of relatively small trees and the low density of large snags. The beetles existed on Site 8 at an endemic population level. The lodgepole forest was too young to provide optimal conditions for a mountain pine beetle epidemic, but that remains a possibility for the future.

Sites 6 and 7 (High elevation mountainsides)

Sites 6 and 7 were not censused in the winter; data for only 2 breeding seasons were collected. Although beetle densities were relatively low in 1978 and 1979 breeding seasons, beetle densities during the 1977-78 winter were probably quite high. This winter food source attracted woodpeckers to the sites. Both Sites 6 and 7 had only 8 large, old snage per acre. The relatively low 1978 breeding season woodpecker densities may reflect a scarcity of suitable nest sites. By the 1979 breeding season, beetle densities in areas adjacent to and on both sites had been quite low for at least 1 year. The 1979 breeding season woodpecker densities were very low, and I found no nests on either site. Apparently, there were not many suitable nest trees on either site, and the woodpeckers moved on to other areas as the local food source dwindled.

Sites 2 and 5 (Mature lodgepole forests)

Sites 2 and 5 had similarities and differences. One difference between the sites was the timing of the beetle infestation. On Site 2, the beetles attacked the most lodgepole in 1978; the heaviest attack on Site 5 occurred in 1977. Another difference was the number of large, old snags per acre. Site 2 had none, and Site 5 had ten. I did not find old woodpecker nest holes on either site.

Woodpecker densities in the 1977-78 winter were very high on Site 5, reflecting the high local beetle population. Breeding season woodpecker densities in 1978 were very similar on both Sites 2 and 5. On Site 2, I observed a pair of Northern Three-toed Woodpeckers excavating a nest in an aspen snag in late May 1978, but the birds abandoned the tree after about 1 week of work. Apparently, it was not acceptable as a nest tree. On Site 5, Yellow-bellied Sapsuckers nested in the largest aspen grove in 1978 and were observed feeding there in 1978 and 1979. The pair of sapsuckers may have occupied the only suitable nest tree in the grove.

It was difficult to reach Site 2 in the winter, and I conducted only 5 1978-79 winter censuses. Because of the inherent variability in winter censuses, I do not believe the 1978-79 mean winter density of 2.2 woodpeckers per 100 acres (40 ha) was accurate.

Woodpecker densities were low through the 1978-79 winter and the 1979 breeding season on both sites. There were no 1979 woodpecker nests on either site. On Site 2, beetle densities were sufficient to support feeding woodpeckers in the 1979 breeding season, but a lack of suitable nest sites may have excluded nesting woodpeckers from the area. Beetle densities on Site 5 were too low to attract feeding woodpeckers, and the scarcity of suitable unoccupied nest trees excluded nesting pairs from the site. Apparently, Sites 2 and 5 provided feeding sites for woodpeckers year-round but lacked suitable nest trees for breeding woodpeckers.

Site 3 (Recently infested by beetles)

Data for only 2 seasons were collected on Site 3. It was the only site that was not heavily infested by beetles before 1978. High beetle densities through the 1978-79 winter attracted flocks of feeding woodpeckers to the area. Although beetle mortality was high, enough beetles survived to support a relatively high 1979 breeding season woodpecker population. There were no 1979 woodpecker nests on the site, and I found no old woodpecker nest holes, indicating that woodpeckers have not often nested on the site in the past. A pair of Northern Three-toed Woodpeckers nested in a live aspen just beyond one end of the transect. Site 3 had more aspen than all other sites except Site 1, and I believe the aspen will provide nest trees in the future.

Beetles probably attacked as many trees in 1979 as in 1978 on Site 3, and this food source would help maintain high winter woodpecker densities. I believe that 1980 breeding season and nesting woodpecker densities on Site 3 probably will exceed the 1979 densities.

Site 1 (Most diverse vegetation) and Site 4 (Old-growth lodgepole forest)

Sites 1 and 4 consistently had the highest densities of feeding and nesting woodpeckers. Beetle densities were very high on Site 4 in the 1976-77 and 1977-78 seasons; on Site 1, beetle densities peaked in the 1977-78 winter. I found old woodpecker nest holes on both sites, indicating use of the areas by nesting woodpeckers in earlier years.

Woodpeckers responded to the local food abundance on Site 4 in 1976 and 1977. Woodpecker densities were very high in the 1977-78 winter. In the following seasons on Site 4, woodpecker densities declined as the food source dwindled. Woodpeckers also responded to high beetle densities on Site 1, but the response occurred at least 1 year later on Site 1 than on Site 4. Beetle densities through the 1978-79 winter remained high enough on Site 1 to continue to support high densities of feeding and breeding woodpeckers.

Both Sites 1 and 4 showed evidence of past woodpecker nesting and maintained pairs of nesting woodpeckers in 1978 and 1979. Apparently, both sites had a relative abundance of suitable nest trees. There were differences between the active nest trees on the two sites. On Site 1, 6 nests (including the 1978 sapsuckers) were in aspen, and only two were in lodgepole pine. On Site 4, all 7 nests (including the 1978 flickers) were in lodgepole pine. There were corresponding differences in the woodpecker species nesting on each site. On Site 1, there were 2 pairs each of Northern Three-toed, Hairy, and Downy Woodpeckers; and 1 pair each of Pileateds and sapsuckers. On Site 4, there were 5 pairs of three-toed woodpeckers, 1 pair of Hairys, and 1 pair of flickers. The different species of woodpeckers selected different species of nest trees.

It appears that the epidemic of mountain pine beetles was the major reason for the high woodpecker densities in the North

Fork study area. The effects of this superabundance of woodpecker food cannot be completely separated from the effects of vegetation (availability of suitable nest sites, large snags) because beetle epidemics do not occur in young forests that are composed primarily of small trees. Woodpecker densities were not estimated before the beetle epidemic in the North Fork study area. But, there were many reports of dramatically increased woodpecker numbers from amateur birdwatchers and outdoor workers in the North Fork area in the early and mid-1970s. I believe the mountain pine beetle epidemic attracted the large numbers of woodpeckers to the area.

Apparently, in the winter, the local beetle density was the most important variable influencing woodpecker densities in the infested area. High beetle densities attracted flocks of feeding woodpeckers to specific sites, but as local beetle populations declined over several seasons, most woodpeckers stopped feeding in those areas. In the breeding season, the availability of suitable nest trees in the infested area appeared to have more effect on woodpecker densities than did beetle densities. High beetle densities may have attracted woodpeckers to a local area at some time during the year, but if there were no suitable unoccupied nest sites in that area, pairs of woodpeckers did not breed there.

Nest Site Selection

The 5 woodpecker species I studied rarely have been investigated in lodgepole pine forests, but general characteristics of their nest sites in other areas may be summarized. Pileated

Woodpeckers have the least flexibility in selection of nest sites of the 5 species. In northwestern Montana, Pileateds generally selected broken-top larch snags over 20 inches (51 cm) dbh in areas of old growth. Large, old ponderosa pine or black cottonwood provided alternative nest sites (McClelland 1979). Downy Woodpecker nests have been reported in dead trees or stubs with rotten cores, usually hardwoods (Bent 1939, Lawrence, Conner and Adkisson 1976). Black-backed Three-toed Woodpeckers have been reported nesting in live and dead trees, and most trees have decayed heartwood (Bent 1939).

In this study, 2 nests of each of these 3 species were located. Although this was a very small sample, the nest trees did not appear to very different from the trees selected by these species in other areas.

Northern Three-toed Compared with Hairy Woodpeckers

Northern Three-toed and Hairy Woodpeckers were the most abundant and frequently seen woodpecker species in the study area, and 76% of the nests I located belonged to these 2 species. Other researchers have observed that Hairy Woodpeckers nested in live or dead trees that had heart rot. They generally selected nest trees in or near relatively wet sites (Bent 1939, Lawrence 1966, Conner and Adkisson 1976). In drier forest types, aspen was used most commonly for nesting (Tatschl 1967). Northern Three-toed Woodpecker nests have been reported in dead trees, dead limbs of live trees, and in live trees with heartwood decay. Most nests were found in spruce (Bent 1939).

Nest site selection and density. In the study area, there was a marked difference in the type of trees Hairys and Northern Three-toeds selected as nest sites. Only 1 of 8 Hairy nests was in lodgepole, and only 2 of 11 Northern Three-toed nests were not in lodgepole. There were also differences in the seasonal densities of Hairy and Northern Three-toed Woodpeckers and differences in the way each species' densities changed over time. Through 4 seasons on the 7 epidemic sites, I collected data to estimate 20 total woodpecker densities (Table 3). In only 3 of the 20 estimates did the mean density of Hairy Woodpeckers exceed the mean density of Northern Three-toed Woodpeckers. Two of those instances were the winter estimates on Site 4. The other estimate was the 1978 breeding season estimate on Site 1. The only season in which Hairys occurred more frequently than Northern Three-toeds was the 1978 breeding season on Site 1.

