AN ABSTRACT OF THE DISSERTATION OF

Kevin J. Dodds for the degree of Doctor of Philosophy in Forest Science presented on December 1, 2003.
Title: Basic and Applied Studies on Douglas-fir Beetle: Spatial Relationships of Infestations, Lipids and Host Habitat, and Attraction Distances of Pheromone-Baited Traps.

Abstract approved:

Darrell W. Ross

Three studies on Douglas-fir beetle (DFB), *Dendroctonus pseudotsugae*, were conducted to investigate its basic and applied biology. Studies included investigations into the spatial relationship of DFB infestations over multiple years and multiple landscapes, relationships between DFB brood adult lipid levels and position of development along the length of tree boles, and determination of the attraction distances of DFB pheromone-baited traps.

Distances between infestations varied, but in general as DFB populations increased, distance to nearest infestation declined. When DFB populations were epidemic, 88% of within-year infestations were ≤ 1,000 m from other infestations. Between-year average nearest neighbor distances followed a similar pattern to within-year distances. During periods of endemic populations, there was a wide range in distances between infestations. Risk ratings were developed for each ranger district studied as well as an overall average risk rating for the region.

There were no significant differences in brood adult lipid levels in relation to bole position, phloem width, or bark width found in the study on brood position and lipid levels. Numbers of attacks, larval galleries, brood adults, and parasitoids did not differ significantly by tree bole position. Results from this study suggest Douglas-fir beetle does not benefit, in the form of increased lipid levels, from oviposition at different bole positions.

The study on attraction distances of DFB pheromone-baited traps determined distances helpful for management of this bark beetle. Two mark-recapture and one trap interference study were conducted to determine the sampling range and range of attraction of DFB pheromone-baited traps. Mark-recapture studies indicated that most *D. pseudotsugae* were recaptured from distances ≤ 200 m from the pheromone-baited trap. Results of the trap interference experiment provided no insight into the range of attraction of *D. pseudotsugae* pheromones.

Basic and Applied Studies on Douglas-fir Beetle: Spatial Relationships of Infestations, Lipids and Host Habitat, and Attraction Distances of Pheromone-Baited Traps

by
Kevin J. Dodds

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APPROVED:

Major Professor, representing Forest Science

Head of the Department of Forest Science

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State libraries. My signature below authorizes release of my dissertation to any reader upon request.

Kevin J. Dodds, Author

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CONTRIBUTION OF AUTHORS

Dr. Darrell W. Ross was involved in the experimental design and fieldwork associated with chapter 4. Dr. Steve Garman was involved in the study design and data analyses in chapter 2.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

LIST OF FIGURES

LIST OF FIGURES (Continued)

LIST OF FIGURES (Continued)

LIST OF TABLES

LIST OF TABLES (Continued)

DEDICATION

This dissertation is dedicated to the memory of my grandfather, Carroll Doran of Annapolis, Maryland. As an avid Chesapeake Bay and Severn River fisherman, he helped introduce me to the wonders of nature.

Basic and Applied Studies on Douglas-fir Beetle: Spatial Relationships of Infestations, Lipids and Host Habitat, and Attraction Distances of Pheromone-Baited Traps

CHAPTER 1

INTRODUCTION

Kevin J. Dodds

Scolytidae

Bark beetles (Coleoptera: Scolytidae) are important components of forested ecosystems and are found throughout North American forests. Scolytidae influence forest stand dynamics (Veblen et al., 1991; Hadley and Veblen, 1993; Hadley, 1994; Parish et al., 1999), nutrient cycling (Edmonds and Eglitis, 1989), wildlife habitat (Ross and Niwa, 1997), local food web dynamics, and create habitat for other forest invertebrates (Dahlsten and Stephen 1974; Stephen and Dahlsten, 1976; Dodds et al. 2002). Although bark beetles are ecologically important, they often cause economic losses in forest resources. For example, in the United States it has been estimated that over 60% of tree mortality can be attributed to Scolytidae (Anderson, 1960). This dissertation focuses on several aspects of the biology and management of one scolytid, the Douglas-fir beetle (DFB), *Dendroctonus pseudotsugae* Hopk. in the western United States.

Douglas-fir Beetle Biology

While it is found primarily in Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, DFB can successfully colonize freshly felled western larch, *Larix occidentalis* Nutt. (Schmitz and Gibson, 1996). Douglas-fir beetle is univoltine, with brood overwintering as either fully developed adults or as late stage larvae. Brood over-wintering as adults emerge and attack new host material in early spring when temperatures begin to warm. Brood that over-wintered as larvae complete development in the spring and subsequently emerge and attack new host material in early to mid summer. Adult DFB disperse from trees they developed in and attack damaged, freshly downed, or standing Douglas-fir trees. Upon successful attack, host defenses are overwhelmed and parent beetles begin constructing egg galleries and females oviposit eggs along its length. Eggs hatch and brood develop through the summer.

Like many other *Dendroctonus* species, DFB rely on complex chemical cues to attack and overwhelm host trees, and to eventually terminate colonization (Wood, 1982). Aggregation pheromones including frontalin (1,5-dimethyl-6,8-dioxabicyclo [3.2.1] octane) and seudenol (3-methylcyclohex-2-en-1-ol) are necessary for successful attack and colonization of host trees, while the anti-aggregation pheromone MCH (3-methylcyclohex-2-en-1-one) stops attack on trees to avoid overpopulation of the host resource. Host released volatiles also are important factors in the colonization of trees.

Population Biology of Douglas-fir Beetle

Douglas-fir beetle populations are found at a variety of densities. Low density populations usually subsist in downed, damaged, or weakened trees and are often associated with some type of moderate natural disturbance (i.e., small fires, ice storms, windstorms, and associations with root rot). If disturbances are large and available resources are plentiful, DFB populations often increase substantially in an area. Consequently, these high density populations often attack and kill living trees, causing serious economic losses in Douglas-fir forests. In the years following the 1933 Tillamook Fire in Oregon, 200 million board feet of timber were lost to DFB (Chamberlin 1939; Bedard 1950). In addition, outbreaks occurring between 1950 and 1969 in Oregon and Washington caused the loss of 7.4 billion board feet (Schmitz and Gibson, 1996).

Several factors may contribute to fluctuations in DFB populations. Abiotic factors, such as winter temperatures (Johnson, 1967) can affect brood production and survivorship. Drought conditions can also influence the abundance of suitable habitat available (i.e., stressed trees) for DFB. Biotic factors, including predators (Cowan and Nagel, 1965; Zhou et al., 2001), parasitoids (Ryan and Rudinsky, 1962), competitors, and intraspecific competition (McMullen and Atkins, 1961) likely influence brood survival and subsequent population levels.

Douglas-fir Beetle Management

Silvicultural treatments can be used to minimize the impacts of DFB infestation on forest stands (Schmitz and Gibson, 1996). Stand thinning and removal of highly susceptible Douglas-fir, downed or damaged tree material, and DFB-infested trees may help in minimizing local beetle populations and reduce future tree losses. Silvicultural treatments guided by hazard ratings can be especially useful at reducing the susceptibility of a stand to infestation by DFB. Several hazard ratings have been developed for DFB (Randall and Tensmeyer, 1999; Shore et al., 1999; Negron, 1998; Furniss et al. 1981). These hazard ratings consider tree and stand level factors such as average dbh, percent Douglas-fir, stand age, aspect, and other relevant features that influence a stands susceptibility to DFB attack.

Several pheromones have been used in the management of local DFB populations in the western United States. The aggregation pheromones, frontalin and seudenol, are effective at attracting and capturing large numbers of DFB from local populations (Ross and Daterman 1997). Traps baited with these aggregation pheromones plus ethanol removed more beetles from a local population than trap trees, demonstrating their potential efficacy in management programs (Dodds et al., 2000). In contrast, the anti-aggregation pheromone, MCH, has been used to prevent infestation of windthrown timber (McGregor et al., 1984) and to protect high-risk stands and individual trees (Ross and Daterman 1994, 1995a; Ross et al., 2001).

Dissertation Objectives

The objective of this dissertation was to gain a better understanding of the spatial relationship of DFB infestations on landscape scales and to integrate basic and applied studies that would provide insight into factors that may influence dispersal potential and improve existing management techniques. To complete this task, three studies on DFB were conducted.

Analyses were conducted to provide insights into the spatial relationship of DFB infestations over large landscapes and through multiple years. Analyses were accomplished using geographic information systems, USDA Forest Service aerial detection survey maps, and nearest neighbor measurements. Landscape scale studies on the spatial ecology of bark beetles are becoming more common (Gilbert et al., 2003; Wichmann and Ravn, 2001; Gilbert et al., 2001; Gumpertz et al., 2000; Coulson et al., 1999) and one study has been completed on DFB (Powers et al., 1999). However, there has not been a DFB study that investigated the spatial relationship of DFB infestations on multiple landscapes over consecutive years. Research on the spatial relationship of DFB infestations was used to develop risk ratings for interior western forests that should be helpful to natural resource managers facing epidemic populations of this beetle. Patch metrics were described for two ranger districts and provided information on the area affected and number of trees killed. Finally, management implications of this work are also discussed.

The second study in this dissertation focused on how developmental position along the length of a tree bole and host tree characteristics may influence DFB lipid content and subsequent dispersal potential. Several studies have found correlations between lipid levels and bark beetle flight potential (Atkins, 1966; Slansky and Haack, 1986; Jactel, 1993). However, few studies have investigated how host tree characteristics influence lipid levels. To gain a better understanding of the effects of bole position and host tree characteristics, DFB brood adult lipid levels were compared from three heights along the length of infested Douglas-fir trees. Understanding factors that potentially affect DFB dispersal, like position of brood development along a tree bole, could provide insights into the spatial relationships of inter-annual infestations. Such insights could provide information helpful for predicting where infestations may occur.

Pheromone-baited traps provide natural resource managers a tool for managing DFB populations. Douglas-fir beetle pheromones are well studied and optimal pheromone blends have been determined for use in pheromone-baited traps (Ross and Daterman, 1995b). To effectively integrate pheromone-baited traps into management strategies, knowledge of attraction distances of these traps would be helpful. Two concepts, the sampling range and range of attraction, are important in determining the attraction distance of pheromone-baited traps (Wall and Perry, 1987). The sampling range is the greatest distance that insects can be shown to move to a pheromone source in a given time period, while the range of attraction is the greatest distance over which insects can be shown to direct their movements to a pheromone source. The range of attraction consists of only the distance from which insects begin directed movement to the pheromone signal. To determine these two distances, two mark-recapture studies and a trap interference experiment were conducted. Knowledge of attraction distances of pheromone-baited traps and the spatial relationship of existing and new infestations could be helpful in determining placement of traps in a trapping program.

The three studies undertaken in this dissertation contribute important information about the biology and management of DFB in the interior western US. An understanding of the spatial relationship of DFB infestations over large landscapes provides relevant information for natural resource managers that will allow for more effective use of current management techniques. In addition, the spatial analysis of DFB infestations provides information pertinent to the other studies undertaken in this dissertation.

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CHAPTER 2

LANDSCAPE SCALE ANALYSES OF DOUGLAS-FIR BEETLE INFESTATIONS AND THE DEVELOPMENT OF A RISK RATING SYSTEM USING SPATIAL DATA

Kevin J. Dodds, Steven L. Garman, and Darrell W. Ross

Abstract

Spatial relationship of Douglas-fir beetle (DFB), *Dendroctonus pseudotsugae*, infestations were examined over a 13-year period on four USDA Forest Service ranger districts in Idaho, USA. Using aerial detection survey maps and GIS to derive nearest neighbor distances, trends in the proximity of DFB infestations within a single year (*t*), between years (*t + 1*), and between 2 years (*t + 2*) were determined. Nearest neighbor frequency distributions were used to create DFB risk ratings. Patch metrics for DFB infestations (trees killed, area affected) were described on two ranger districts.

When DFB populations were low, average within-year nearest neighbor distances were typically above 1,000 m. As DFB populations increased, average nearest neighbor distances dropped to below 1,000 m. When DFB populations were epidemic, 88% of within-year infestations were ≤ 1,000 m from other infestations. Between-year average nearest neighbor distances followed a similar pattern to within-year distances. Three of the four ranger districts had the highest number of infestations occurring directly adjacent to previous year infestations. All ranger districts had approximately 50% of infestations occurring ≤ 200 m from previous year infestations during epidemic populations. During periods of endemic populations, infestations were found in various distance classes (0 – 5000+ m) from other infestations. Between 2-year average nearest neighbor distances ranged from 133 m to 12,948 m over all ranger districts.

Risk ratings created from between-year nearest neighbors were developed for epidemic DFB populations. On average, there was a 50% chance of an infestation occurring within a radius of 176 m from previous year infestations, 75% chance from within a radius of 517 m, and 90% chance from within a radius of 1,188 m. The between 2-year risk rating determined that there is a 50% chance of infestation

occurring on average within a radius of 249 m, 75% within 627 m, and 90% within 1,332 m from previous year infestations.

Average patch size of infestations on two ranger districts varied from 0.8 ha to 19.7 ha and was negative exponentially related to number of infestations. On the same ranger districts, average number of trees killed per infestation ranged from 4.8 to 124.3 and was also negative exponentially related to number of infestations. As numbers of infestations increased, infestations formed larger patches with an increasing number of trees killed.

Introduction

Douglas-fir beetle (DFB), *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae), is an important component of Douglas-fir, *Pseudotsugae menziesii* (Mirb.) Franco, and mixed conifer ecosystems in western North America. Douglas-fir beetle influences forest structure (Hadley and Veblen, 1993; Hadley, 1994), nutrient cycling (Edmonds and Eglitis, 1989), and wildlife habitat (Ross and Niwa, 1997). In addition, DFB are important components of local food web dynamics. Although Douglas-fir beetle are an integral part of Douglas-fir forest ecosystems, epidemic populations can cause tree mortality that conflicts with forest management objectives. Timber losses, reduction or loss of wildlife habitat, and diminished aesthetic values of forests often coincide with epidemic populations of Douglas-fir beetle.

Interest in landscape scale studies of bark beetles is increasing. Studies on the spatial ecology of *Dendroctonus micans* (Kugelann) have been conducted at the regional (Gilbert et al., 2003) and smaller local scales (Gilbert et al., 2001). Population behavior of *Ips typographus* (L.) after a windstorm was investigated using GIS (Wichmann and Ravn, 2001). Gumpertz et al. (2000) used regression techniques accounting for spatial and temporal autocorrelation to study *Dendroctonus frontalis* in the southeastern US. Landscape structure and its affect on *D. frontalis* populations were investigated by Coulson et al. (1999). Powers et al. (1999) investigated spatial patterns of DFB on a landscape scale and factors that influence population levels in Oregon. While previous work has investigated the spatial ecology of DFB on a single landscape, more research is needed to gain a better understanding of the spatial and temporal relationship of DFB infestations on landscape scales. Knowledge of landscape-scale patterns of DFB infestations would provide important information to aid in the management of epidemic populations and contribute to a better understanding of the spatial ecology of this species.

Spatial ecology is not a new concept in bark beetle research as several DFB studies have investigated this species at various spatial scales. Spatial distribution of attacks (Hedden and Gara, 1976), spatial relationship of colonization along the length of tree boles (Furniss, 1962), stand level distribution of host tree mortality (Negron et al., 2001), and landscape level (i.e., Oregon) studies (Powers et al. 1999) have been completed on DFB. However, there is still a need for research that focuses on the spatial relationship of annual DFB infestations over large landscapes and multiple years.

Information gleaned from studies on the spatial and temporal relationships of DFB infestations could be incorporated into the development of a risk rating. A risk rating used in conjunction with a currently implemented DFB hazard rating system (Randall and Tensmeyer 1999; Dodds et al., 2003) would be useful for managing DFB in the interior western US. While hazard and risk have often been used interchangeably, there are distinct differences between the two terms and how they relate to insect pest management.

Hazard is a measure that projects where damage may occur and the severity that could be expected given certain stand criteria (i.e., relates to stand conditions) (Hicks et al. 1987). Hazard ratings or stand susceptibility factors are easier to develop and have been created for several bark beetle species (Reynolds and Holsten 1994; Amman and Anhold 1989; Hicks et al. 1980). Risk is the probability or chance that an outbreak event will occur in a given area (i.e., relates to insect population levels in addition to hazard). Risk ratings are more difficult to quantitatively define because they relate to dynamic and spatially variable insect populations.

The objective of this research was to use a retrospective approach to investigate the spatial relationship of DFB infestations over large landscapes and multiple years in the interior western US and to use results in the development of a DFB risk rating. Patch metrics on DFB infestations also were described.

Methods

Study Areas

Four USDA Forest Service ranger districts were used to describe the spatial relationship among DFB infestations (Figure 2.1). These ranger districts included Priest Lake (154,276 ha), Salmon River (142,716 ha), St. Joe (312,222 ha), and Bonners Ferry (194,383 ha). These ranger districts were selected based on the availability of data and the degree of DFB activity occurring over time.

GIS Data Description

GIS data consisted of digitized aerial detection surveys (scale = 1:100,000) conducted from 1989 to 2001, and contained locations of individual DFB infestations in a polygonal format. Maps also contained information on number of trees killed per polygon. Aerial detection surveys were overlayed on ranger district shapefiles that provided spatial boundaries to each area. Because it usually takes up to a year for DFB-killed trees to change to a color detectable by aerial observers (Belluschi and Johnson, 1969), aerial detection survey maps actually represent trees killed the year before surveys are taken (i.e., 1988-2000). Analyses were completed using ArcView 3.2 (ESRI, Redmond, USA).

The term infestation is used to describe a forested patch affected by DFB. Each infestation was mapped by aerial observers to estimate tree mortality occurring within spatially discrete patches. Tree mortality caused by DFB within each infestation varied from only a few trees to large numbers of trees that were in close proximity to one another. The minimum grain of an infestation on the aerial detection survey maps is 0.8 ha.

Nearest Neighbor Measurements

Distances to the first nearest neighbor were measured for all infestations that occurred on each ranger district. Nearest neighbor distances were measured on infestations occurring within the same year (t), between consecutive years (t + 1) and between a 2-year period (t + 2). Hereafter, these combinations will be referred to as within-year, between-year, and between 2-year nearest neighbor distances. Because data were polygons, nearest neighbor distances were measured from the nearest edge of one polygon to the nearest edge of another. To conserve data, polygons lying outside the sampling area were used as nearest neighbors to those within the sampling area when they were nearest neighbors. Nearest neighbors of polygons lying outside the boundary, however, were not determined. Descriptive statistics (mean, SE, minimum, maximum, 95% CL) were determined for all within-year, between-year, and between 2-year distances. Nearest neighbor frequency distributions were plotted to more thoroughly investigate the spatial relationships among DFB infestations. Frequency distributions were plotted using 200 m distance classes. For example, the 0 distance class included all infestations directly touching another infestation, while the 200 m class included all distances between 1-200 m.

Two districts were chosen to illustrate the frequency distributions of within-year nearest neighbors. However, between-year nearest neighbor frequency distributions for the four ranger districts are included because of their value to natural resource managers. Between 2-year frequency distributions from two ranger districts showing four combinations of years are also included.

Development of Risk Rating System

Information from between-year and between 2-year nearest neighbor distances were used to develop a DFB risk rating system. Between 2-year measurements were used because trees take up to a year to fade before they are detected from aerial surveys. Consequently, by using the between 2-year measurements time is allowed for managers to fly aerial surveys, map the infestations, and have a year to implement management strategies. If managers know the location of a DFB infestation, or as detection technology advances, the between-year risk rating system could be used.

Percentiles for nearest neighbor distances were determined for each combination of years as the basis for developing the risk rating system. From these percentiles, the distance at which 50%, 75%, and 90% of infestations occurred were determined. These distances were considered to represent the radii for a circular area surrounding a previous year infestation within which there was a 50%, 75%, or 90% chance of an infestation occurring the following year.

To determine the between-year risk rating distances, two between-year combinations from each ranger district were selected. Between-year combinations were selected based on the presence of high or expanding DFB populations. An average risk model that could potentially be used in other areas in Idaho was developed by averaging radii distances of the four ranger districts used in this study. Only one 2-

year period was used to create the between 2-year risk rating because of data limitations (i.e., populations were high for only 3-4 years).

Patch Analysis

Two ranger districts were selected to investigate two landscape metrics over the 13-year period: average infestation size and average number of trees killed. Frequency distributions of hectares affected and number of trees killed were plotted for each ranger district. Relationships between the number of infestations and mean number of trees and hectares in infestations were also determined.

Results

The patterns in number of DFB infestations occurring over the 13-year period were similar for the four ranger districts (Figure 2.2). Infestation numbers were low on all ranger districts between 1992 and 1996. Numbers of infestations increased significantly on the Salmon River Ranger and St. Joe Ranger Districts in 1997 and on the Priest Lake and Bonners Ferry Ranger Districts in 1998. Trends in hectares affected (Figure 2.3) and number of trees killed (Figure 2.4) paralleled trends in infestation numbers.

Nearest Neighbor Measurements

Within-year

The average nearest neighbor distances on Priest Lake Ranger District are shown in Table 2.1. From 1988-1997, the average nearest neighbor distance was less than 1,000 m in only one year, while the average nearest neighbor distances were less than 500 m each year from 1998-2000. When DFB populations were low, there was no distinct pattern to the nearest neighbor frequency distributions. As DFB populations increased, more infestations occurred in smaller distance classes and the highest number of infestations was always in the 400 m distance class (Figure 2.5).

The average nearest neighbor distances on Bonners Ferry Ranger District were similar to Priest Lake Ranger District. Average nearest neighbor distances were greater than 1,500 m during 1988-1997, and dropped below 750 m during 1998-2000 (Table 2.2). Overall average nearest neighbor distances ranged from 607 m to 8,957 m.

Average nearest neighbor distances on Salmon River Ranger District were above 1,000 m during the period of 1988-1996, and dropped below 700 m during the next 4 years (Table 2.3). Nearest neighbor distances among infestations were highly variable when populations were low (Figure 2.6). As DFB populations increased, the majority of infestations were within 1,200 m of their nearest neighbor, although a small number of infestations were farther apart.

St. Joe Ranger District nearest neighbor distances varied more than other ranger districts. Average nearest neighbor distances were below 900 m in 1988-1989, and then increased and remained relatively high until 1997-2000 (Table 2.4). For the 13-year period, average nearest neighbor distances ranged from 571 m to 5,933 m.

Combining data from the four ranger districts (N = 52), there was a strong relationship ($r^2 = 0.79$) between number of infestations and the average nearest neighbor distance (Figure 2.7).

Between-year

Because between-year nearest neighbor distances had a more obvious direct applied use, details of results from each ranger district are included. Average nearest neighbor distances were over 1,000 m for the period of 1988-1989 to 1996-1997 on Priest Lake Ranger District, while they dropped below 600 m for 1997-1998 to 1999-

2000 (Table 2.5). Frequency distributions of nearest neighbor distances are shown in Figure 2.8. Most infestations occurred >5,000 m from previous year infestations in five of the twelve year combinations. In the 1997-1998, 1998-1999, and 1999-2000 year combinations, highest number of infestations occurred directly adjacent (i.e., 0 distant class) to previous year infestations. In 1998-1999, 63% of infestations occurred at distances of ≤ 200 m, 77% ≤ 400 m, and 90% at distances ≤ 1,200 m from previous year infestations. In 1999-2000, 50% of infestations occurred at distances ≤ 200 m, 76% ≤ 600 m, and 91% ≤ 1,400 m.

Average nearest neighbor distances on Bonners Ferry Ranger District were similar to those on Priest Lake Ranger District. From 1988-1989 to 1996-1997, average nearest neighbor distances were above 2,000 m (Table 2.6). Average nearest neighbor distances dropped to below 800 m during the period 1997-1998 to 1999-2000. Frequency distributions of nearest neighbor distances are shown in Figure 2.9. Six years had the highest number of infestations occurring in the >5,000 m class. The 1998-1999 and 1999-2000 combinations had the highest number of infestations directly adjacent to previous year infestations. In 1998-1999, 49% of infestations occurred within 200 m from a previous year infestation, while 72% were ≤ 600 m and 91% were ≤ 1,400 m from previous year infestations. Similar patterns were found in 1999-2000, with 48% of infestations occurring within 200 m, 71% within 600 m, and 90% within 2,000 m from previous year infestations.

With the exception of the 1996-1997 and 1997-1998 year combinations, Salmon River Ranger District average nearest neighbor distances were above 1,400 m (Table 2.7). Distances ranged from 397 m to 7,172 m. Nearest neighbor frequency distributions for the twelve between-year combinations are shown in Figure 2.10. Only four years had the highest number of infestations in the > 5,000 m class. Between-year 1997-1998 and 1998-1999, the largest number of infestations occurred directly adjacent to previous year infestations. In 1997-1998, 54% of infestations were ≤ 200 m, 79% were ≤ 600 m, and 90% were ≤ 1,200 m from previous year infestations.

Average nearest neighbor distances on St. Joe Ranger District followed a pattern similar to Bonners Ferry and Priest Lake Ranger Districts (Table 2.8). From 1988-1989 to 1996-1997, average nearest neighbor distances were over 1,000 m. During the years 1997-1998 to 1999-2000, average distances dropped to below 850 m. The highest number of infestations was in the > 5,000 m distance class for four years (Figure 2.11). Two periods with high levels of DFB activity occurred on St. Joe Ranger District, 1988-1991 (4 years) and 1997-1999 (3 years). Nearest neighbor distances from 1988-1989, 1989-1990, and 1990-1991 had similar patterns with 50% of infestations occurring ≤ 800 m and 75% occurring between 1,400 and 2,800 m from previous year infestations. The 1991-1992 combination differed, with only 26% of infestation occurring at distances ≤ 3,200 and the large majority of infestations occurring > 5,000 m from previous year infestations. In 1997-1998, 68% of infestations occurred ≤ 200 m, with 82% and 91% occurring at 400 m and 600 m respectively, from previous year infestations. In 1998-1999, 48% of infestations occurred ≤ 200 m, 76% ≤ 600 m, and 91% ≤ 1,200 m from previous year infestations. In 1999-2000, 57% of infestations occurred ≤ 600 m, 78% ≤ 1,200 m, and 90% ≤ 2,200 m from previous year infestations.

Between 2-year

Priest Lake and Bonners Ferry Ranger Districts had similar average nearest neighbor distance patterns (Table 2.9 and Table 2.10). With the exception of one year on Bonners Ferry Ranger District, both districts had average nearest neighbor distances over 1,979 m for the period 1988-1990 to 1993-1995. From 1996-1998 to 1998-2000, average nearest neighbor distances were below 829 m on Priest Lake and Bonners Ferry Ranger Districts. Frequency distributions for four 2-year combinations on Priest Lake and Bonners Ferry Ranger Districts during periods of expanding DFB populations are shown in Figures 2.12 and 2.13. Only limited activity occurred in the 1995-1997, 1996-1998, and 1997-1999 years on both districts. In the 1998-2000 combination, highest number of infestations occurred directly adjacent to previous year infestations. Eighty percent of infestations were ≤ 1,000 m on Priest Lake and Bonners Ferry Ranger Districts.

Salmon River Ranger District had average nearest neighbor distances over 1,400 m for all but two years (1995-1997, 1996-1998) (Table 2.11). Distances ranged from 353 m to 5,303 m. Salmon River Ranger District nearest neighbor frequency distributions are shown in Figure 2.14. Salmon River Ranger District had high numbers of infestations occurring directly adjacent to previous infestations in 1997-1999, but the highest number of infestations was found in the > 5,000 m distance class. In the 1998-2000 combination, highest number of infestations was also found in the > 5,000 m distance class.

Between 1988-1990 to 1996-1998, St. Joe Ranger District average nearest neighbor distances ranged from 1,144 m to 6,560 m (Table 2.12). In 1997-1999 and 1998-2000, distances were 245 m and 807 m respectively. St. Joe Ranger District frequency distributions are shown in Figure 2.15. Low DFB activity occurred during the 1995-1997 and 1996-1998 combinations, but the 1997-1999 combination had highest number of infestations found in the 200 m distance class with most infestations occurring below 600 m. The 1998-2000 year combination had highest numbers of infestations in the 200 m and 400 m distance classes.

Development of Risk Rating System

Two-year combinations of high DFB populations were used to develop between-year risk ratings for each ranger district and an overall average risk rating system (Table 2.13). Over the two time periods chosen for each ranger district, all four districts had a 50% chance of an infestation occurring within a radius of 249 m from previous year infestations, a 75% chance that an infestation would occur within a radius of between 272 and 696 m, and a 90% chance of an infestation occurring within a radius of between 578 and 1926 m. For the overall average risk rating system, radii were 175.8 m, 516.5 m, and 1187.5 m, respectively, for the 50, 75, and 90% risk categories.

Only one 2-year period from each ranger district was used to determine the between 2-year risk rating (Table 2.14). The radii associated with a 50%, 75%, and 90% chance of an infestation occurring were ≤ 415 m, 319-964 m, and 571-2644 m, respectively. The overall average radii were 249.3 m, 626.8 m, and 1332 m, for the 50%, 75%, and 90% risk categories, respectively.