Northern Three-toed Woodpeckers were generally more common in the study area than Hairys. But, if Hairys outnumbered Northern Three-toeds in both winters on Site 4, why did they never outnumber them in the following breeding seasons? I believe that Site 4 was not a "traditional" nesting area for Hairy Woodpeckers, either because it lacked suitable nest sites for Hairys, or there were more suitable nest sites in other nearby areas. In a forest so strongly dominated by lodgepole pine, suitable nest trees for Hairy Woodpeckers were generally limited to scattered aspen groves, which did not occur on Site 4. In contrast, Northern Three-toed Woodpeckers located nests in the large numbers of dead lodgepole pine.

In the winters, high densities of Hairy and Northern Three-toed Woodpeckers represented the addition of juveniles to wandering, feeding flocks of woodpeckers. The juveniles of all species probably dispersed to suitable unoccupied areas or died before the next breeding season. Hairys that were breeding for the first time were forced to travel greater distances than Northern Three-toeds, perhaps to the fringe of the beetle infestation, to locate unoccupied aspen, cottonwood, or birch. Northern Three-toed Woodpeckers were able to locate nest sites throughout the infested area, and first-year breeders may have been recruited into the local populations and increased local densities of this species.

I believe Site 1 had consistently high densities of Hairy Woodpeckers because it had more suitable nest trees for Hairys than any other site. A pair of Hairy Woodpeckers probably has nested in the aspen on Site 1 for many seasons, and will continue to occupy the grove as long as there are suitable nest trees. They probably defend the grove against other members of their own species which prevents an increase in the breeding season and nesting densities of Hairy Woodpeckers on the site. The year-to-year densities of Hairy Woodpeckers did not fluctuate greatly with changing beetle densities. Changes in year-to-year densities of Northern Three-toed Woodpeckers often corresponded with changes in local beetle densities.

First-year breeders and immigrant adults of all woodpecker species had to compete with local breeding pairs of woodpeckers for nest sites. Sapsuckers and flickers were not observed feeding on mountain pine beetles, and their densities probably did not respond to the infestation. However, locally breeding pairs of these migrants may have a competitive advantage in nest site selection over Hairys and Northern Three-toeds breeding for the first time. Lawrence (1966) reported that migrants were more likely to return to the same nesting territory than were Hairy or Downy Woodpeckers. This may have reduced numbers of available nest sites for Hairys because they appeared to select the same type of nest tree as the sapsuckers. Since the three-toeds were able to use lodgepole, the presence of the sapsuckers probably had little effect on their nesting and breeding season densities.

The presence of conks on all active aspen, birch, and cottonwood nest trees indicated that decay was present before woodpeckers selected these trees for nest excavation. Heartwood rot existed immediately above and below the nest holes in all lodgepole snags sampled. This decay was quite advanced, thus it is more likely that the decay existed before the woodpeckers selected the trees than that the woodpecker excavations served as the routes of infection for the fungi. Since advanced heartwood decay is relatively uncommon in lodgepole stands less than 100 years old (Loman and Paul 1963), Northern Three-toed Woodpeckers appeared to be showing a preference for lodgepole snags with pre-existing decay.

Response to the beetle epidemic. Northern Three-toed Woodpeckers were particularly well-adapted to exploit the abundant food source. They responded to the mountain pine beetle epidemic by increasing their densities in the infested area. They reduced competition with local woodpecker pairs for nest sites by utilizing lodgepole pine, a species generally not selected by other woodpecker species, for nest trees. Because of this adaptability, as beetle densities decrease to endemic levels in some areas, Northern Three-toeds probably will follow the infestation as it develops in other areas.

Hairy Woodpeckers, because of their dependence on more specific types of nest trees, did not show as great a response to the mountain pine beetle epidemic as did the Northern Three-toed Woodpeckers. In particular, I believe the local breeding populations of Hairy Woodpeckers did not change significantly with the increase in beetle densities. Reproductive success may have increased, and undoubtedly Hairys responded functionally to the abundance of mountain pine beetles, but scarcity of suitable nest sites appeared to prevent an increase in density of breeding Hairy Woodpeckers.

Limiting factors. Food did not appear to be a limiting factor for either Hairy or Northern Three-toed Woodpeckers in the North Fork study area, although local beetle densities affected woodpecker numbers, especially in the winter, in local areas. The scarcity of suitable nest sites appeared to limit the Hairy Woodpecker population. Availability of suitable nest sites had a strong effect on Northern Three-toed Woodpeckers, but social and territorial behavior probably was equally important in regulating Northern Three-toed densities. Social interactions were not studied in this project, but defense of the nesting territory against conspecifics has been discussed by other researchers (Kilham 1962, Lawrence 1966, Kilham 1968). The maximum density of breeding Northern Three-toeds probably was determined by the availability of suitable nest trees and the size of the territory defended against conspecifics.

Beetle Mortality

Mortality of mountain pine beetles may be caused by many interacting factors. Generally, intraspecific competition for food is cited as the major mortality factor (Amman 1977); however, low temperatures also may cause significant mortality (Amman 1973, Cole 1973). I believe severe winter weather greatly affected the 1978 beetle brood in the study area. The exact temperature required to cause significant mortality of mountain pine beetle broods in a natural setting is not known. Cold-hardiness of larvae is greatest from December through February, but winter survival of larvae depends on the life stage at the onset of winter temperatures. Epidemic beetle populations are more likely to be affected by cold weather than are endemic populations (Cole 1973). Crowding of beetles in the phloem is much greater in an epidemic than an endemic population. Increased crowding shortens the developmental stages within a single generation. Many larvae enter the winter without achieving the level of cold-hardiness necessary to survive normal winter temperatures.

In late December 1978 and early January 1979, temperatures in the study area reached -40° F (-40° C) for 3 consecutive nights. Laboratory estimates indicate the lethal low temperature for larvae is between -29° F (-33.9° C) and -36° F (-37.7° C) (Somme 1940, Safranyik 1978). In the study area, high temperatures of the days following the 3 cold nights varied from -18° F (-28° C) to 21° F (-6° C), and the skies were clear. The south faces of the trees probably were several degrees warmer than the ambient temperature. Beetle samples from December through February did not show any major brood mortality. However, by the end of March, the 3 sites sampled showed 78-83% reductions in beetle densities. Apparently, the severe temperatures did not kill the larvae outright, but the physiological stress caused by low temperatures may have increased the susceptibility of the larvae to mortality by starvation, dessication, disease, and parasitism.

Cole (1975) reported that cold winter weather followed by severe drying of the phloem drastically reduced a beetle population and accounted for about 75% mortality in trees 9 inches (22.9 cm) dbh. Temperature and precipitation figures indicate that conditions to cause severe drying prevailed in the study area through the 1979 spring and summer (Fig. 4). About 64% of the beetles alive in May did not survive to adulthood. For this same period, Cole (1970, 1975) reported 22-42% mortality. The severity of both winter and summer weather in the study area probably combined to cause unusually high beetle mortality.

Impact of Woodpeckers on Mortality of Mountain Pine Beetles

Isolating the impact of woodpeckers on beetle mortality from other effects is virtually impossible. However, no mortality factors operate totally independently of other factors. In the 1978-79 season, I observed the most intensive woodpecker feeding during the winter (December through February). The bark disturbance caused by this feeding contributed to exposure of the larvae to lethal low temperatures and drying of the phloem. Beetles killed directly by woodpeckers may have died later in the season from other causes if the woodpeckers had not eaten them; there is no way to determine this probability. However, regardless of the severe weather conditions during the 1978-79 season, I beleive overall beetle mortality would have been somewhat less than the 96-97% estimate if the woodpeckers had not been present in the study area. I do not believe the woodpeckers alone regulated or significantly reduced the mountain pine beetle population in the study area, although their contribution to beetle mortality probably varied from year to year.

Management Implications and Recommendations

In Glacier National Park

In Glacier National Park, USFS entomologists recommended spraying all green lodgepole 7 inches (17.8 cm) or larger in high use recreational and administrative sites with an insecticide to prevent beetle attack. They also stated that dead and infested trees should be cut and removed or used for firewood (McGregor et al. 1978). I believe the expense of this type of operation would be extremely prohibitive. The cost to spray one tree is about $2, and each tree must be sprayed at least every other year throughout the duration of the epidemic. The manpower and time required to cut and remove all the dead trees in the Park campgrounds and along the Park roads would be more than the budget of the Park could afford.