Patch Analysis

There was a positive exponential relationship ($r^2 = 0.65$) between the number of infestations occurring per year and average size of infestations on the Priest Lake and Salmon River Ranger Districts (Figure 2.16). There was also a positive exponential relationship ($r^2 = 0.73$) between the number of infestations per year and average number of trees killed in an infestation (Figure 2.17). Patch metrics associated with Priest Lake and Salmon River Ranger Districts are shown in table 2.15. Priest Lake

Ranger District infestation size ranged from 0.8-19.7 ha, with between 4.7 and 124.3 trees killed per infestation. Frequency distributions of numbers of hectares affected and number of trees killed on Priest Lake Ranger District are shown in Figure 2.18 and 2.19, respectively.

Salmon River Ranger District average infestation size ranged from 0.96-9.7 ha, with an average of 7.2 to 90.5 trees killed per infestation. Frequency distributions of number of hectares affected by year for Salmon River Ranger District are shown in Figure 2.20. For every year, the largest proportion of infestations were less than 1 ha. As populations of DFB increased, more infestations had larger areas affected by beetles. Most infestations consisted of between 5-10 trees for all years (Figure 2.21). The numbers of trees killed per infestation increased with increasing DFB population density.

Discussion

Douglas-fir beetle is an important bark beetle found throughout the western United States. Endemic populations are important contributors to ecosystem processes, but epidemic populations often cause serious economic losses to timber resources. While several management alternatives exist for DFB populations (Schmitz and Gibson, 1996; Ross and Daterman, 1995, 1997; Dodds et al. 2000; Ross et al., 2001), a better understanding of the temporal and spatial patterns of DFB infestations may increase the effectiveness of current management techniques.

Population Trends

Overall population trends were similar among the four ranger districts. On Priest Lake, Salmon River, and Bonners Ferry Ranger Districts populations seemed to be declining before 1988, remained low and then started to increase between 1997 and

1998. St. Joe followed a similar pattern except relatively high numbers of infestations occurred between 1988-1991. In general, populations were low for 5-10 years and then rapidly increased and remained high for 3 to 4 years with declining but relatively high populations occurring during the last two years. Number of hectares affected and trees killed followed similar patterns, with numbers lower in the early-mid 1990's and increasing in 1997 or 1998.

Endemic DFB populations typically survive in downed wood or injured or stressed trees. If large-scale forest disturbances occur and large numbers of suitable hosts become available, DFB populations can increase substantially and then attack and overwhelm apparently healthy living trees in subsequent years. This behavior is also common in other bark beetle species (Wermelinger et al., 1999; Schroeder and Lindelöw, 2002; Schroeder and Lindelöw, 2003). In Oregon, epidemic DFB populations were correlated with windstorm events and drought (Powers et al., 1999). Widespread ice storms occurred during winter 1996-1997 over large parts of Idaho and likely were responsible for the switch from endemic to epidemic populations that occurred in 1997-1998. This area also suffered droughts in the late 1990's likely rendering Douglas-fir more susceptible to DFB attack.

Nearest Neighbor Measurements

Within-year

For most years, as numbers of infestations increased average within-year nearest neighbor distance decreased following a negative exponential relationship. When infestation numbers were between 0-100, average nearest neighbor distances were usually greater than 1,000 m. When there were over 100 infestations per year, average nearest neighbor distances dropped below 1,000 m. Two biological factors could help explain within-year distributions of DFB infestations. First, areas containing DFB susceptible trees are likely spatially grouped (Negron et al., 2001) because of past forest management history or other factors (e.g., aspect, pathogens, etc.) that make trees susceptible to bark beetles. Second, pheromone behavior in forests likely influences DFB over large areas. The distance from which trees undergoing attack and providing a source of semiochemicals attract DFB is unknown. However, DFB pheromone-baited traps attracted beetles from up to 400 m, and larger proportions of those released from distances less than 200 m (Dodds and Ross, 2002). It seems likely natural pheromone dispersal emanating from an infestation is at least equivalent to pheromone-baited traps and can lure DFB into large areas surrounding initial infestations. Consequently, in years of high DFB populations, more beetles would be attracted to stands undergoing attack and ultimately shift to other host trees within stands. Powers et al. (1999) found beetle killed patches were clustered at a scale of 1 km and 4 km. Results from this study further support the claim that at epidemic levels, DFB infestations are typically found less than 1 km away from one another. In our study, 88% of within-year infestations were within 1000 m of other infestations. Similarly, Franklin et al. (2000) determined that *Ips typographus* (L.) (Coleoptera: Scolytidae) trap catches were spatially autocorrelated up to distances of 265 m.

Between-year

Between-year nearest neighbor distances provided information on the relationship of DFB infestations from one year to another. However, it is important to note that DFB were not followed from one infestation to the next and results from this research do not relate to beetle movements between infestations. Therefore, this research does not provide information about DFB dispersal behavior or the distances traveled by beetles after emerging from a previous year infestation before colonizing a new host.

When DFB populations were low, there were few distinct patterns found to between-year nearest neighbor distances on ranger districts or between years. On all ranger districts, between four and five years of sampling showed the highest number of infestations occurring in the > 5,000 m class. During years of low populations, infestations occurred in various distance classes, indicating infestations were spread throughout the landscape and rarely grouped together.

As populations increased, several patterns of between-year nearest neighbor distances were found. Frequency distributions of between-year nearest neighbors became skewed towards the right with fewer infestations occurring at larger distances. The four ranger districts had almost one half of all infestations occurring at or below 200 m from previous year infestations. Three of the ranger districts had the highest number of infestations occurring directly adjacent to previous year infestations.

In a two-year study following *Ips typographus* populations after a windstorm event, Wichmann and Ravn (2001) found 80% of new attacks occurred within 250 m of old attacks and all attacks were below 650 m from previous years infestations. We also found a large proportion of infestations occurring directly adjacent to or very near previous year infestations. Douglas-fir beetle vary in their dispersal potential, with some beetles only able to fly short distances, while others can fly long distances (Atkins, 1966). Consequently, beetles developing in host trees may have encountered conditions that led to limited energy stores and shorter dispersal distances and therefore attacked trees adjacent to previous year infestations. Temperatures also influence flight behavior and may influence dispersal behavior (Atkins, 1959). Unless growing conditions, stand management practices, climate or drought conditions, or other factors that might alleviate tree susceptibility have changed, unattacked trees within the same area where DFB is present would likely remain susceptible to attack the following year.

Between 2-year

Between 2-year nearest neighbors were investigated because Douglas-fir trees take up to a year to fade to a color detectable by aerial observation. Therefore, these distances could be useful for natural resource managers who are relying on aerial detection survey maps to detect infestations and thus working with a one-year information lag. While average between 2-year nearest neighbor distances were determined and provide estimates of distances between infestations, frequency distributions provided limited information because populations stayed high for only three to four years. If populations are increasing and information on DFB infestations location is only available through aerial detection survey maps, then average nearest neighbor distances may be useful to natural resource managers.

Data Limitations

While aerial detection survey maps contain important information on forest insects and disease, important considerations arise when using these maps in a quantitative study. First, there is some inherent error associated with mapping the location of infestations from above while flying over an area. Most aerial observers are highly trained and have conducted these surveys for numerous years within the same region. Consequently, we believe these estimates are sound and useful for describing spatial relationships of DFB infestations. Second, estimates of area affected by DFB are influenced by beetle population levels. For example, in areas where a number of small infestations occur adjacent to one another, aerial mapping often groups these infestations as a single polygon with an estimate of trees per area killed. Therefore, while number of trees remains a dependable estimate, it is important to acknowledge that estimates of acres affected is higher than the actual area of trees killed and infested by DFB. In instances where multiple infestations are grouped as one polygon, nearest neighbor distances are likely overestimated for that polygon because the nearest infestation is grouped within the same polygon. Finally, aerial detection survey maps locate infestations that occur in standing timber, they do not detect DFB populations that occur in downed wood. Therefore, these maps provide a conservative estimate of DFB populations, especially in years where there are large-scale forest disturbances that provide downed host material for beetles.

While forest stand conditions were not considered in the current study, various stand and individual tree level characteristics affect a trees susceptibility to DFB attack (Furniss et al., 1981; Negron, 1998; Shore et al., 1999). Also, the distribution of susceptible host trees over a landscape influences bark beetle distribution. However, at epidemic levels bark beetles can overcome the defenses of most host trees by force of numbers. Because of difficulties associated with determining individual tree susceptibility over large spatial and temporal scales, it was not feasible to consider potential host tree distribution when determining nearest neighbor distances. Therefore, distances to nearest available host patch were not determined and it was not possible to assess DFB resource use in the context of available resources on the landscape. Knowledge of the distribution of available DFB susceptible habitat would have enhanced these analyses and improved estimates of distance between infestations. Future research should concentrate on estimating available and suitable DFB habitat and incorporating this information into determining nearest neighbor distances in a more realistic setting.

Development of Risk Rating System

Risk rating systems are important tools for management of bark beetles and have been developed for several species (Weslien et al., 1989; Paine et al., 1985; Shore and Safranyik, 1992). However, use of aerial detection survey maps, GIS, and nearest neighbor estimates represents a novel approach to creating a risk rating system. While several years of data were available to develop between-year risk ratings, only limited data for between 2-year risk ratings were available. Therefore, the results and subsequent between 2-year risk rating may not be as strong as the between-year risk model. Also, because populations of DFB remained high for 3-4 years, the between 2-year risk rating has limited application if this is typical of most outbreaks.

The risk rating system was developed for use in years when DFB populations are high or expanding. Because some level of DFB activity is to be expected regardless of stand conditions, it is not appropriate to use this risk rating system when populations are low and landscapes are large. Natural resource managers should expect some level of DFB activity regardless of population levels. However, as populations increase, the risk ratings (Table 2.13 and 2.14) provides general guidelines as to where infestations are likely to occur in the coming year relative to previous year infestations. While some of the risk rating radii are over 1,000 m and represent large areas that could potentially include DFB infestations, the lower percent risk rating categories cover areas more manageable for natural resource managers. Natural resource managers could minimize the at-risk area by combining these risk rating radii with the Randall and Tensmeyer (1999) hazard rating system to prioritize management activities in high risk, high hazard areas or areas of special concern (e.g., wildlife habitat, old-growth reserves, riparian buffers, recreational sites, etc.). If large-scale natural disturbances occur, the risk ratings could provide general guidelines for protecting surrounding forests two years after the event.

Patch Analysis

As infestation numbers increased, there was a positive exponential relationship with the average size of DFB infestations. This relationship indicates that not only are infestation numbers growing, but that there are also larger areas affected by DFB activity in years when epidemic populations occur. Average infestation size was generally smaller on Priest Lake Ranger District compared to Salmon River Ranger District. Frequency distributions show that during years of low DFB populations, most areas affected were ≤ 1 ha. However, as populations increased there were more infestations distributed over various size classes of area affected. This pattern was consistent over all of the ranger districts. Estimates of area affected must be viewed cautiously because of methodological techniques used in aerial detection surveys. Individual tree kills within close proximity to one another will be grouped as one infestation in larger polygons during periods of high DFB populations. Consequently, estimates of area affected are likely higher during DFB outbreaks.

As with area affected, there was a positive exponential relationship between number of infestations and average number of trees killed per infestation. This suggests that as DFB populations increase, not only do the number of infestations increase, but also the average number of trees killed per infestation. For most years, average numbers of trees per infestation were higher on Salmon River Ranger District than on Priest Lake Ranger District. Frequency distributions of trees killed on Priest

Lake Ranger District show most infestations occurring in classes with less than 20 trees killed, with the majority being 10 trees or fewer, during years of low populations. As with area affected, as populations increase infestations are distributed more evenly among classes of trees killed. In comparison, Salmon River Ranger District had infestations with various numbers of trees killed occurring even at low populations. As populations increased, patterns were similar to those occurring at high population levels on Priest Lake Ranger District.

Management Implications

Several results from this study could be helpful for natural resource managers attempting to manage DFB populations. First, managers can use the risk rating system developed from percentiles of nearest neighbor distances to protect areas where DFB infestations are expected to interfere with management objectives. If managers are aware of current infestations, they can use between-year risk models to determine where beetle infestations are likely to occur next year. While the risk model only provides a radius distance from current infestations, managers can use stand information (i.e., hazard ratings), or other resource variables (e.g., endangered species habitat, riparian buffers, old-growth reserves), to determine if a given area should be prioritized for management activities. If management is needed, pheromone-baited traps (Dodds and Ross, 2002; Laidlaw and Wieser, 2002; Dodds et al. 2000; Ross and Daterman, 1997), antiaggregation pheromones (Ross et al., 2001; Ross and Daterman,; 1995; McGregor et al. 1984), or silvicultural treatments can be undertaken.

The between 2-year risk rating can be used if populations are on the rise in areas and forest survey information is only acquired from aerial detection survey maps. However, if populations follow patterns determined from this study, the between 2-

year risk rating will only provide useful information for the first year of increasing DFB populations. After that, by the time data is acquired populations should be returning to endemic populations.

Patch analyses provided information that is relevant to forecasting DFB related forest damage. As DFB populations increase, natural resource managers can expect not only more infestations, but also infestations that contain higher average number of trees killed and larger areas affected. Estimates of area affected, while problematic in some ways, provide relative estimates of DFB activity and could be useful to quantify some management variables (e.g., wildlife habitat, CWD inputs, etc.).

Combining forest stand information, an estimate of DFB risk, and any other relevant forest data in a GIS format, allows managers to have a proactive tool for managing DFB populations in northern Idaho. In addition, the information provided on the spatial relationship of DFB infestations through multiple years provides insights into the spatial ecology of this species.

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Table 2.1. Summary statistics for within year nearest neighbor (NN) distances on Priest Lake Ranger District, 1988-2000.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988	65	1,171.8	163.6	208.0	6,926.2	326.8
1989	57	1,422.5	268.9	190.4	12,567.0	538.6
1990	16	2,224.0	534.1	406.0	7,950.2	1,138.5
1991	43	2,467.6	285.9	283.2	6,896.0	577.0
1992	10	4,698.7	2,315.4	290.2	24,574.0	5,237.7
1993	12	4,528.3	2,542.6	370.3	31,960.7	5,596.1
1994	25	3,082.9	1,318.2	85.5	32,790.0	2,720.7
1995	12	5,029.4	901.5	1,714.1	13,641.6	1,984.1
1996	15	555.0	162.1	144.8	2,390.0	347.6
1997	8	7,169.0	3,110.4	283.6	24,916.7	7,354.9
1998	351	291.6	17.3	0	2,794.2	33.9
1999	418	438.6	22.2	0	3,846.4	43.6
2000	357	496.5	29.0	0	6,140.5	57.0

Table 2.2. Summary statistics for within year nearest neighbor (NN) distances on Bonners Ferry Ranger District, 1988-2000.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988	8	3,709.3	1915.0	451.2	12,473.5	4,528.3
1989	4	1,914.9	419.1	1,188.9	2,640.8	1,333.9
1990	15	3,308.8	757.9	387.3	8,640.3	1,625.5
1991	32	2,597.8	544.2	384.6	13,406.2	1,109.8
1992	9	1,623.1	942.3	273.7	8,801.1	2,172.9
1993	24	2,475.3	420.9	124.4	6,487.8	870.9
1994	18	2,699.8	846.4	192.8	11,981.0	1,785.8
1995	21	3,516.2	928.1	238.7	19,200.0	1,936.0
1996	5	8,554.6	1,920.3	3,931.7	12,931.2	5331.6
1997	4	8,956.9	5,042.8	1,830.5	23,225.3	16,048.5
1998	200	642.2	46.2	109.5	3,937.5	91.0
1999	241	606.9	43.5	81.4	5,581.7	85.7
2000	227	730.3	89.5	72.8	11,876.7	176.3

Table 2.3. Summary statistics for within year nearest neighbor (NN) distances on Salmon River Ranger District, 1988-2000.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988	78	1,313.1	114.4	167.2	4,511.3	227.9
1989	70	1,559.7	145.0	264.9	5,370.4	289.4
1990	49	1,267.2	161.6	166.2	5,171.3	325.0
1991	73	1,365.5	183.6	201.2	9,464.6	366.0
1992	36	2,217.9	568.5	273.3	17,345.7	1,154.2
1993	13	4,794.7	1,494.3	305.5	18,059.2	3,255.8
1994	30	1,938.9	425.0	289.2	9,420.6	869.3
1995	51	1,820.0	336.0	172.9	12,107.0	674.8
1996	93	1,172.2	168.3	120.7	8,170.2	334.3
1997	295	683.1	41.0	0	5,872.4	80.7
1998	448	481.7	22.4	46.9	4,140.4	44.0
1999	393	336.8	14.0	0	1,777.8	27.6
2000	185	579.1	49.4	91.9	5,543.9	97.4

Table 2.4. Summary statistics for within year nearest neighbor (NN) distances on St. Joe Ranger District, 1988-2000.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988	256	860.0	44.9	0	5,371.2	88.6
1989	187	735.7	57.5	48.9	5,829.2	113.5
1990	123	1,170.6	101.2	88.9	7,681.7	200.3
1991	198	936.1	81.9	167.3	8,747.2	161.6
1992	21	3,539.9	752.8	601.5	11,231.3	1,570.2
1993	18	3,111.4	1,208.6	336.9	21,048.5	2,549.9
1994	9	5,932.1	3,527.7	658.1	33,764.8	8,134.9
1995	45	1,536.3	340.1	99.9	10,146.6	685.4
1996	6	4,573.8	2,318.4	932.7	15,886.6	5,959.5
1997	156	808.9	95.2	120.6	9,675.9	188.1
1998	558	562.1	35.4	44.2	10,917.1	69.6
1999	537	571.1	27.4	0	4,639.9	53.9
2000	362	765.2	43.8	107.4	8,514.7	86.2

Table 2.5. Summary statistics for between-year nearest neighbor (NN) distances on Priest Lake Ranger District.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988-1989	65	1,380.1	179.6	0	6,429.3	359.0
1989-1990	57	3,334.8	449.7	0	20,461.0	900.9
1990-1991	16	2,861.5	375.6	206.2	5,973.9	800.6
1991-1992	43	7,201.0	693.0	1,404.2	16,737.0	1,398.4
1992-1993	10	2,358.8	662.3	527.0	7,170.2	1,498.3
1993-1994	12	1,911.9	898.9	0	11,117.3	1,978.4
1994-1995	25	4,087.7	784.8	58.5	11,636.6	1,619.8
1995-1996	12	9,157.0	1,286.8	34.4	16,843.6	2,832.2
1996-1997	15	6,042.9	1,520.0	0	15,589.8	3,260.2
1997-1998	8	598.7	345.7	0	2,287.9	817.4
1998-1999	351	440.8	110.1	0	37,313.6	216.6
1999-2000	418	446.9	32.8	0	4,349.7	64.5

Table 2.6. Summary statistics for between-year nearest neighbor (NN) distances on Bonners Ferry Ranger District.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988-1989	8	7,849.7	1,984.6	149.5	14,568.9	4,692.9
1989-1990	4	2,978.3	406.7	1,795.5	3,612.2	1,294.2
1990-1991	15	2,118.8	622.1	282.0	8,158.4	1,334.2
1991-1992	32	11,438.6	1,014.5	2,743.7	19,982.1	2,068.9
1992-1993	9	13,469.6	2,893.7	2,616.6	24,793.6	6,672.8
1993-1994	24	3,850.3	527.9	0	10,042.1	1,091.9
1994-1995	18	2,263.9	464.7	52.5	7,632.3	980.3
1995-1996	21	7,834.4	1,389.6	101.5	25,364.0	2,898.6
1996-1997	5	7,477.3	2,950.1	701.1	16,954.6	8,190.8
1997-1998	4	414.9	359.9	0	1,492.1	1,145.3
1998-1999	200	588.1	77.6	0	9,503.2	153.1
1999-2000	241	765.9	112.7	0	20,058.4	222.0

Table 2.7. Summary statistics for between-year nearest neighbor (NN) distances on Salmon River Ranger District.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988-1989	78	1,597.5	220.9	0	11,517.2	439.8
1989-1990	70	3,849.4	545.9	110.1	20,365.3	1,089.0
1990-1991	49	1,447.3	157.1	0	4,974.4	315.9
1991-1992	73	2,453.3	278.4	0	9,170.9	554.9
1992-1993	36	4,682.6	902.9	0	17,745.1	1,833.1
1993-1994	13	2,646.7	918.4	0	9,647.5	2,001.0
1994-1995	30	1,938.5	323.9	0	7,309.4	662.4
1995-1996	51	1,915.6	363.4	0	10,092.6	730.0
1996-1997	93	396.9	48.0	0	2,098.5	95.3
1997-1998	295	410.8	38.2	0	5,825.5	75.2
1998-1999	448	3,003.9	294.9	0	28,167.38	579.5
1999-2000	393	7,170.9	424.6	0	30,403.9	834.7

Table 2.8. Summary statistics for between-year nearest neighbor (NN) distances on St. Joe Ranger District.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988-1989	256	2,052.2	180.9	0	12,670.5	356.3
1989-1990	187	1,106.3	90.4	0	7,439.9	178.3
1990-1991	123	1,316.9	137.1	0	7,427.4	271.3
1991-1992	198	6,586.5	443.5	0	74,601.0	874.7
1992-1993	21	2,528.7	384.4	129.2	6,441.7	801.8
1993-1994	18	9,012.1	1,548.1	375.3	22,085.6	3,266.1
1994-1995	9	9,250.8	906.6	5,835.4	14,418.7	2,090.7
1995-1996	45	6,941.7	714.8	0	16,162.2	1,440.6
1996-1997	6	1,842.7	1,034.3	0	5,708.9	2,658.8
1997-1998	156	252.6	39.3	0	4,105.4	77.6
1998-1999	558	423.4	29.7	0	7,252.8	58.4
1999-2000	537	840.4	52.0	0	11,174.6	102.2

Table 2.9. Summary statistics for between 2-year nearest neighbor (NN) distances on Priest Lake Ranger District.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988-1990	65	3,159.8	384.5	147.2	18,907.3	768.1
1989-1991	57	1,979.3	230.5	25.8	6,764.9	461.2
1990-1992	16	10,759.9	1,796.6	884.3	20,489.5	3,829.4
1991-1993	43	5,736.3	624.0	160.2	15,795.4	1,259.3
1992-1994	10	4,459.9	1,342.1	1,180.4	13,032.6	3,036.0
1993-1995	12	10,355.6	2,121.6	99.8	19,142.5	4,669.5
1994-1996	25	4,973.1	1,106.3	0	20,512.7	2,283.2
1995-1997	12	7,813.7	1,913.3	1,124.6	22,158.1	4,211.2
1996-1998	15	133.0	44.0	0	496.3	94.4
1997-1999	8	316.9	172.6	0	1,355.0	408.2
1998-2000	351	485.4	34.5	0	3,555.8	67.9

Table 2.10. Summary statistics for between 2-year nearest neighbor (NN) distances on Bonners Ferry Ranger District.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988-1990	8	3,287.8	632.7	362.3	6,304.9	1,495.9
1989-1991	4	687.4	422.8	106.5	1,940.7	1,345.6
1990-1992	15	12,948.3	1,292.8	3,828.2	24,312.1	2,772.9
1991-1993	32	2,726.6	502.6	109.7	11,806.2	1,024.9
1992-1994	9	5,661.1	1,432.2	1,915.4	15,690.7	3,302.6
1993-1995	24	3,010.9	394.9	63.1	7,783.4	817.1
1994-1996	18	7,088.5	1,065.7	1,612.3	16,123.9	2,248.4
1995-1997	21	10,071.9	1,880.6	879.5	33,040.8	3,922.9
1996-1998	5	535.3	200.2	101.4	1,264.5	555.8
1997-1999	4	475.4	387.5	0	1,633.9	1,233.0
1998-2000	200	828.7	84.0	0	6,951.4	165.7

Table 2.11. Summary statistics for between 2-year nearest neighbor (NN) distances on Salmon River Ranger District.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988-1990	78	2,359.6	250.2	0	10,828.7	498.3
1989-1991	70	2,407.4	468.7	0	17,324.4	935.1
1990-1992	49	2,812.3	241.4	139.0	6,852.2	485.4
1991-1993	73	4,132.2	416.2	0	16,324.4	829.6
1992-1994	36	2,187.0	412.5	0	11,256.0	837.4
1993-1995	13	1,401.5	390.5	0	3,792.7	850.8
1994-1996	30	2,495.5	519.0	0	9,550.5	1,061.5
1995-1997	51	530.0	91.9	0	3,661.3	184.5
1996-1998	93	353.3	48.9	0	3,006.2	97.0
1997-1999	295	4,004.9	364.8	0	22,644.6	717.9
1998-2000	448	5,303.4	355.0	0	31,813.7	697.6

Table 2.12. Summary statistics for between 2-year nearest neighbor (NN) distances on St. Joe Ranger District.

Year	Number of infestations	Average NN (m)	SE	Minimum NN (m)	Maximum NN (m)	95% CL (m)
1988-1990	256	1,684.9	99.7	0	8,045.9	196.3
1989-1991	187	1,143.8	145.4	0	22,456.3	286.9
1990-1992	123	6,560.1	373.3	0	17,521.9	739.0
1991-1993	198	4,698.4	229.6	0	18,034.1	452.7
1992-1994	21	5,984.5	1,158.6	185.1	18,720.0	2,416.9
1993-1995	18	5,348.1	1,259.2	58.4	14,320.5	2,656.6
1994-1996	9	5,170.1	832.2	1,762.9	8,882.2	1,919.1
1995-1997	45	1,572.6	309.6	0	8,977.2	624.1
1996-1998	6	1,249.2	760.3	0	4,379.8	1,954.5
1997-1999	156	245.1	32.1	0	3,766.5	63.4
1998-2000	558	807.3	40.4	0	5,397.9	79.4

Table 2.13. Risk rating for 2 two-year combinations on ranger districts in northern Idaho and an overall average risk rating model. Percentiles where 50, 75, and 90% of infestations occurred are shown.

	1st year combination			**2nd Year Combination**		
	Risk Rating Radius (m)					
Ranger District	**50%**	**75%**	**90%**	**50%**	**75%**	**90%**
Priest Lake	39	360	1106	204	580	1236
Bonners Ferry	215	657	1342	227	696	1926
Salmon River	249	501	1050	145	512	1193
St. Joe	112	272	578	215	554	1069
Average	153.8	447.5	1019	197.8	585.5	1356
Std Error	48.1	84.3	160	18.2	39.4	193.3
Upper 95% CL	306.7	715.7	1528.3	255.7	710.9	1971.1
Overall Average	**175.8**	**516.5**	**1187.5**			

Table 2.14. Between 2-year risk rating system for the four ranger districts and an overall average risk rating model. Percentiles where 50, 75, and 90% of infestations occurred are shown.

	Risk Rating Radius (m)		
Ranger District	**50%**	**75%**	**90%**
Priest Lake	221	755	1220
Bonners Ferry	415	964	2644
Salmon River	231	469	893
St. Joe	130	319	571
Overall Average	**249.3**	**626.8**	**1332.0**
Std Error	59.7	144.3	457.0
Upper 95% CL	439.4	1085.9	2786.3

Table 2.15. Average area affected (ha) per infestation and average number of trees killed per infestation by DFB on Priest Lake and Salmon River Ranger Districts from 1988-2000.