An extensive management effort within the Park would contradict the nature of the Park as a preserve for all forms of wildlife. The mountain pine beetle is a native species, and the epidemic is a natural occurrence. The dead trees are an integral part of the ecosystem. I observed them being used as foraging and nesting sites by squirrels and other insectivorous, cavity-nesting birds as well as woodpeckers. Standing and fallen trees provide cover for many large and small wildlife species. Eventually, the nutrients contained in the dead wood will be recycled through the ecosystem. Runoff from chemical sprays would affect areas around each tree as well as the tree itself. It will be necessary to remove fallen trees when they obstruct traffic in campground and on roads, but I do not believe it is necessary or practical to cut and remove all standing dead trees. However, if snags in high use areas appear to be hazardous, it would be possible to reduce the hazard by removing the upper half to two-thirds of the trees and allowing stubs to remain. These would provide potential nest sites for woodpeckers and other cavity-nesting birds and foraging sites for many animal species.

In Commercial Lodgepole Forests

This field work was not conducted in a commerical forest. General silvacultural recommendations for managing lodgepole pine to prevent beetle epidemics are to use short (60 year) rotations and encourage a mosaic of even-aged stands within the forest. Management for lodgepole pine snags has been nonexistent because it is difficult (lodgepole snags blow down easily), and little research has been done regarding their use by cavity-nesting birds. My data indicated that three-toed woodpeckers were very capable of nesting in lodgepole pine.

The retention of lodgepole snags may maintain resident pairs of three-toed woodpeckers. The presence of other species of snags and aspen groves may enhance an area for all woodpeckers. The presence of abandoned and old woodpecker cavities is important to other insectivorous hole-nesting birds that cannot excavate their own nests. An effort to manage all kinds of snags may result in enhanced populations of insectivorous cavity-nesting birds. This not only helps to maintain some natural diversity in a managed ecosystem, but the combined impacts of several populations of insectivorous birds on the mortality of endemic populations of harmful forest insects may be significant. Beebe (1974) summarized the conclusions of many researchers:

> . . . in many instances, birds act as important components of natural biological regulation of insect population dynamics at endemic, or "normal" population levels. In some rather unusual circumstances birds may act together, each species and sometimes each sex in its own specialized way, to be a major cause of the suppression of an insect outbreak. Most authors agree, however, that the most important role of birds is in the prevention of insect epidemics, rather than their suppression. This important role is probably still underestimated because the vast majority of research has been conducted during insect epidemics in which sheer numbers of insects simply overwhelm the bird's ability to exert a regulating influence.

I believe that before initiation of active timber management in a commerical lodgepole forest, there should be a site by site evaluation of the value of each area to woodpeckers. Certain areas become traditional nesting areas because of the presence of suitable nest sites. Areas that show evidence of past use by nesting woodpeckers require careful examination. Any trees with old nest holes should not be cut. Aspen groves should not be disturbed. Whenever possible, patches of snags should be left intact in these breeding areas. Snags over 9 inches (23 cm) dbh are most suitable for nesting woodpeckers. However, buffer zones including live and dead trees should be left to help protect nest trees from windthrow. Since there will be attrition of snage, live trees with the potential of becoming suitable nest trees should be left standing. These trees include those with external evidence of decay (conks) and those with broken tops and fire scars that can serve as routes of infection for heartwood decay. If clearcutting is the only feasible harvest method, clearcuts should be small and alternated with uncut blocks of timber. Trees in uncut areas may provide alternative foraging and nesting sites when other areas are disturbed. Most importantly, certain sizes and/or species of snags, such as lodgepole pine, should not be eliminated categorically from management plans simply because of a scarcity of evidence of their importance to cavity-nesters. Under some circumstances, these species may be heavily utilized and their presence may be essential to the maintenance of some woodpecker populations. The forest manager should determine the relative importance of areas within the forest to woodpeckers, and place restrictions on timber harvesting practices in those areas that appear to have high value for woodpeckers and other cavity-nesting birds.

CHAPTER VI

SUMMARY

High densities of woodpeckers were attracted to the North Fork study area because of the epidemic of mountain pine beetles that began in the early 1970s. Northern Three-toed Woodpeckers were the most abundant woodpecker species in the infested area. Their winter densities in local areas appeared to correspond to local beetle densities. Most Northern Three-toed Woodpeckers nested in lodgepole pine snags that had heartwood decay at the nest holes. As a result of the beetle infestation, lodgepole pine snags were common, and there probably were many that had decay. Because of this relative abundance of potential nest trees, Northern Three-toeds were able to increase their breeding population in the infested area greatly. Territorial behavior and availability of suitable nest sites probably determined the maximum density of nesting Northern Three-toed Woodpeckers in local areas. Because of their year-round abundance, Northern Three-toed Woodpeckers probably had more impact on the beetle population than any other woodpecker species.

Hairy Woodpeckers were the second most abundant woodpecker species in the infested area. Their winter densities appeared to be related to local beetle densities, but breeding season densities probably were determined by the availability of suitable nest sites. Almost all Hairy Woodpecker nests were located in aspen or birch that had evidence of heartwood decay. The relative scarcity of these types of trees in the study area limited the population of resident, breeding Hairy Woodpeckers, and the mountain pine beetle epidemic probably did not cause a major increase in their numbers.

The mountain pine beetle epidemic was in a decline by the 1978-79 season. Estimates of initial 1978 beetle densities ranged from 216,000 to 484,000 larvae per acre (540,000 - 1,210,000 larvae per ha). By the summer of 1979 beetle densities ranged from 7200 to 19,500 beetles per acre (18,000 - 48,750 beetles per ha). Total beetle mortality was 96-97%. Extremely cold winter temperatures followed by dry spring and summer weather probably accounted for the high mortality of the 1978 beetle brood.

About 10% of the bark on 1978-attacked lodgepole pine that showed evidence of woodpecker feeding was disturbed. Woodpecker-related mortality of beetles was about 30%, but because of the severe weather conditions, many of these beetles would have died before adulthood regardless of the woodpeckers' activity. Woodpeckers contributed to overall beetle mortality, but did not appear to regulate or control the epidemic beetle population.

REFERENCES CITED

Amman, G. D. 1969. Mountain pine beetle emergence in relation to depth of lodgepole pine bark. USDA Forest Serv. Res. Note Int-96. Intermtn. Forest and Range Exp. Sta., Ogden, UT 8 pp.

________. 1973. Population changes of the mountain pine beetle in relation to elevation. Env. Ent. 2:541-547.

________. 1975. Abandoned mountain pine beetle galleries in lodgepole pine. USDA Forest Serv. Res. Note INT-197. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 6 pp.

________. 1977. The role of the mountain pine beetle in lodgepole pine ecosystems: impact on succession. From Proceedings in Life Sciences.

________, and P. H. Baldwin. 1960. A comparison of methods for censusing woodpeckers in spruce-fir forests of Colorado. Ecol. 41:699-706.

________, M. D. McGregor, D. B. Cahill, and W. H. Klein. 1977. Guidelines for reducing losses of lodgepole pine to the mountain pine beetle in unmanaged stands in the Rocky Mountains. USDA Forest Serv. Gen. Tech. Rep. INT-36. Intermtn. Forest and Range Exp. Sta., Ogden, UT. 19 pp.

Ayres, H. B. 1900. The Flathead Forest Reserve. 20th Ann. Rep., US Geol. Surv. Part V (1898-1899). pp. 245-316.

Baldwin, P. H. 1968. Predator-prey relationships of birds and spruce beetles. Proc. North Central Branch - ESA 23:90-00.

Beebe, S. B. 1974. Relationships between insectivorous hole-nesting birds and forest management. Unpubl. lit. review. Yale Univ. School of Forestry and Environ. Studies. New Haven, CT. 49 pp.

Bent, A. C. 1939. Life histories of North American Woodpeckers. Dover Publ., Inc. New York. 334 pp.

Berryman, A. A. 1976. Theoretical explanation of mountain pine beetle dynamics in lodgepole pine forests. Env. Ent. 5:1225-1233.

Burt, W. H. 1930. Adaptive modifications in woodpeckers. Univ. Calif. Publ. Zool. 32:455-524.

Cole, W. E. 1970. The statistical and biological implications of sampling units for mountain pine beetle populations in lodgepole pine. Res. Popul. Ecol. XII:243-248.

________. 1973. Crowding effects among single-age larvae of the mountain pine beetle. Env. Ent. 2:285-293.

________. 1975. Interpreting some mortality factor interactions within mountain pine beetle broods. Env. Ent. 4:97-102.

Conner, R. H., and C. S. Adkisson. 1976. Discriminant function analysis: a possible aid in determining the impact of forest management on woodpecker nesting habitat. For. Sci. 22:122-127.

Habeck, J. R. 1970a. The vegetation of Glacier National Park, Montana. Dept. of Botany, Univ. of Montana, Missoula. 132 pp.

________. 1970b. Fire ecology investigations in Glacier National Park. Historical considerations and current observations. Dept. of Botany, Univ. of Montana, Missoula. 80 pp.

Hutchinson, F. I. 1951. The effects of woodpeckers on the Engelmann spruce beetle, _Dendroctonus engelmanni_ Hopk. M.S. Thesis. Colo. State Univ., Fort Collins, CO. 73 pp.

James, F. C., and H. H. Shugart, Jr. 1970. A quantitative method of habitat description. Audubon Field Notes 24:727-736.

Kilham, L. 1962. Reproductive behavior of Downy Woodpeckers. Condor 64:126-133.

________. 1966. Nesting activities of Black-backed Three-toed Woodpeckers. Condor 68:308-310.

________. 1968. Reproductive behavior of Hairy Woodpeckers. II. Nesting and habitat. Wils. Bull. 80:286-305.

Knight, F. B. 1958. The effects of woodpeckers on populations of the Engelmann spruce beetle. J. Econ. Ent. 51:603-607.

Koplin, J. R. 1969. The numerical response of woodpeckers to insect prey in a subalpine forest in Colorado. Condor 71:436-438.

________, and P. H. Baldwin. 1970. Woodpecker predation on an endemic population of Engelmann spruce beetles. Am. Mid. Nat. 83:510-515.

Kotok, E. S. 1971. Lodgepole pine. American Woods - FS - 253. USDA Forest Serv. 7 pp.

Lawrence, L. deK. 1966. A comparative life history of four species of woodpeckers. AOU Ornithol. Monog. No. 5. Lawrence, KS. 156 pp.

Little, E. L., Jr. 1971. Atlas of United States trees. I. Conifers and important hardwoods. USDA Misc. Publ. 1146, Vol. I. 9 pp. 200 maps.

Loman, A. A., and G. D. Paul. 1963. Decay of lodgepole in two foothills sections of the boreal forest in Alberta. For. Chron. 39:422-435.

McClelland, B. R. 1977. Relationships between hole-nesting birds, forest snags, and decay in western larch-Douglas-fir forests of the northern Rocky Mountains. Ph.D. Dissertation. School of Forestry, Univ. of Montana, Missoula. 495 pp.

________. 1979. The Pileated Woodpecker in forests of the northern Rocky Mountains. In The Role of Insectivorous Birds in Forest Ecosystems. J. G. Dickson, R. N. Conner, R. R. Fleet, J. C. Kroll, and J. A. Jackson, eds. Academic Press, Inc. New York. 381 pp.

________, and S. S. Frissell. 1975. Identifying forest snags useful for hole-nesting birds. J. For. 73:414-417.

McGregor, M. D., D. R. Hamel, and S. Kohler. 1978. Status of mountain pine beetle infestation, Glacier National Park and Glacier View Ranger District, Flathead National Forest, Montana, 1977. Report No. 78-6, Forest Insect and Disease Mgt., USDA Forest Serv. Northern Region, State and Private Forestry, Missoula.

Nelson, R. M. 1934. Effect of blue-stain fungi on southern pines attacked by bark beetles. Phytopathology 7:327-353.

Ott, L. 1977. An introduction to statistical methods and data analysis. Duxbury Press, Wadsworth Publishing Co., Inc. Belmont, CA. 730 pp.

Otvos, I. S. 1964. Studies on avian predators of *Dendroctonus brevicomis* LeConte (Coleptera: Scolytidae) with special reference to Picidae. Can. Ent. 97:1184-1199.

Pfister, R. D., and R. Daubenmire. 1975. Ecology of lodgepole pine, *Pinus contorta* Dougl. In Management of Lodgepole Pine Ecosystems. Symp. Proc. D. M. Baumgartner, ed. Wash. State Univ., Pullman, WA 495 pp.

Pitman, G. B., J. P. Vité, G. W. Kinzer, and A. F. Fentiman, Jr. 1968. Bark beetle attractants: *Trans*-verbenol isolated from *Dendroctonus*. Nature 218:168-169.

Rasmussen, L. A. 1974. Flight and attack behavior of mountain pine beetles in lodgepole pine of northern Utah and southern Idaho. USDA Forest Serv. Res. Note INT-180. Intermtn. Forest and Range Exp. Sta., Ogden, UT 7 pp.

Reid, R. W. 1963. Biology of the mountain pine beetle, *Dendroctonus monticolae* Hopkins, in the east Kootenay region of British Columbia. III. Interaction between the beetle and its host, with emphasis on brood mortality and survival. Can. Ent. 95: 225-238.

Rudinsky, J. A., M. E. Morgan, L. M. Libbey, and T. B. Putnam. 1974. Antiaggregative rivalry pheromone of the mountain pine beetle, and a new arrestant of the southern pine beetle. Env. Ent. 3: 90-98.

Safranyik, L. 1978. Effects of climate and weather on mountain pine beetle populations. Symp. Proc. Theory and Practice of Mountain Pine Beetle Management in Lodgepole Pine Forests. Publ. by Forest, Wildlife, and Range Exp. Sta., Univ. of Idaho, Moscow with USDA Forest Serv., Forest Insect and Disease Research, Wash., DC and Intermtn. Forest and Range Exp. Sta., Ogden, UT 224 pp.

________, D. M. Shrimpton, and H. S. Whitney. 1973. An interpretation of the interaction between lodgepole pine, the mountain pine beetle and its associated blue-stain fungi in western Canada. From Management of Lodgepole Pine Ecosystems. D. M. Baumgartner, ed. Wash. State Univ., Pullman. 495 pp.

________, ________, and ________. 1974. Management of lodgepole pine to reduce losses from the mountain pine beetle. Can. Dept. Environ., For. Serv., Pac. For. Res. Cent. Tech. Rep. 1. 24 pp.

Scott, V. E. 1978. Characteristics of ponderosa pine snags used by cavity-nesting birds in Arizona. J. For. 76:26-28.

________, J. A. Whelan, and R. R. Alexander. 1978. Dead trees used by cavity-nesting birds on the Fraser Experimental Forest: a case history. USDA Forest Serv. Res. Note RM-360. Rocky Mtn. Forest and Range Exp. Sta., Fort Collins, CO 4 pp.

Shepherd, R. F. 1965. Distribution of attacks by Dendroctonus ponderosae Hopk. on Pinus contorta Dougl. var. latifolia Engelm. Can. Ent. 97:207-215.

Somme, L. 1964. Effects of glycerol on cold hardiness in insects. Can. J. Zool. 42:87-101.

Spring, L. 1965. Climbing and pecking adaptations in some North American woodpeckers. Condor 67:457-488.

Tatschl, J. J. 1967. Breeding birds of the Sandia Mountains and their ecological distributions. Condor 69:479-490.

Tunnock, A., Jr. 1960. A biological evaluation of a mountain pine beetle infestation in Glacier National Park, Montana, season of 1959. Unpubl. Rep. Intermtn. Forest and Range Exp. Sta., Ogden, UT 4 pp.

Vité, J. P., and G. B. Pitman. 1968. Bark beetle aggregation: effects of feeding on the release of pheromones in Dendroctonus and Ips. Nature 218:169-170.

Wellner, C. A. 1975. The importance of lodgepole pine in the United States. Symp. Proc. Management of Lodgepole Pine Ecosystems. D. M. Baumgartner, ed. Wash. State Univ., Pullman. 495 pp.

Whitney, H. S. 1971. Association of Dendroctonus ponderosae (Coleoptera: Scolytidae) with blue-stain fungi and yeasts during brood development in lodgepole pine. Can. Ent. 103:1495-1503.

Yeager, L. E. 1955. Two woodpecker populations in relation to environmental change. Condor 57:148-153.

APPENDIX A

VEGETATIVE CHARACTERISTICS OF THE STUDY SITES

Site 1

Date established: June 1978

Location: 3.5 miles (5.6 km) southeast of Polebridge RS

Elevation: 3690 feet (1125 m)

Slope: 5-10%

Aspect: SE

Tree species	Stems per acre (ha)	Relative density	Basal area ft^2/acre (m^2/ha)	Relative dominance
Lodgepole pine	152 (380)	.517	96.8 (22.2)	.528
Douglas-fir	86 (215)	.292	39.0 (8.9)	.213
Spruce	22 (55)	.075	9.2 (2.1)	.050
Subalpine fir	16 (40)	.055	5.6 (1.3)	.030
Larch	8 (20)	.027	14.6 (3.3)	.080
Ponderosa pine	2 (5)	.007	14.2 (3.3)	.077
Aspen	8 (20)	.027	4.0 (0.9)	.022
Alder	0 (0)	0	0 (0)	0
Total	294 (735)	1.000	183.4 (42.0)	1.000

Site 2

Date established:	May 1978
Location:	15 miles (24.1 km) northwest of the Polebridge RS
Elevation:	3740 feet (1140 m)
Slope:	level
Aspect:	level