	Priest Lake Ranger District				Salmon River Ranger District			
	Size of Area		Number Trees Killed		Size of Area		Number Trees Killed	
Year	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**	**Mean**	**SE**
1988	1.0	0.18	12.55	3.18	6.49	4.88	16.76	2.4
1989	0.83	0.00036	4.77	0.64	1.83	0.47	16.44	3.11
1990	0.75	0.05	3.88	0.84	0.96	0.1	9.16	1.42
1991	1.09	0.17	4.7	0.37	3.41	0.72	20.85	2.36
1992	0.79	0.01	6.3	0.92	4.5	1.85	11.75	1.58
1993	1.83	0.56	8.92	2.03	1.53	0.43	7.15	1.14
1994	0.81	0.0004	7.64	1.11	1.65	0.28	15.17	2.09
1995	0.97	0.17	5.67	0.66	2.51	0.74	19.49	3.1
1996	0.81	0.0008	5.3	0.33	2.14	0.42	18.92	1.78
1997	2.01	1.19	8.25	2.73	4.65	0.63	24.98	2.15
1998	19.71	2.09	124.34	16.1	4.44	0.55	29.1	1.9
1999	15.51	1.73	85.93	12.72	9.73	1.68	90.47	18.99
2000	8.36	1.2	46.23	6.6	5.5	1.07	23.45	2.82

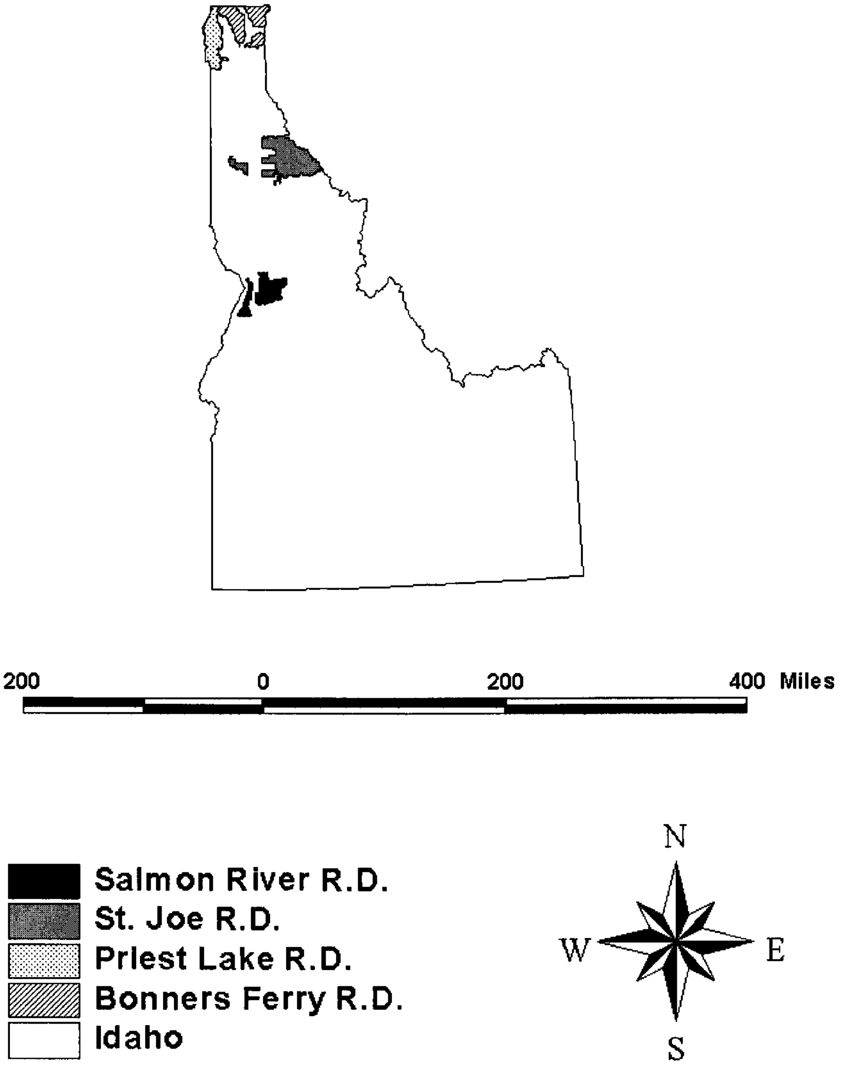


Figure 2.1. Location of USDA Forest Service ranger districts used to study the spatial relationships among Douglas-fir beetle infestations.

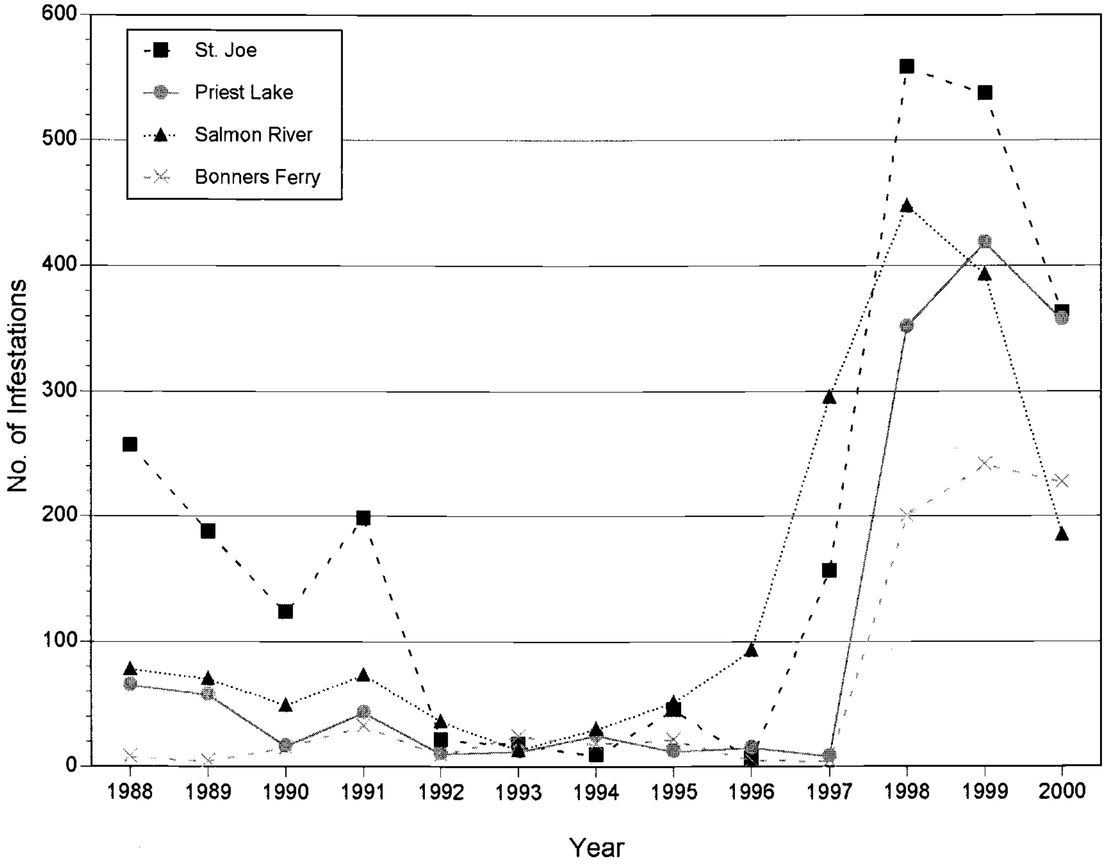


Figure 2.2. Number of infestations occurring on each of four ranger districts in northern Idaho from 1988-2000.

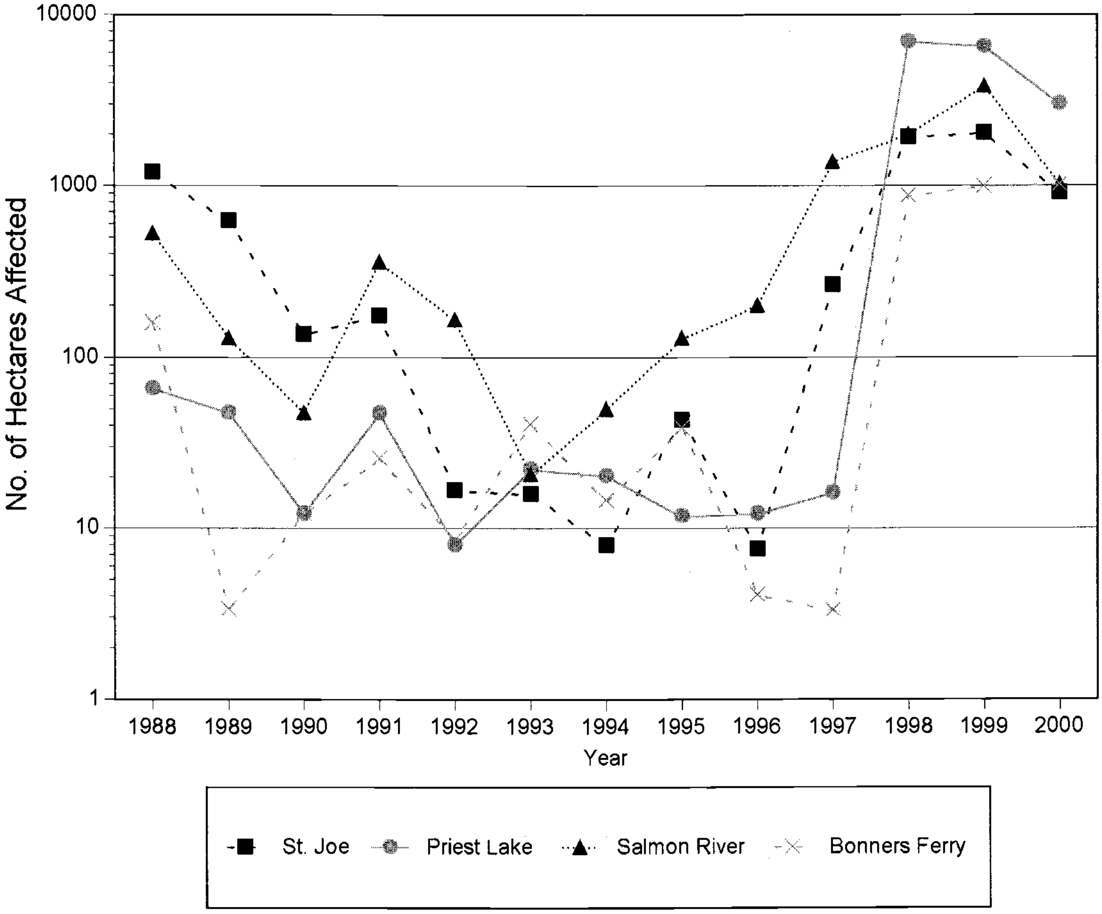


Figure 2.3. Total number of hectares affected by Douglas-fir beetle on four ranger districts in northern Idaho from 1988-2000.

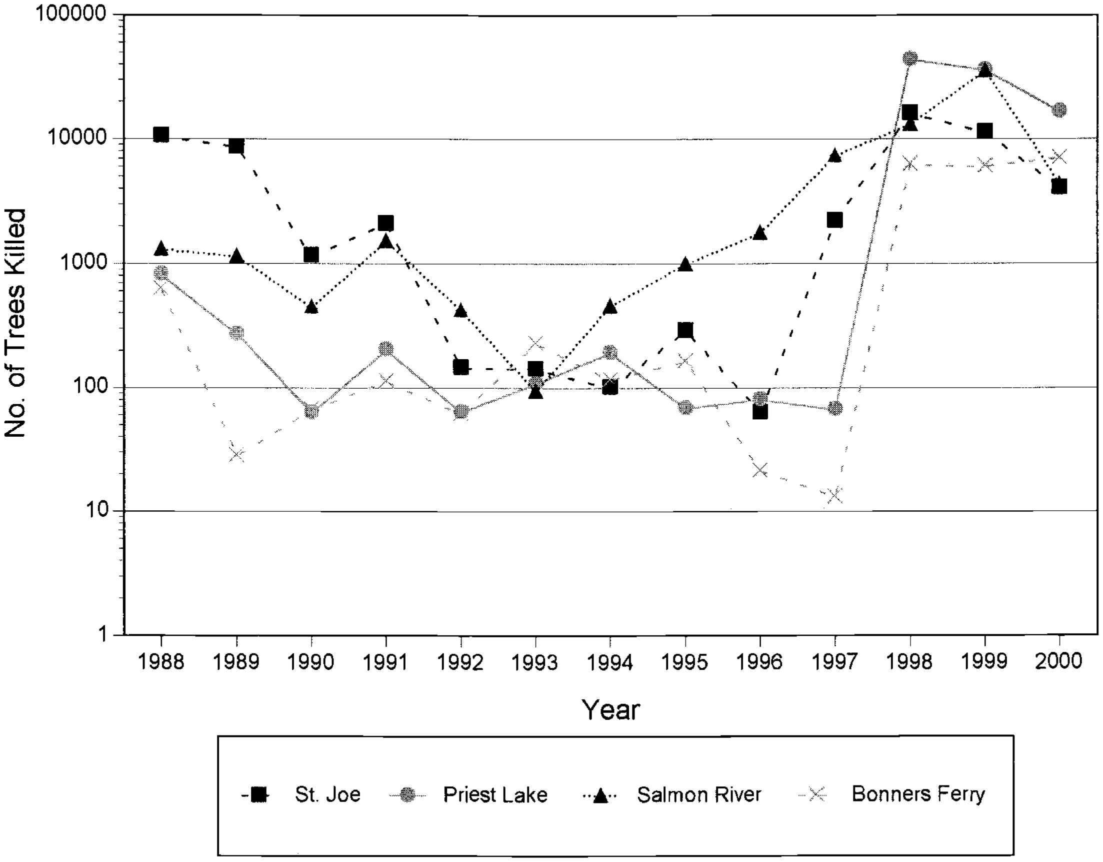


Figure 2.4. Total number of trees killed on four ranger districts in northern Idaho from 1988-2000.

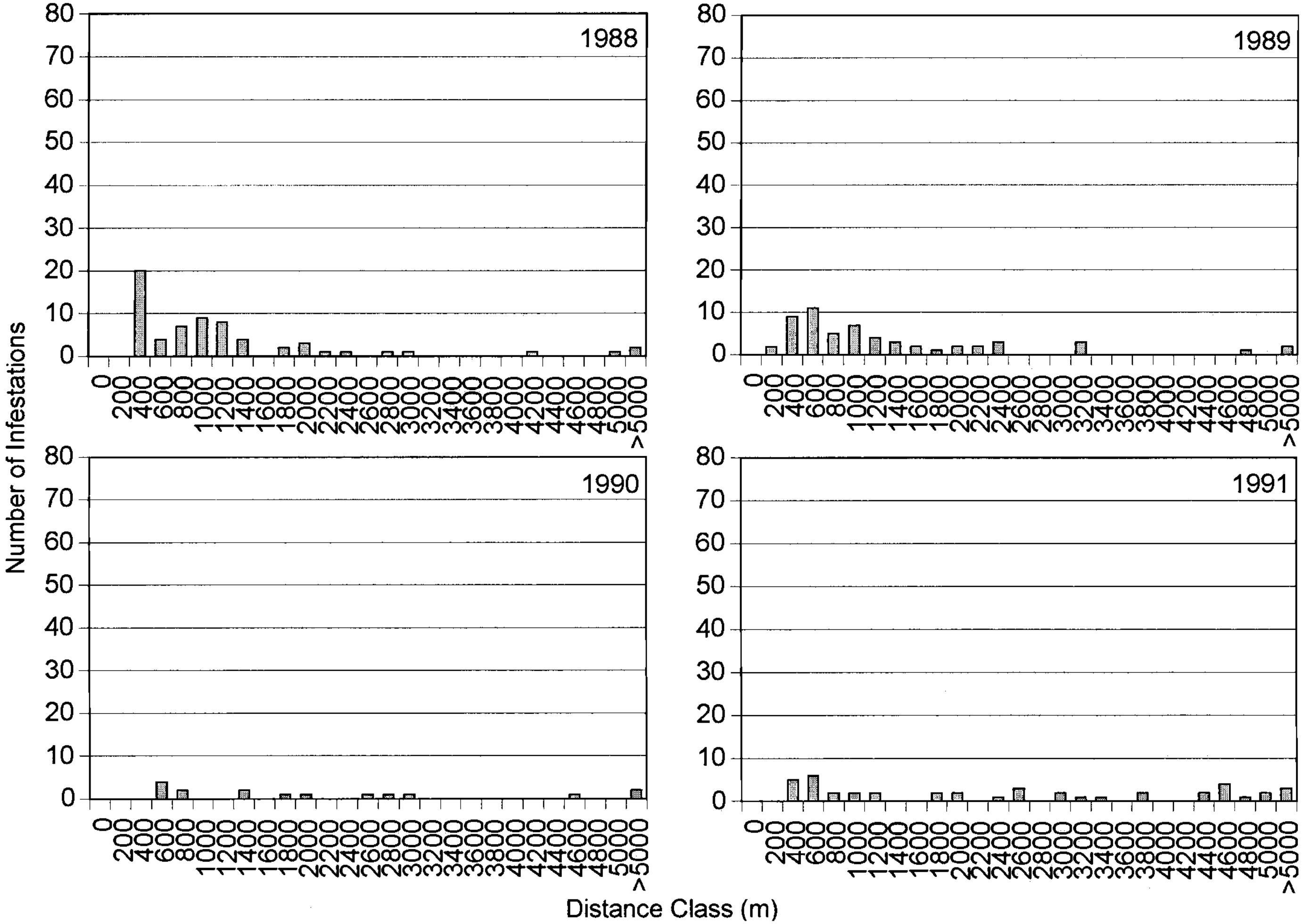


Figure 2.5. Number of infestations by nearest neighbor distance class for within-year infestations occurring on Priest Lake Ranger District.

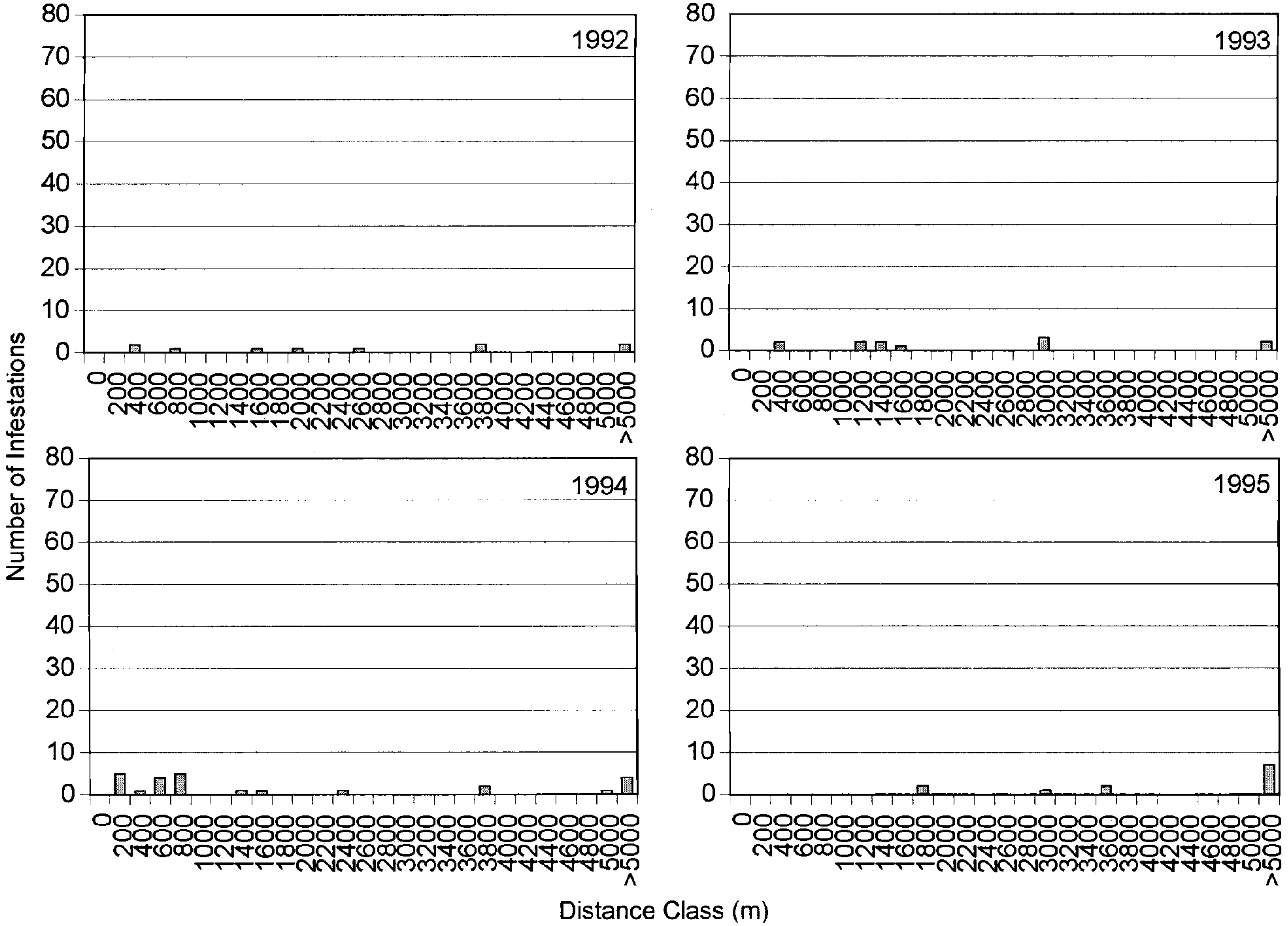


Figure 2.5 cont.

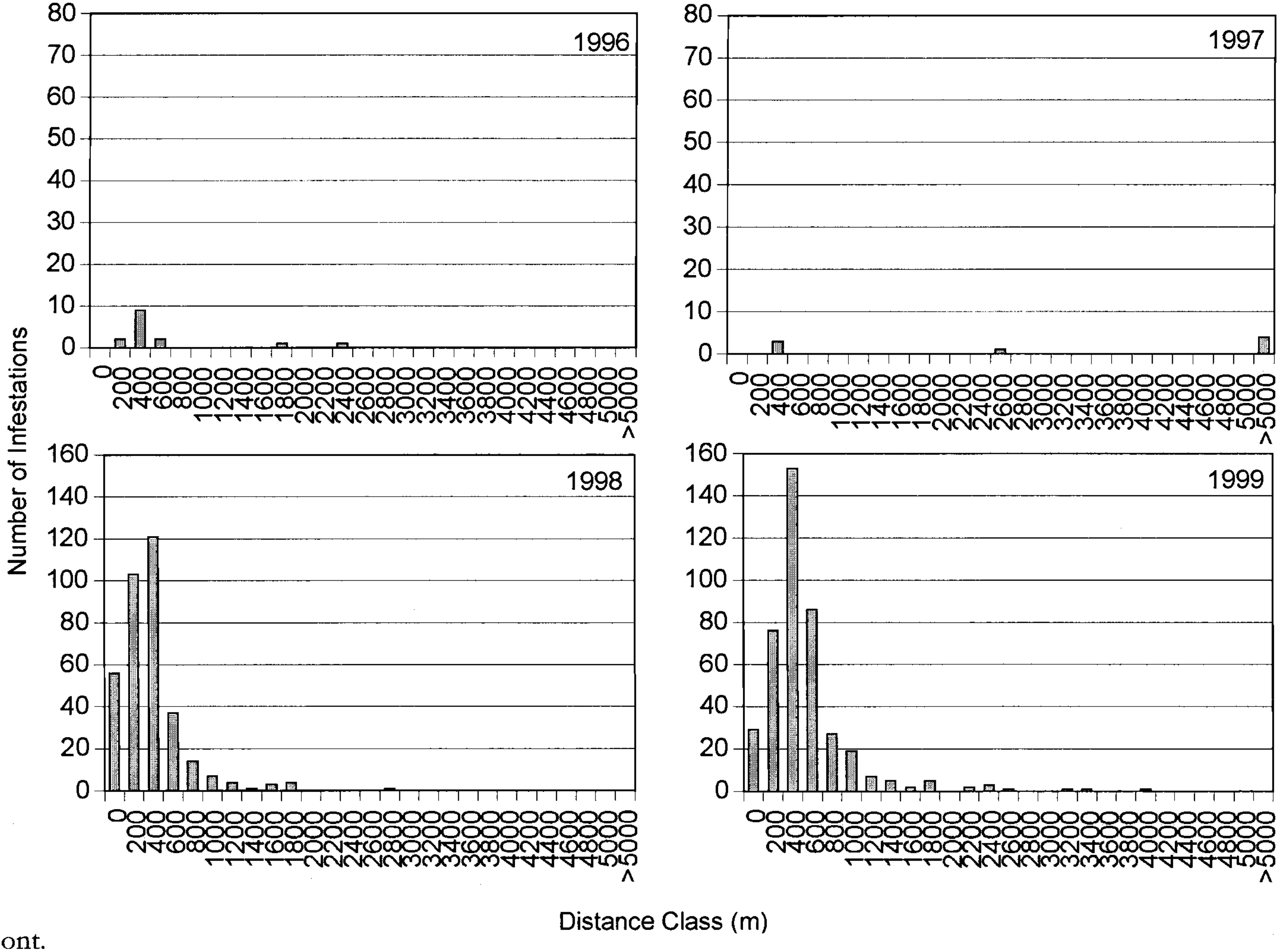
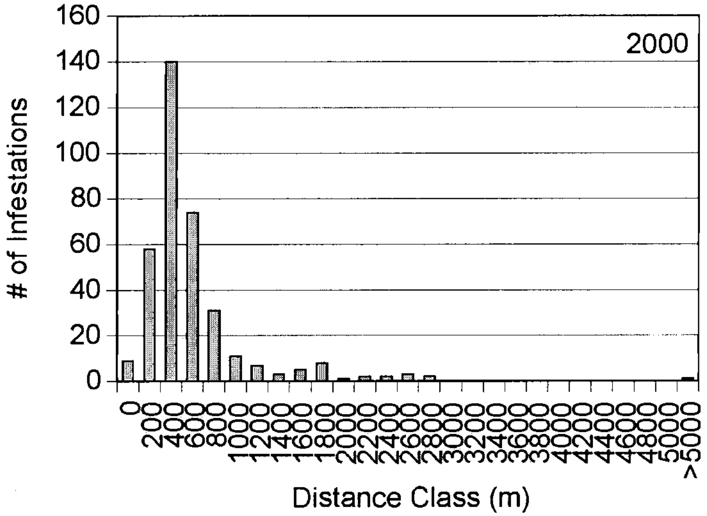


Figure 2.5 cont.



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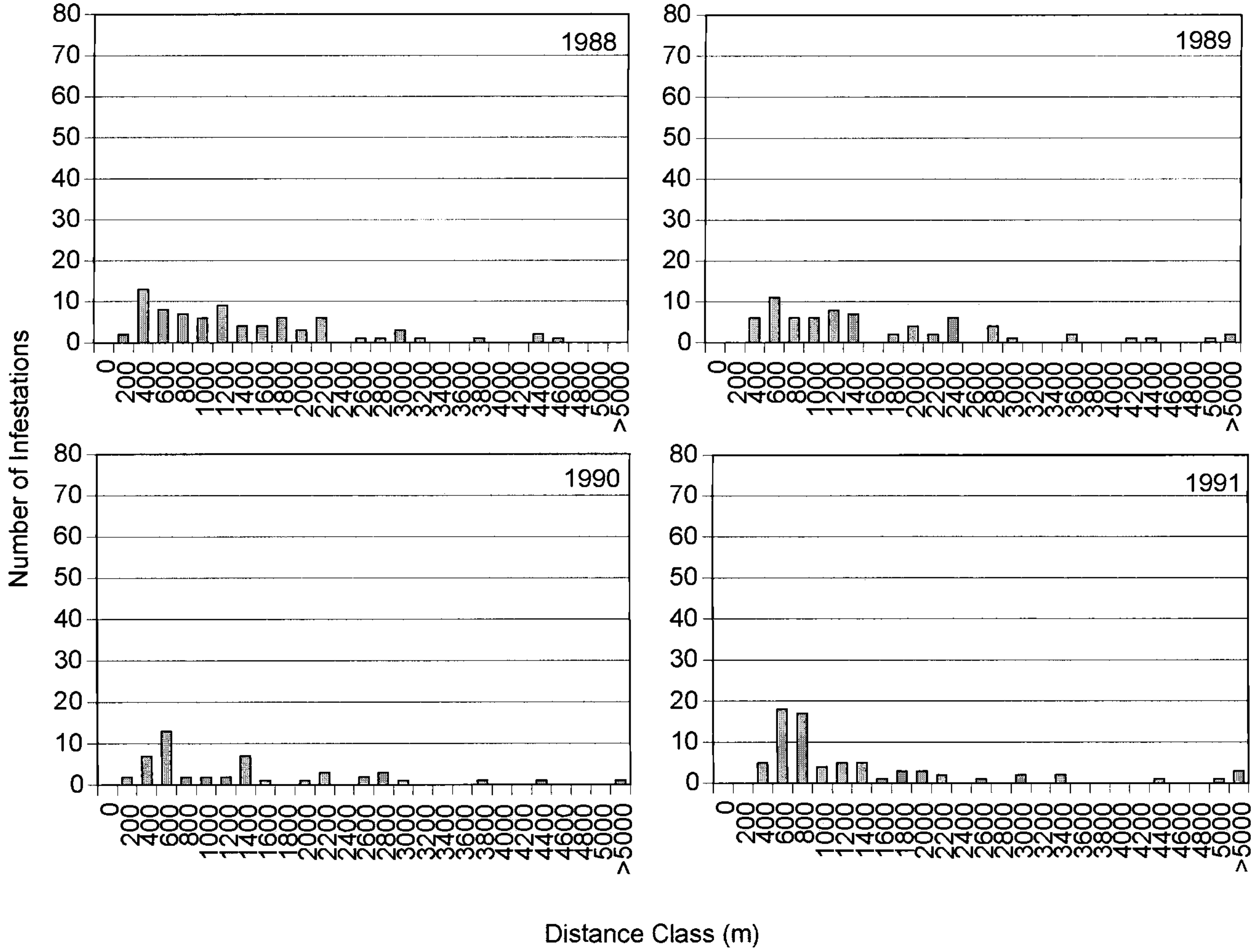
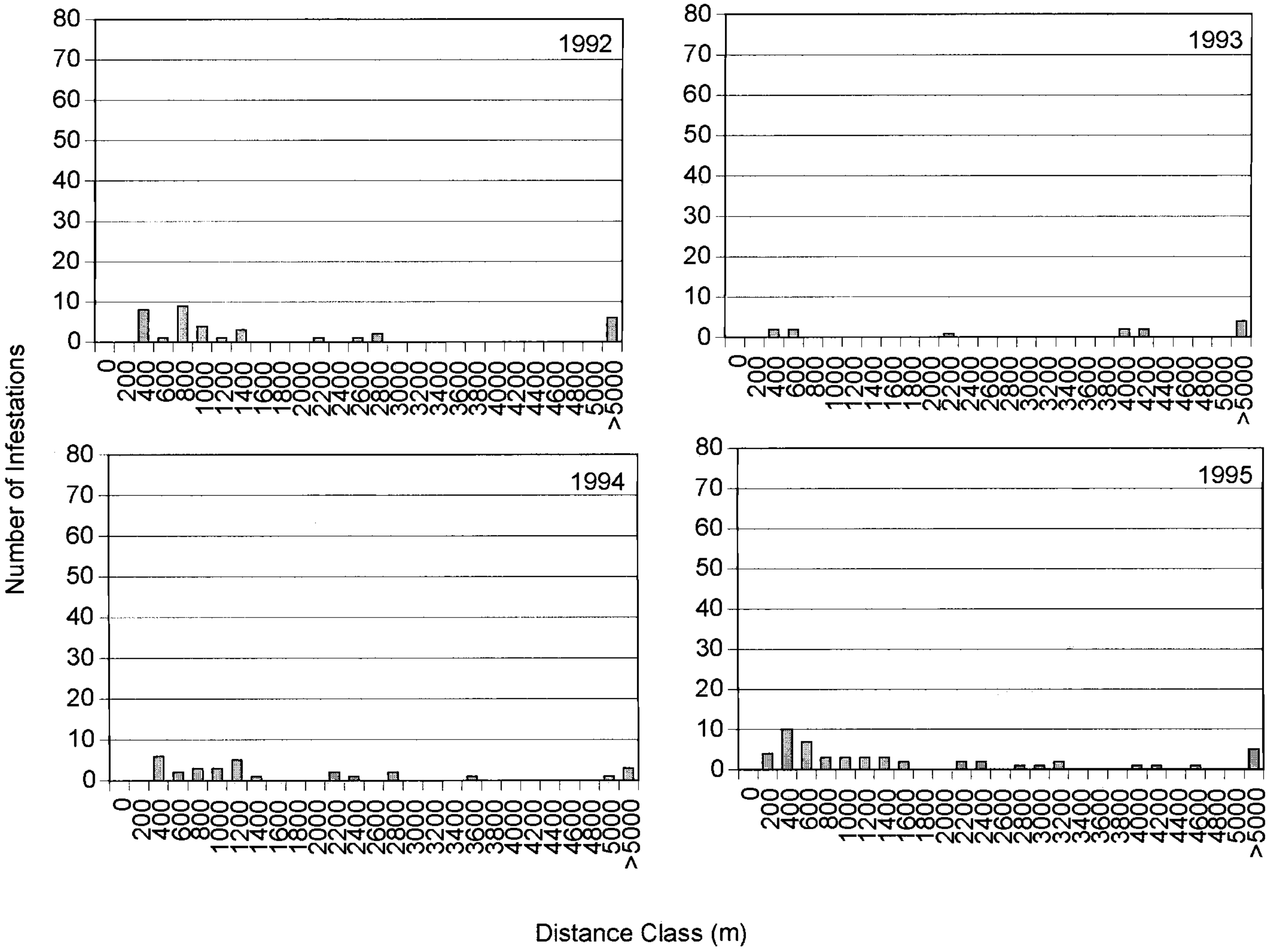