Tree species	Stems per acre (ha)	Relative density	Basal area ft^2/acre (m^2/ha)	Relative dominance
Lodgepole pine	346 (865)	.721	149.6 (34.3)	.798
Douglas-fir	36 (90)	.075	10.4 (2.4)	.056
Spruce	86 (215)	.179	25.8 (5.9)	.138
Subalpine fir	0 (0)	0	0 (0)	0
Larch	4 (10)	.008	0.8 (0.2)	.004
Ponderosa pine	0 (0)	0	0 (0)	0
Aspen	8 (20)	.017	0.8 (0.2)	.004
Alder	0 (0)	0	0 (0)	0
Total	480 (1200)	1.000	187.4 (43.0)	1.000

Site 3

Date established:	November 1978
Location:	12 miles (19.3 km) southeast of the Polebridge RS
Elevation:	3550 feet (1080 m)
Slope:	level
Aspect:	level

Tree species	Stems per acre (ha)	Relative density	Basal area ft^2/acre (m^2/ha)	Relative dominance
Lodgepole pine	256 (640)	.703	125.0 (28.7)	.684
Douglas-fir	0 (0)	0	0 (0)	0
Spruce	16 (40)	.044	8.8 (2.0)	.048
Subalpine fir	0 (0)	0	0 (0)	0
Larch	44 (110)	.121	16.0 (3.7)	.088
Ponderosa pine	36 (90)	.099	27.2 (6.2)	.149
Aspen	12 (30)	.033	5.6 (1.3)	.031
Alder	0 (0)	0	0 (0)	0
Total	364 (910)	1.000	182.6 (41.9)	1.000

Site 4

Data established:	April 1978
Location:	1.5 miles (2.4 km) northwest of the Polebridge RS
Elevation:	3550 feet (1080 m)
Slope:	level
Aspect:	level

Tree species	Stems per acre (ha)	Relative density	Basal area ft^2/acre (m^2/ha)	Relative dominance
Lodgepole pine	116 (290)	.853	109.8 (25.2)	.874
Douglas-fir	2 (5)	.015	1.6 (0.4)	.013
Spruce	14 (35)	.103	13.8 (3.2)	.110
Subalpine fir	0 (0)	0	0 (0)	0
Larch	0 (0)	0	0 (0)	0
Ponderosa pine	0 (0)	0	0 (0)	0
Aspen	0 (0)	0	0 (0)	0
Alder	4 (10)	.029	0.4 (0.1)	.003
Total	136 (340)	1.000	125.6 (28.9)	1.000

Site 5

Date established:	March 1978
Location:	2 miles (3.2 km) north of the Polebridge RS
Elevation:	3640 feet (1110 m)
Slope:	level
Aspect:	level

Tree species	Stems per acre (ha)	Relative density	Basal area ft^2/acre (m^2/ha)	Relative dominance
Lodgepole pine	276 (690)	.711	174.0 (39.9)	.837
Douglas-fir	4 (10)	.010	0.4 (0.1)	.002
Spruce	100 (250)	.258	28.6 (6.6)	.137
Subalpine fir	0 (0)	0	0 (0)	0
Larch	0 (0)	0	0 (0)	0
Ponderosa pine	2 (5)	.005	3.6 (0.8)	.017
Aspen	6 (15)	.016	1.4 (0.3)	.007
Alder	0 (0)	0	0 (0)	0
Total	388 (970)	1.000	208.0 (47.7)	1.000

Site 6

Date established:	May 1978
Location:	1 mile (1.6 km) north of the foot of Bowman Lake
Elevation:	5120 feet (1560 m)
Slope:	15-45%
Aspect:	SE

Tree species	Stems per acre (ha)	Relative density	Basal area ft^2/acre (m^2/ha)	Relative dominance
Lodgepole pine	150 (375)	.429	78.2 (17.9)	.317
Douglas-fir	86 (215)	.246	91.2 (20.9)	.370
Spruce	2 (5)	.006	0.2 (0)	.001
Subalpine fir	8 (20)	.022	0.8 (0.2)	.003
Larch	104 (260)	.297	76.2 (17.5)	.309
Ponderosa pine	0 (0)	0	0 (0)	0
Aspen	0 (0)	0	0 (0)	0
Alder	0 (0)	0	0 (0)	0
Total	350 (875)	1.000	246.6 (56.5)	1.000

Site 7

Date established: May 1978

Location: 1 mile (1.6 km) south of the foot of Bowman Lake

Elevation: 4900 feet (1500 m)

Slope: 20-45%

Aspect: NW

Tree species	Stems per acre (ha)	Relative density	Basal area ft^2/acre (m^2/ha)	Relative dominance
Lodgepole pine	372 (930)	.579	134.8 (30.9)	.582
Douglas-fir	158 (395)	.247	37.6 (8.6)	.162
Spruce	40 (100)	.062	23.8 (5.5)	.103
Subalpine fir	0 (0)	0	0 (0)	0
Larch	72 (180)	.112	35.4 (8.1)	.153
Ponderosa pine	0 (0)	0	0 (0)	0
Aspen	0 (0)	0	0 (0)	0
Alder	0 (0)	0	0 (0)	0
Total	642 (1605)	1.000	231.6 (53.1)	1.000

Site 8

Date established:	July 1978
Location:	11 miles (17.7 km) southwest of the Spotted Bear RS (FNF) on the South Fork of the Flathead River
Elevation:	3890 feet (1185 m)
Slope:	level
Aspect:	level

Tree species	Stems per acre (ha)	Relative density	Basal area ft^2/acre (m^2/ha)	Relative dominance
Lodgepole pine	508 (1270)	.646	148.6 (34.1)	.690
Douglas-fir	138 (345)	.176	37.6 (8.6)	.175
Spruce	88 (220)	.112	14.4 (3.3)	.067
Subalpine fir	36 (90)	.046	3.6 (0.8)	.017
Larch	16 (40)	.020	11.0 (2.5)	.051
Ponderosa pine	0 (0)	0	0 (0)	0
Aspen	0 (0)	0	0 (0)	0
Alder	0 (0)	0	0 (0)	0
Total	786 (1965)	1.000	215.2 (49.3)	1.000

APPENDIX B

WOODPECKER DENSITIES ON THE STUDY SITES

Site 1

Transect length: 2485 feet (756.7 m)

Woodpecker species	Areas censused for feeding woodpeckers	
	Strip width ft. (m)	Area censused acres (ha)
Downy	400 (122.0)	28.5 (11.4)
Hairy	400 (122.0)	28.5 (11.4)
Northern Three-toed	520 (158.5)	29.7 (11.9)
Black-backed Three-toed	400 (122.0)	28.5 (11.4)
Pileated	400 (122.0)	28.5 (11.4)

Nesting woodpeckers:

1978:	1979:
1 pr. Downy	1 pr. Downy
1 pr. Hairy	1 pr. Hairy
1 pr. Pileated	2 pr. Northern Three-toed

Strip width: 490 feet (149.2 m)

Area censused: 28.0 acres (11.2 ha)

(continued)

Woodpecker species	Mean densities per 100 acres (40 ha)					
	1977-78 Winter	1978 Breeding season	1978 Nesting pairs	1978-79 Winter	1979 Breeding season	1979 Nesting pairs
Downy	-	7.3	3.6	0	2.0	3.6
Hairy	-	6.6	3.6	7.3	3.9	3.6
Northern Three-toed	-	1.1	0	7.9	8.6	7.1
Black-backed Three-toed	-	0	0	2.9	0.5	0
Pileated	-	0	3.6	0	0	0

Site 2

Transect length: 2500 feet (761.2 m)

Woodpecker species	Areas censused for feeding woodpeckers	
	Strip width ft. (m)	Area censused acres (ha)
Downy	400 (122.0)	22.8 (9.1)
Hairy	400 (122.0)	22.8 (9.1)
Northern Three-toed	400 (122.0)	22.8 (9.1)
Black-backed Three-toed	400 (122.0)	22.8 (9.1)
Pileated	400 (122.0)	22.8 (9.1)

Nesting woodpeckers:

1978: none 1979: none

(continued)

Woodpecker species	1977-78 Winter	1978 Breeding season	1978 Nesting pairs	1978-79 Winter	1979 Breeding season	1979 Nesting pairs
	Mean densities per 100 acres (40 ha)					
Downy	-	0	0	0	0	0
Hairy	-	1.1	0	0	1.6	0
Northern Three-toed	-	7.6	0	2.2	5.4	0
Black-backed Three-toed	-	0	0	0	0	0
Pileated	-	3.2	0	0	0	0

Site 3

Transect length: 2490 feet (758.2 m)

Woodpecker species	Areas censused for feeding woodpeckers: Strip width ft. (m)	Areas censused for feeding woodpeckers: Area censused acres (ha)
Downy	400 (122.0)	23.0 (9.2)
Hairy	400 (122.0)	23.0 (9.2)
Northern Three-toed	400 (122.0)	23.0 (9.2)
Black-backed Three-toed	400 (122.0)	23.0 (9.2)
Pileated	400 (122.0)	23.0 (9.2)