Figure 2.6. Number of infestations by nearest neighbor distance class for within-year infestations occurring on Salmon River Ranger District.



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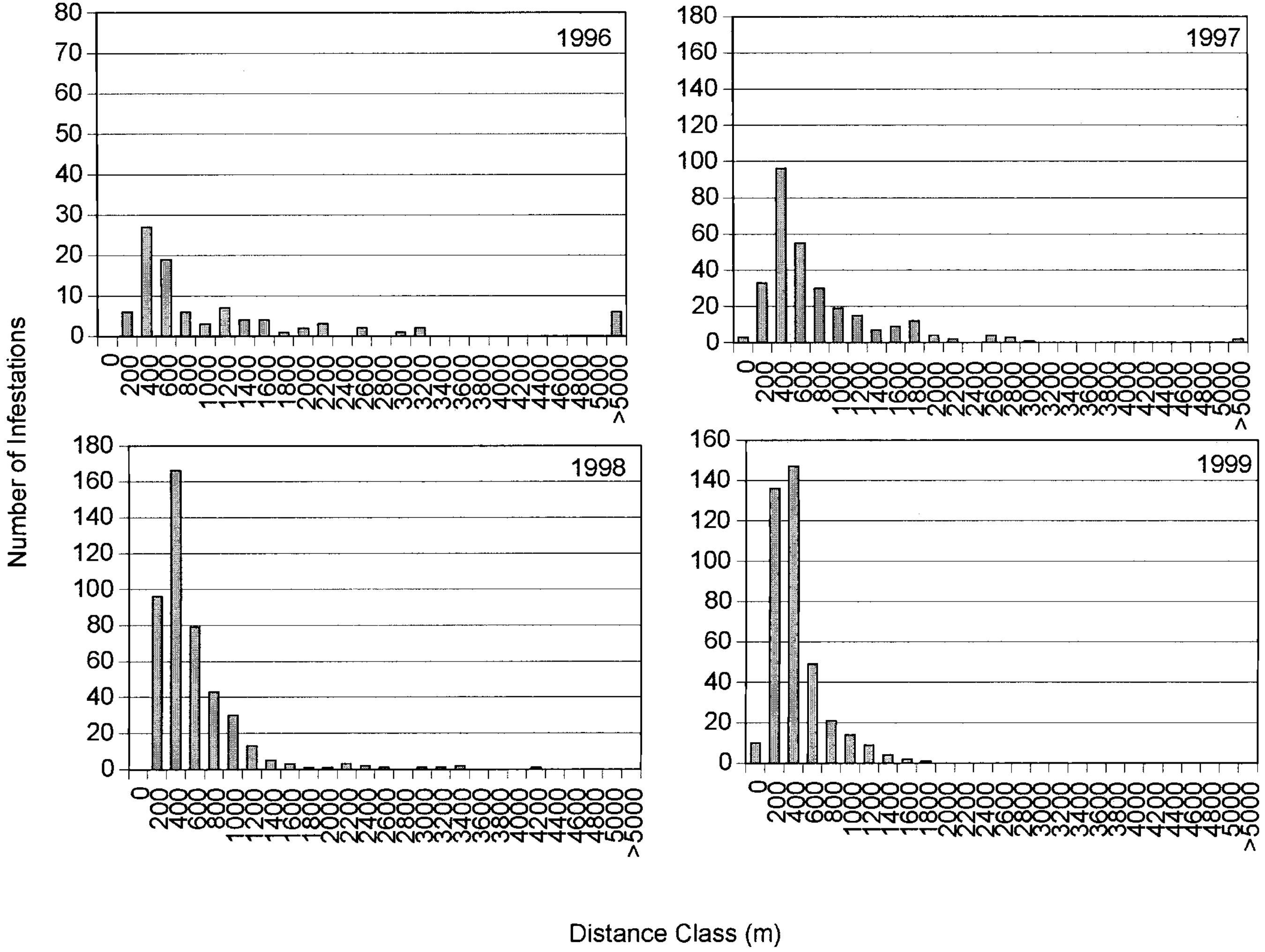

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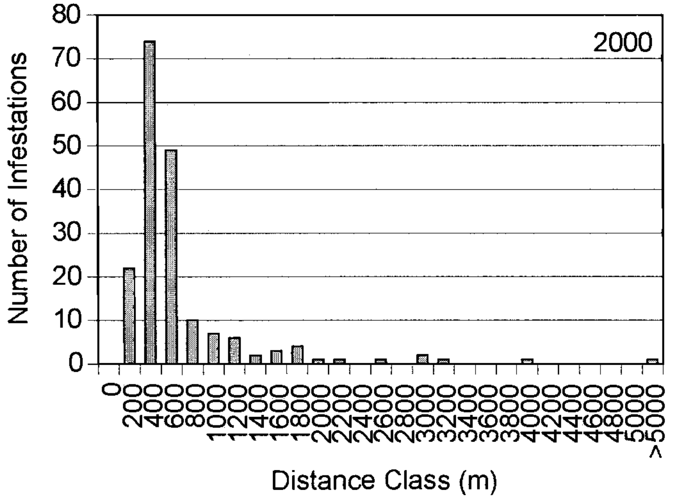

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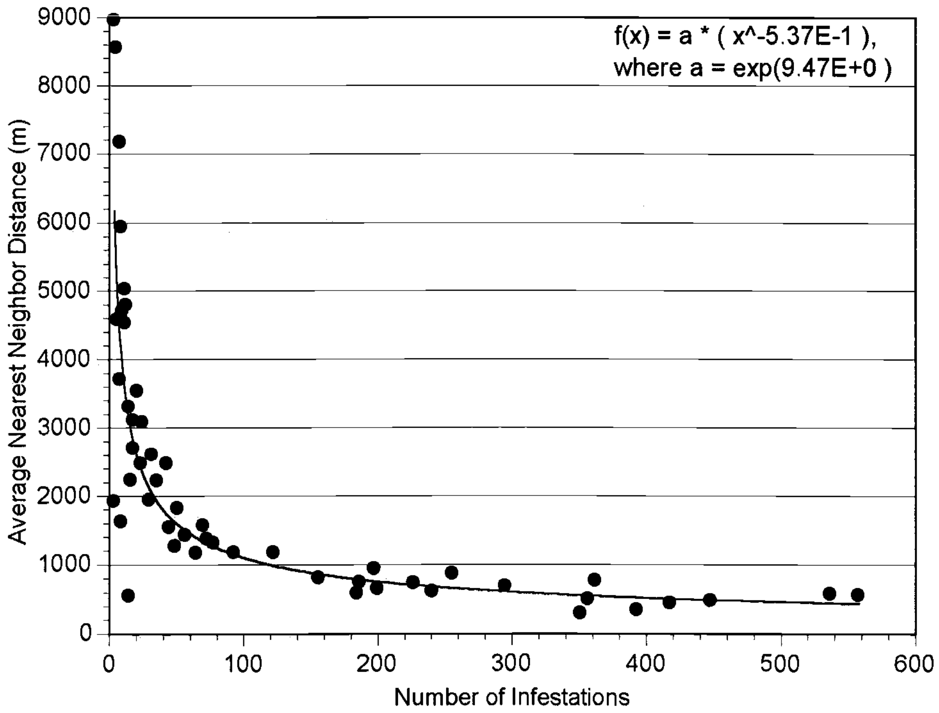


Figure 2.7. Relationship of number of infestations and average nearest neighbor distance for all ranger districts combined.

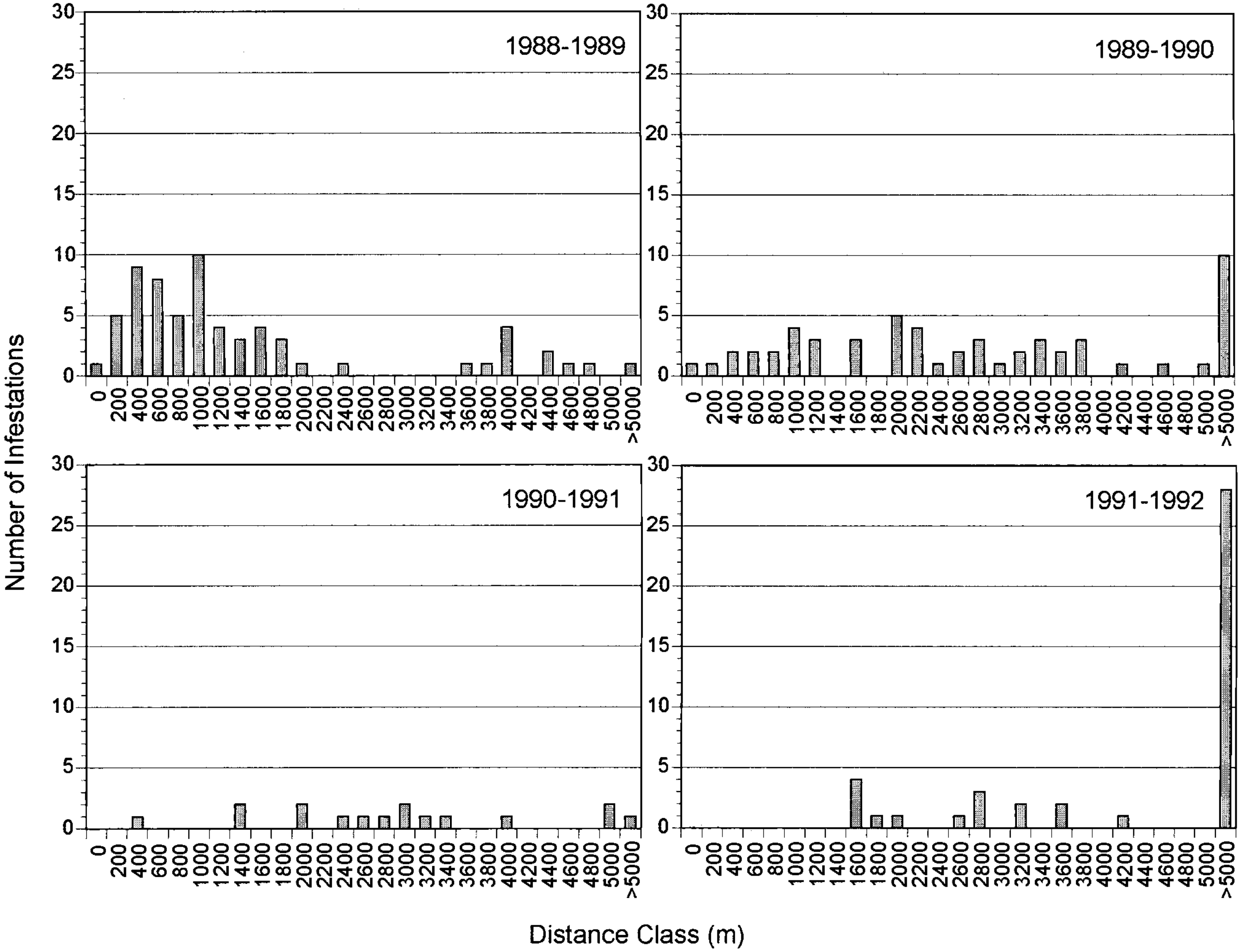
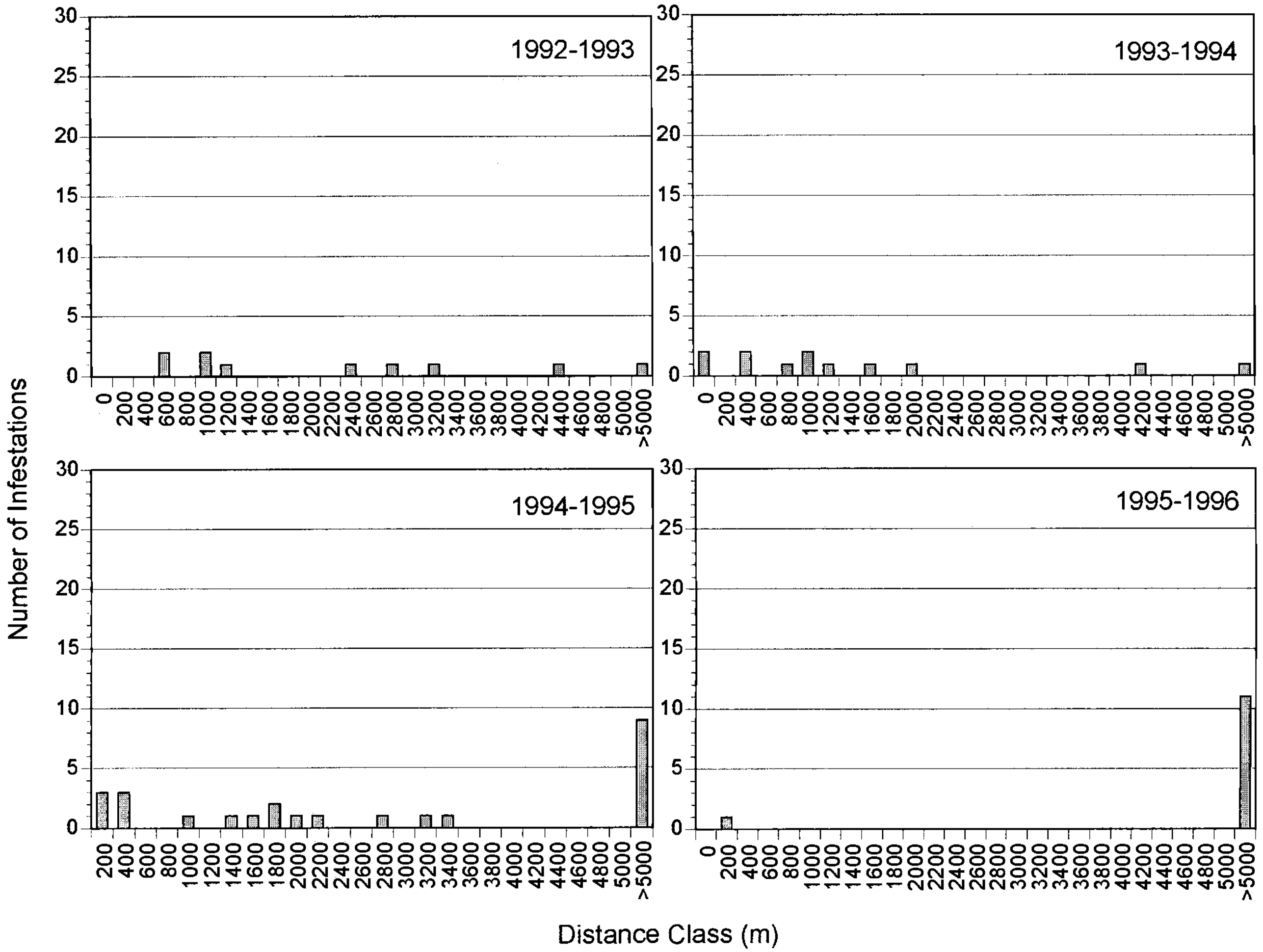