Nesting woodpeckers:

1978: none 1979: none

(continued)

Woodpecker species	Mean densities per 100 acres (40 ha)					
	1977-78 Winter	1978 Breeding season	1978 Nesting pairs	1978-79 Winter	1979 Breeding season	1979 Nesting pairs
Downy	-	-	-	0	0.5	0
Hairy	-	-	-	5.5	1.8	0
Northern Three-toed	-	-	-	6.6	8.8	0
Black-backed Three-toed	-	-	-	0	0	0
Pileated	-	-	-	0	0	0

Site 4

Transect length: 2400 feet (730.8 m)

Woodpecker species	Areas censused for feeding woodpeckers	
	Strip width ft. (m)	Areas censused acres (ha)
Downy	400 (122.0)	22.0 (8.8)
Hairy	460 (140.1)	24.3 (9.7)
Northern Three-toed	600 (182.7)	33.0 (13.2)
Black-backed Three-toed	400 (122.0)	22.0 (8.8)
Pileated	400 (122.0)	22.0 (8.8)

Nesting woodpeckers:

1978:	1979:
3 prs. Northern Three-toeds 1 pr. Black-backed Three-toeds	1 pr. Northern Three-toeds 1 pr. Hairys

Strip width: 950 feet (289.3 m)

Area censused: 52.3 acres (20.9 ha)

(continued)

Woodpecker species	Mean densities per 100 acres (40 ha)					
	1977-78 Winter	1978 Breeding season	1978 Nesting pairs	1978-79 Winter	1979 Breeding season	1979 Nesting pairs
Downy	11.3	1.5	0	1.3	0	0
Hairy	20.8	5.3	0	6.8	4.9	1.9
Northern Three-toed	15.2	13.5	5.1	5.2	5.4	1.9
Black-backed Three-toed	0	1.5	2.5	0	0	0
Pileated	0	0	0	0	0	0

Site 5

Transect length: 2325 feet (708.0 m)

	Areas censused for feeding woodpeckers	
Woodpecker species	Strip width ft. (m)	Area censused acres (ha)
Downy	400 (122.0)	21.3 (8.5)
Hairy	400 (122.0)	21.3 (8.5)
Northern Three-toed	600 (182.7)	32.0 (12.8)
Black-backed Three-toed	400 (122.0)	21.3 (8.5)
Pileated	400 (122.0)	21.3 (8.5)

Nesting woodpeckers:

1978: 1 pr. Black-backed Three-toeds   1979: none

Strip width: 400 feet (122.0 m)

Area censused: 21.3 acres (8.5 ha)

(continued)

Woodpecker species	Mean densities per 100 acres (40 ha)					
	1977-78 Winter	1978 Breeding season	1978 Nesting pairs	1978-79 Winter	1979 Breeding season	1979 Nesting pairs
Downy	6.3	1.4	0	0	0	0
Hairy	1.6	2.8	0	1.9	0.7	0
Northern Three-toed	14.6	5.6	0	2.5	2.7	0
Black-backed Three-toed	4.7	1.4	4.8	0	0	0
Pileated	3.1	0	0	0	0	0

Site 6

Transect length: 2450 feet (746.0 m)

Woodpecker species	Areas censused for feeding woodpeckers	
	Strip width ft. (m)	Area censused acres (ha)
Downy	-	-
Hairy	400 (122.0)	22.5 (9.0)
Northern Three-toed	400 (122.0)	22.5 (9.0)
Black-backed Three-toed	-	-
Pileated	-	-

Nesting woodpeckers:

1978: none 1979: none

(continued)

Woodpecker species	Mean densities per 100 acres (40 ha)					
	1977-78 Winter	1978 Breeding season	1978 Nesting pairs	1978-79 Winter	1979 Breeding season	1979 Nesting pairs
Downy	-	0	0	-	0	0
Hairy	-	1.1	0	-	0	0
Northern Three-toed	-	6.9	0	-	4.9	0
Black-backed Three-toed	-	0	0	-	0	0
Pileated	-	0	0	-	0	0

Site 7

Transect length: 2400 feet (730.8 m)

Woodpecker species	Areas censused for feeding woodpeckers	
	Strip width ft. (m)	Area censused acres (ha)
Downy	-	-
Hairy	400 (122.0)	22.0 (8.8)
Northern Three-toed	400 (122.0)	22.0 (8.8)
Black-backed Three-toed	-	-
Pileated	-	-

Nesting woodpeckers:

1978: 1 pr. Northern Three-toeds   1979: none

Strip width: 400 feet (122.0 m)

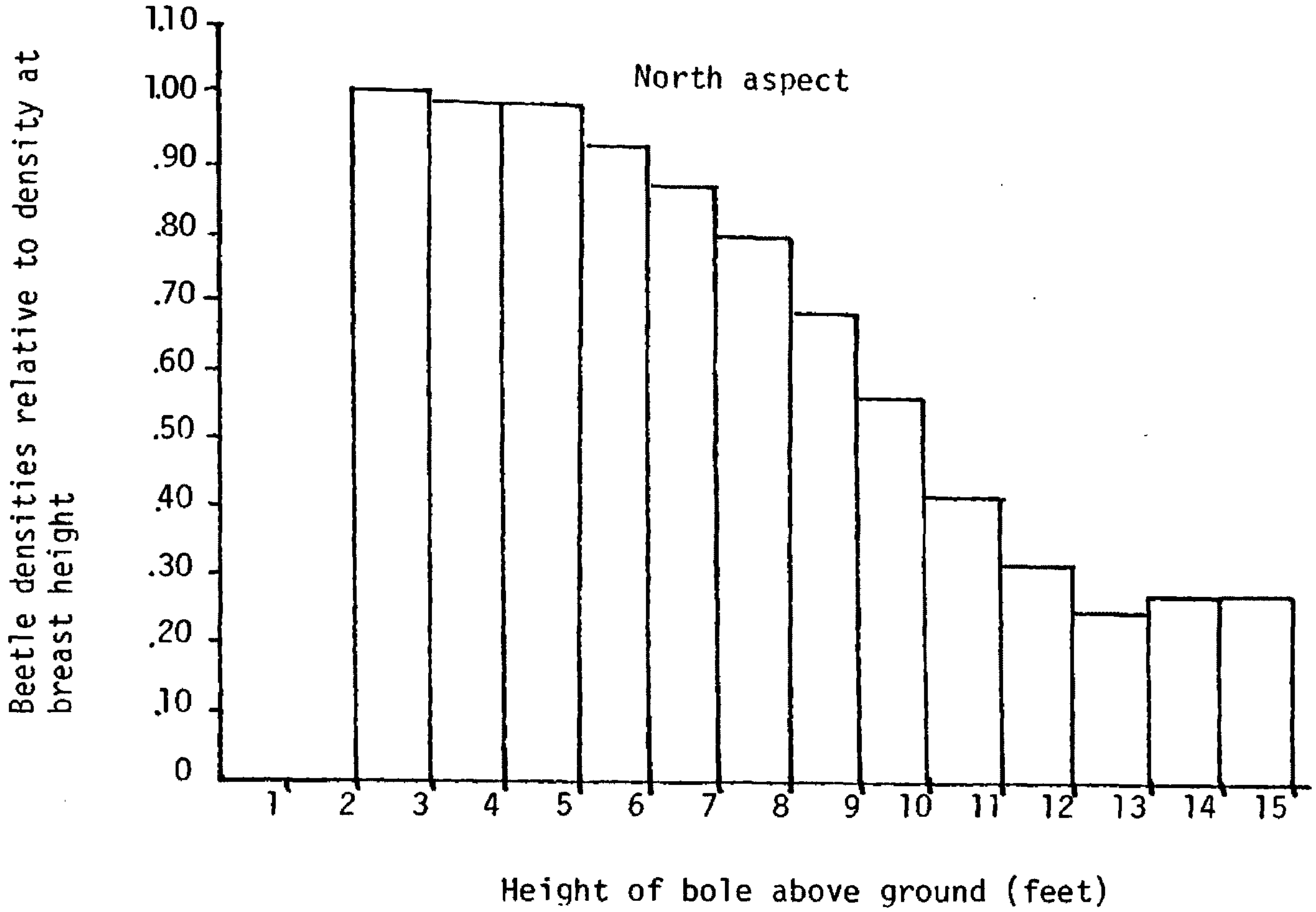
Area censused: 22.0 acres (8.8 ha)

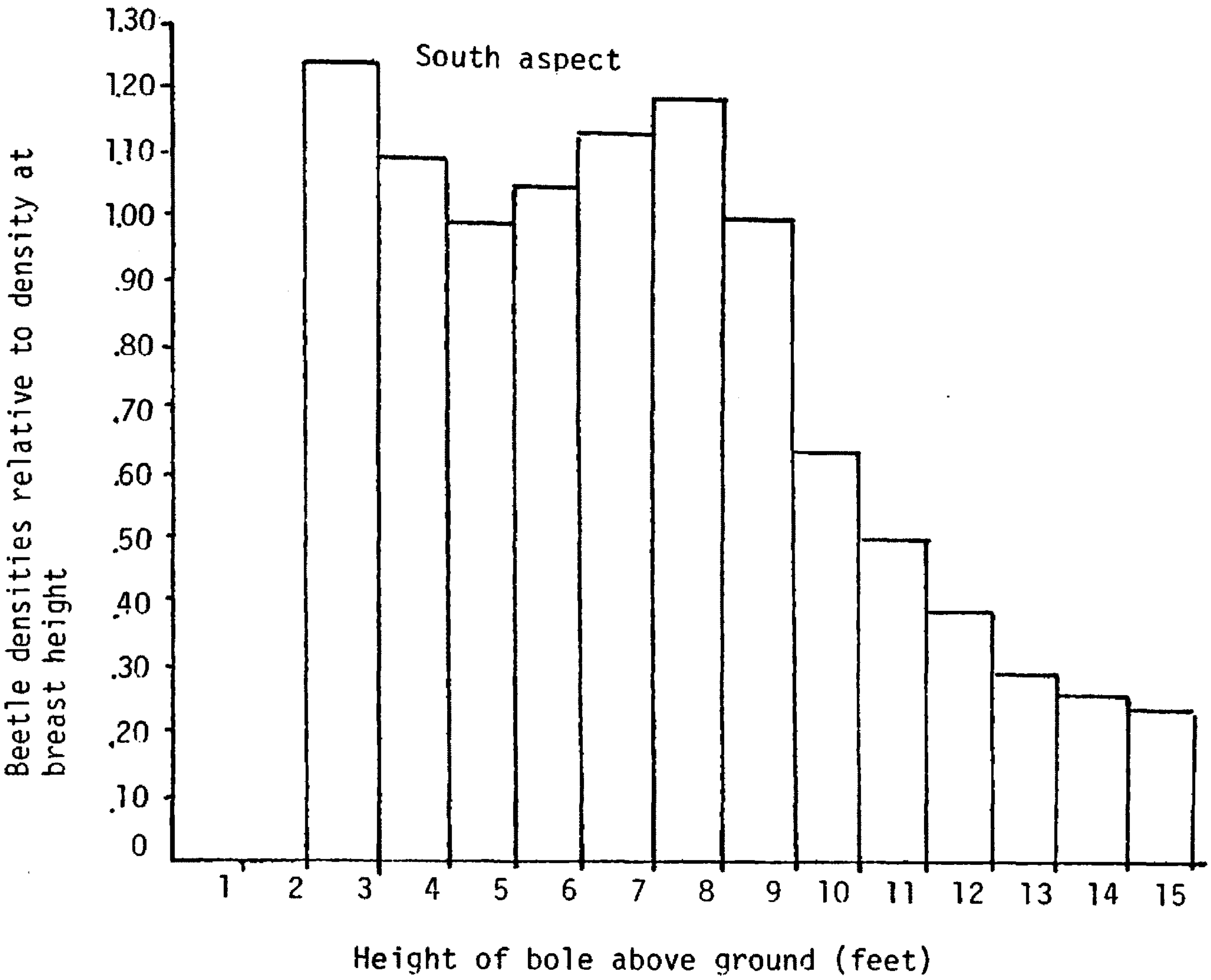
(continued)

Woodpecker species	Mean densities per 100 acres (40 ha)					
	1977-78 Winter	1978 Breeding season	1978 Nesting pairs	1978-79 Winter	1979 Breeding season	1979 Nesting pairs
Downy	-	0	0	-	0	0
Hairy	-	3.9	0	-	1.1	0
Northern Three-toed	-	7.3	4.5	-	4.4	0
Black-backed Three-toed	-	0	0	-	0	0
Pileated	-	0	0	-	0	0

APPENDIX C

BEETLE DENSITIES


North aspect
Beetle densities relative to density at breast height
1.10
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Height of bole above ground (feet)


South aspect
Beetle densities relative to density at breast height
1.30
1.20
1.10
1.00
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
Height of bole above ground (feet)

Total surface area of bark and numbers of successful 1978 brood trees by diameter size class

Diameter size class inches (cm)	Surface area of bark, 2-15 feet ft^2 (m^2)	Successful 1978 brood trees/acre (ha)		
		Site 1	Site 2	Site 3
6-7 (15.2-17.8)	21.1 (1.96)	2 (5)	8 (20)	4 (10)
7-8 (17.9-20.3)	24.4 (2.27)	4 (10)	8 (20)	6 (15)
8-9 (20.4-22.8)	28.5 (2.65)	10 (25)	12 (30)	8 (20)
9-10 (22.9-25.4)	34.1 (3.17)	2 (5)	10 (25)	12 (30)
10-11 (25.5-27.9)	36.3 (3.37)	4 (10)	2 (5)	12 (30)
11-12 (28.0-30.4)	39.6 (3.68)	4 (10)	2 (5)	10 (25)
12-13 (30.5-33.0)	42.9 (3.99)	4 (10)	0 (0)	6 (15)
13-14 (33.1-35.5)	45.4 (4.22)	2 (5)	0 (0)	2 (5)
14-15 (35.6-38.1)	47.9 (4.45)	0 (0)	0 (0)	2 (5)

Mean densities of beetles per square foot (9.3 cm^2) at breast height

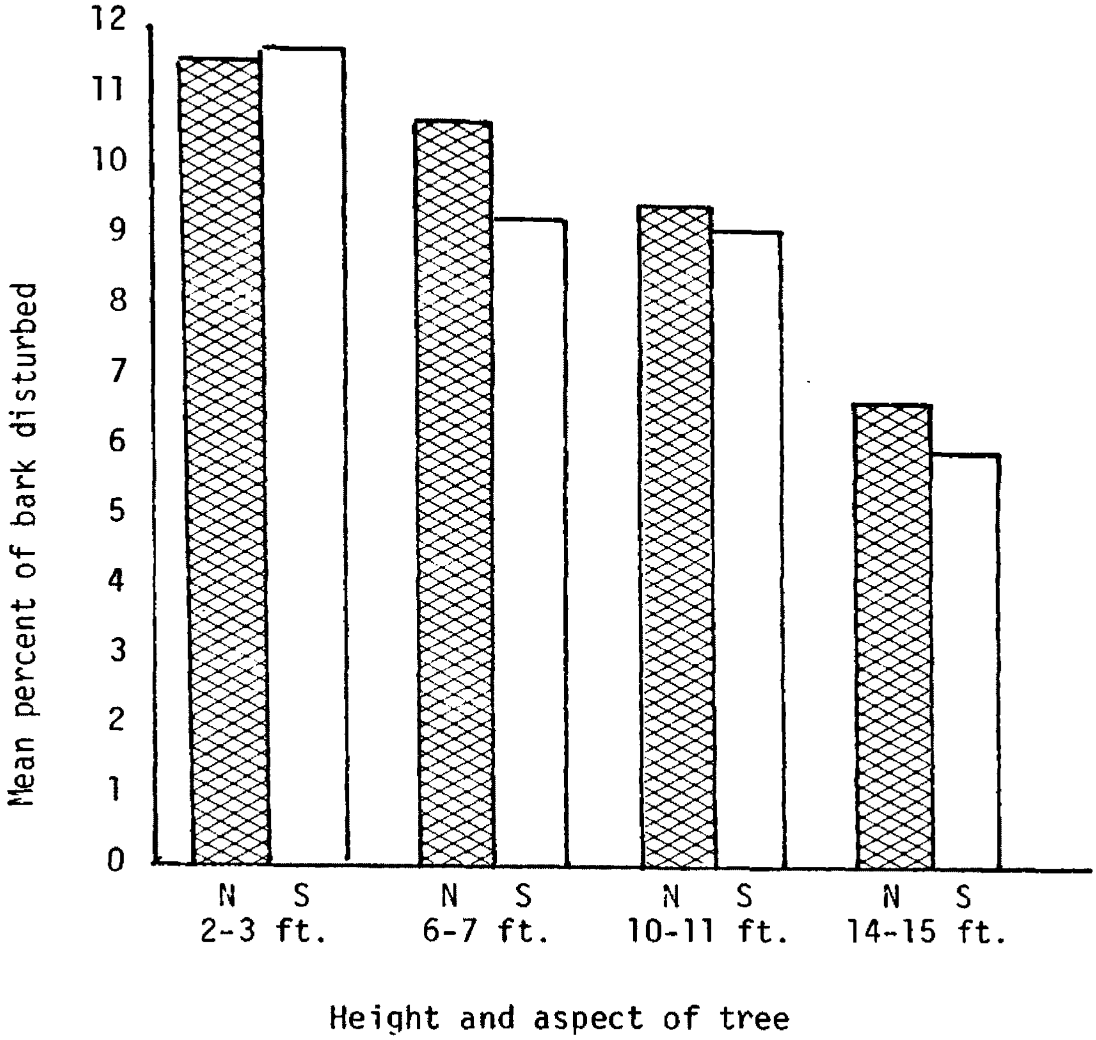
Diameter size class inches (cm)	December 1978		March 1979		May 1979		June 1979		July 1979	
	N	S	N	S	N	S	N	S	N	S
6-7 (15.2-17.8)	129	267	63	52	30	27	2	9	6	5
7-8 (17.9-20.3)	270	216	23	4	18	21	8	12	11	2
8-9 (20.4-22.8)	230	234	56	73	43	38	27	27	7	13
9-10 (22.9-25.4)	324	324	89	5	40	15	31	7	7	4
10-11 (25.5-27.9)	270	225	72	37	53	27	40	27	26	18
11-12 (28.0-30.4)	372	311	108	13	23	36	34	23	18	12
12-13 (30.5-33.0)	258	303	95	99	22	22	24	19	10	13
13-14 (33.1-35.5)	298	260	173	42	18	36	17	21	12	12
14-15 (35.6-28.1)	651	544	306	278	51	24	22	35	19	25

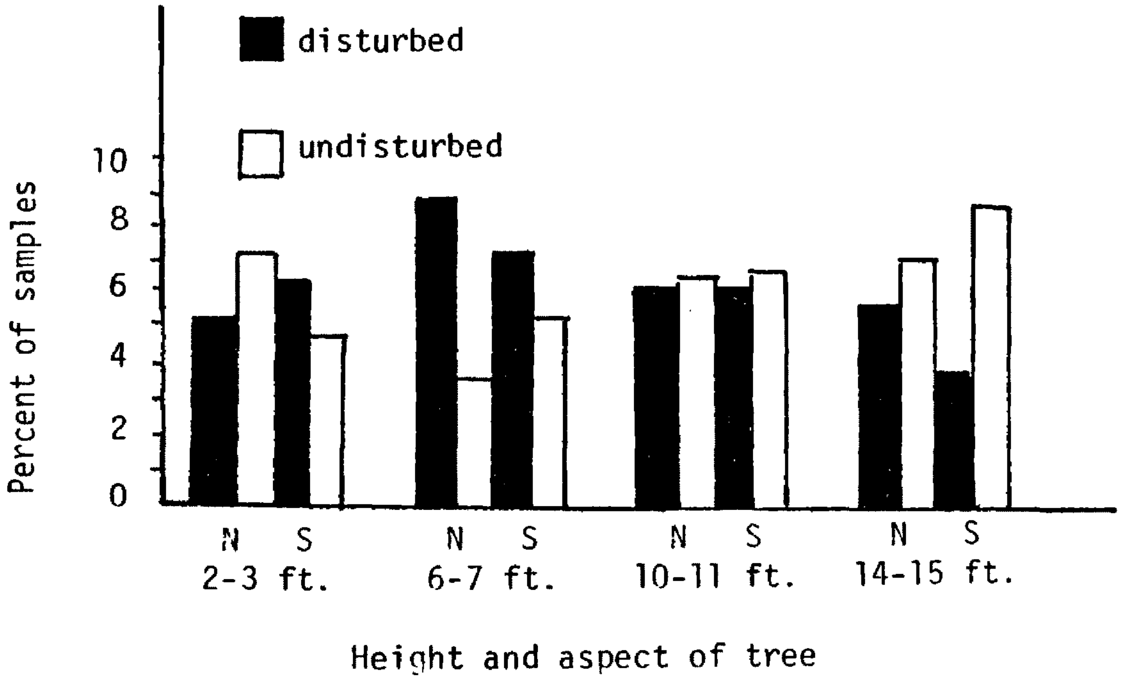
Beetles per tree, 2-15 feet (0.6-4.6 m), by diameter size class

Diameter size class inches (cm)	December 1978	March 1979	May 1979	June 1979	July 1979
6-7 (15.2-17.8)	3,055	853	424	87	80
7-8 (17.9-20.3)	4,162	219	340	176	105
8-9 (20.4-22.8)	4,692	1,319	814	546	208
9-10 (22.9-25.4)	7,833	1,045	640	433	130
10-11 (25.5-27.9)	6,318	1,362	999	847	557
11-12 (28.0-30.4)	9,495	1,578	845	786	414
12-13 (30.5-33.0)	8,593	2,956	669	647	354
13-14 (33.1-35.5)	8,925	3,270	895	617	386
14-15 (35.6-38.1)	20,128	9,874	1,232	988	756

APPENDIX D

BARK DISTURBANCE


Mean percent of bark disturbed
12
11
10
9
8
7
6
5
4
3
2
1
0
N S
2-3 ft.
N S
6-7 ft.
N S
10-11 ft.
N S
14-15 ft.
Height and aspect of tree

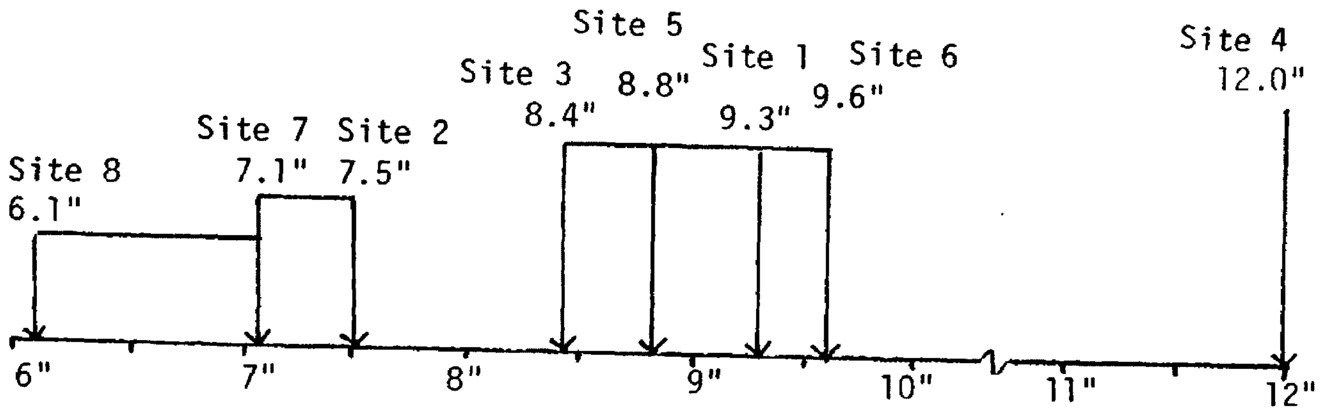

disturbed
undisturbed
Percent of samples
10
8
6
4
2
0
N S
2-3 ft.
N S
6-7 ft.
N S
10-11 ft.
N S
14-15 ft.
Height and aspect of tree

APPENDIX E

STATISTICAL ANALYSES

Statistical Analyses

Differences in mean tree dbh on the study sites (t-test[*])



No significant differences (0.05 level) between:

Sites 7 and 8
Sites 2 and 7
Sites 1, 3, 5, and 6

Mean dbh of Site 4 was significantly different from all other sites.

Differences in beetle densities between north and south aspects (t-test[*]) (Beetles/ft^2 at breast height)

August-December 1978	January 1980-July 1980
North: $\bar{X}$ = 237.4	North: $\bar{X}$ = 77.9
s = 112.7	s = 92.3
South: $\bar{X}$ = 247.5	South: $\bar{X}$ = 64.1
s = 113.3	s = 107.2
df = 24 t = 0.316	df = 35 t = 0.577
No significant difference	No significant difference

---

[*] pp. 116-117. An Introduction to Statistical Methods and Data Analysis by Lyman Ott.

Differences in mean dbhs of woodpeckered and all 1978-attacked lodgepole pine (t-test*)

All 1978-attacked lodgepole pine:	Woodpeckered lodgepole pine:
Mean dbh = 9.1 inches (23.1 cm)	Mean dbh = 9.8 inches (24.9 cm)
s = 1.8 inches (4.6 cm)	s = 2.0 inches (5.1 cm)
n = 116	n = 33

t = 1.812

The difference in mean diameters of all attacked lodgepole pines and those fed on by woodpeckers is significant at the 0.5 level.

Differences in bark disturbance between north and south faces of trees (t-test*)

	North:		South:
North:	$\overline{X}$ = 11.4%	South:	$\overline{X}$ = 10.1%
	s = 19.6		s = 13.8
	n = 33		n = 33

t = 0.3115

There is no significant difference in bark disturbance between the north and south aspects of trees.

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*pp. 116-117. An Introduction to Statistical Methods and Data Analysis by Lyman Ott.