Figure 2.8. Number of infestations by nearest neighbor distance class for between-year infestations occurring on Priest Lake Ranger District.



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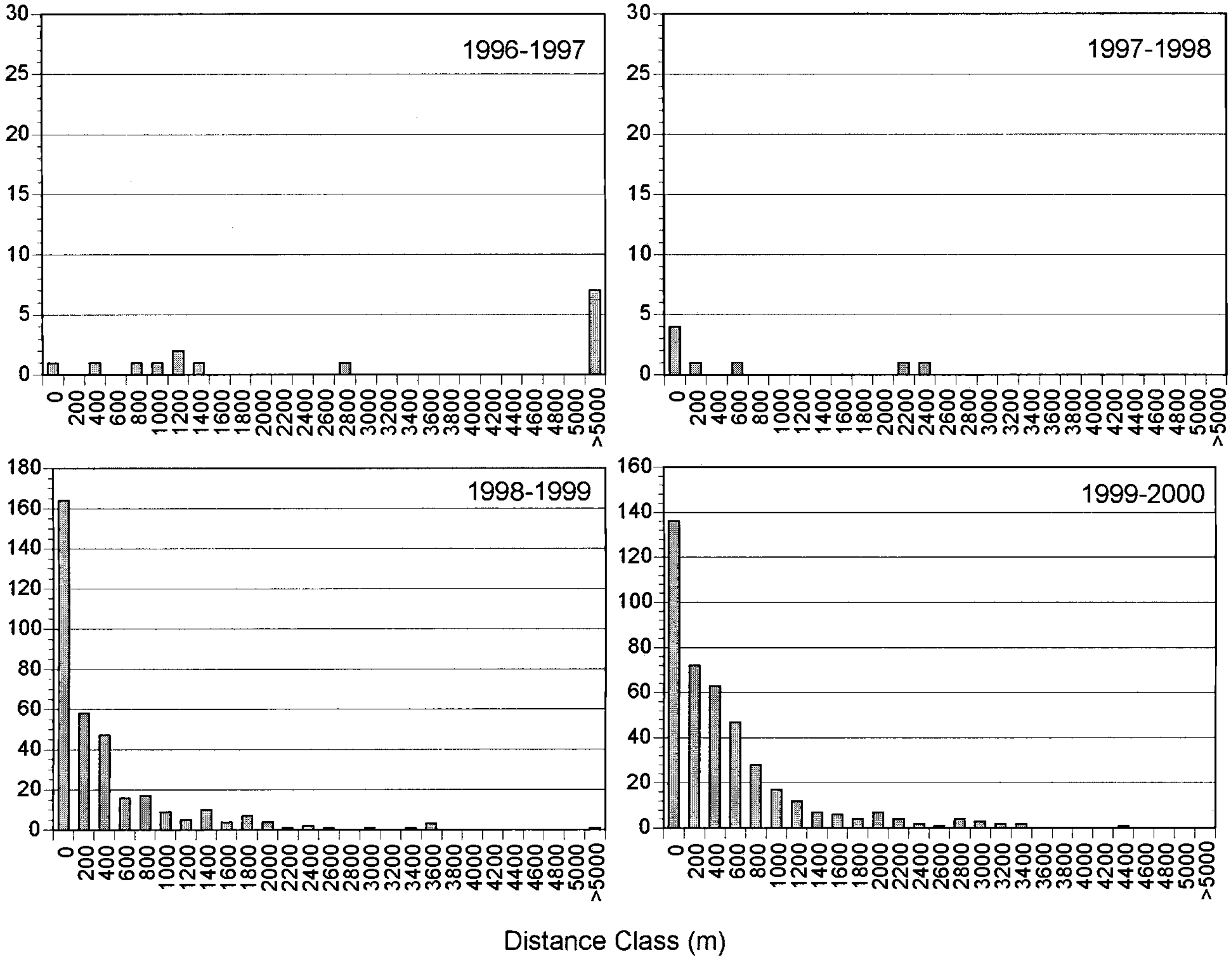

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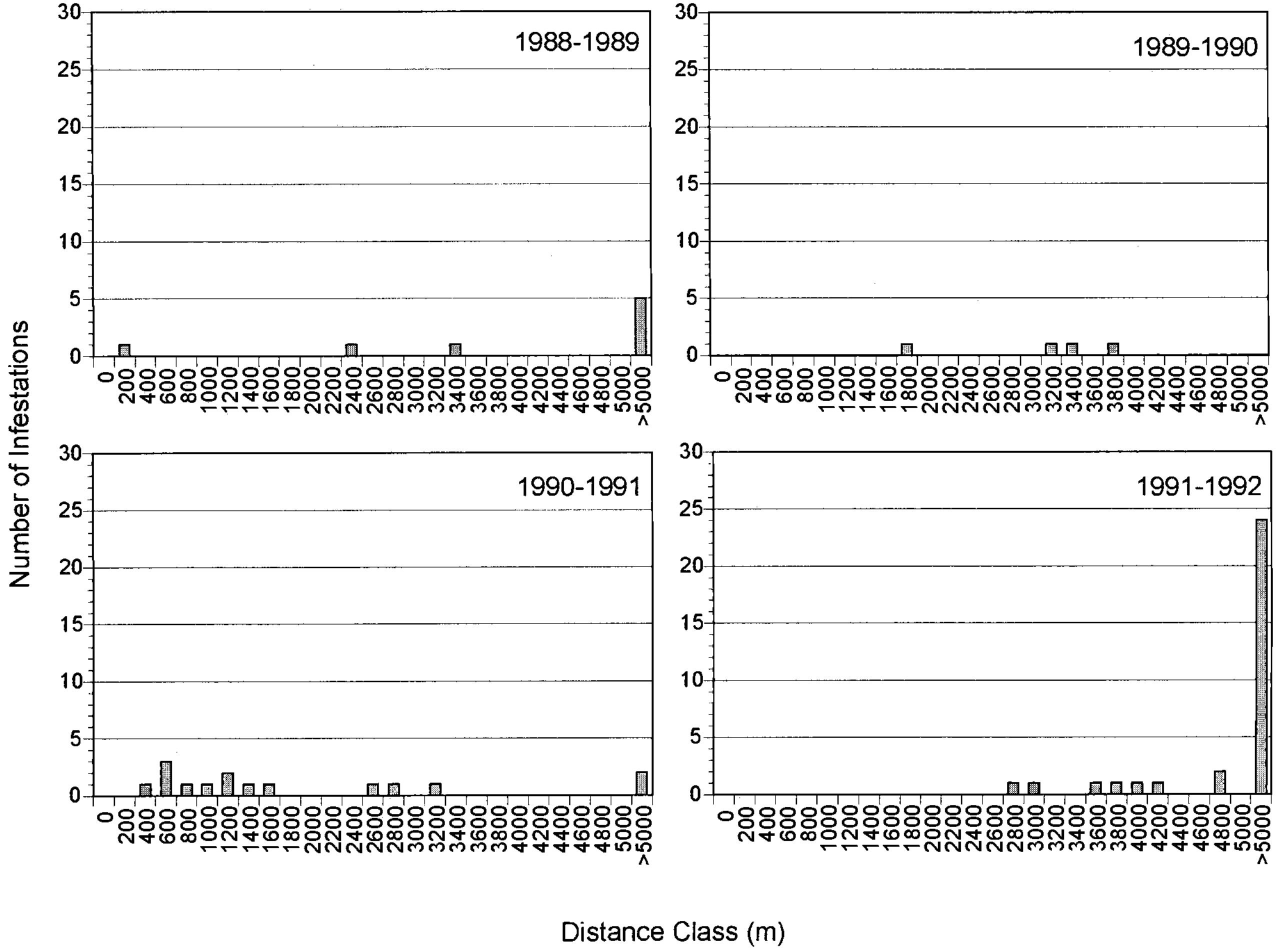
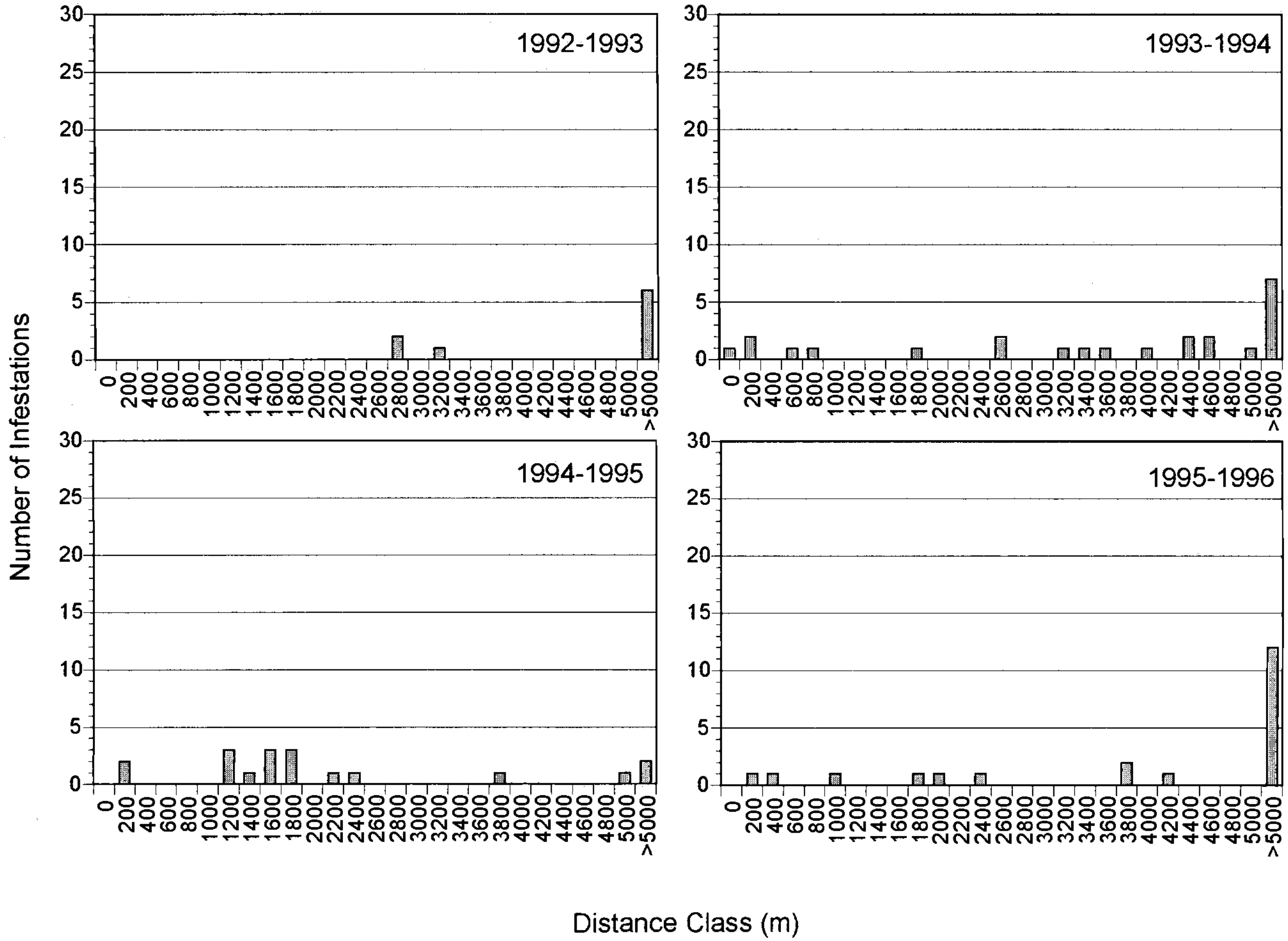


Figure 2.9. Number of infestations by nearest neighbor distance class for between-year infestations occurring on Bonners Ferry Ranger District.



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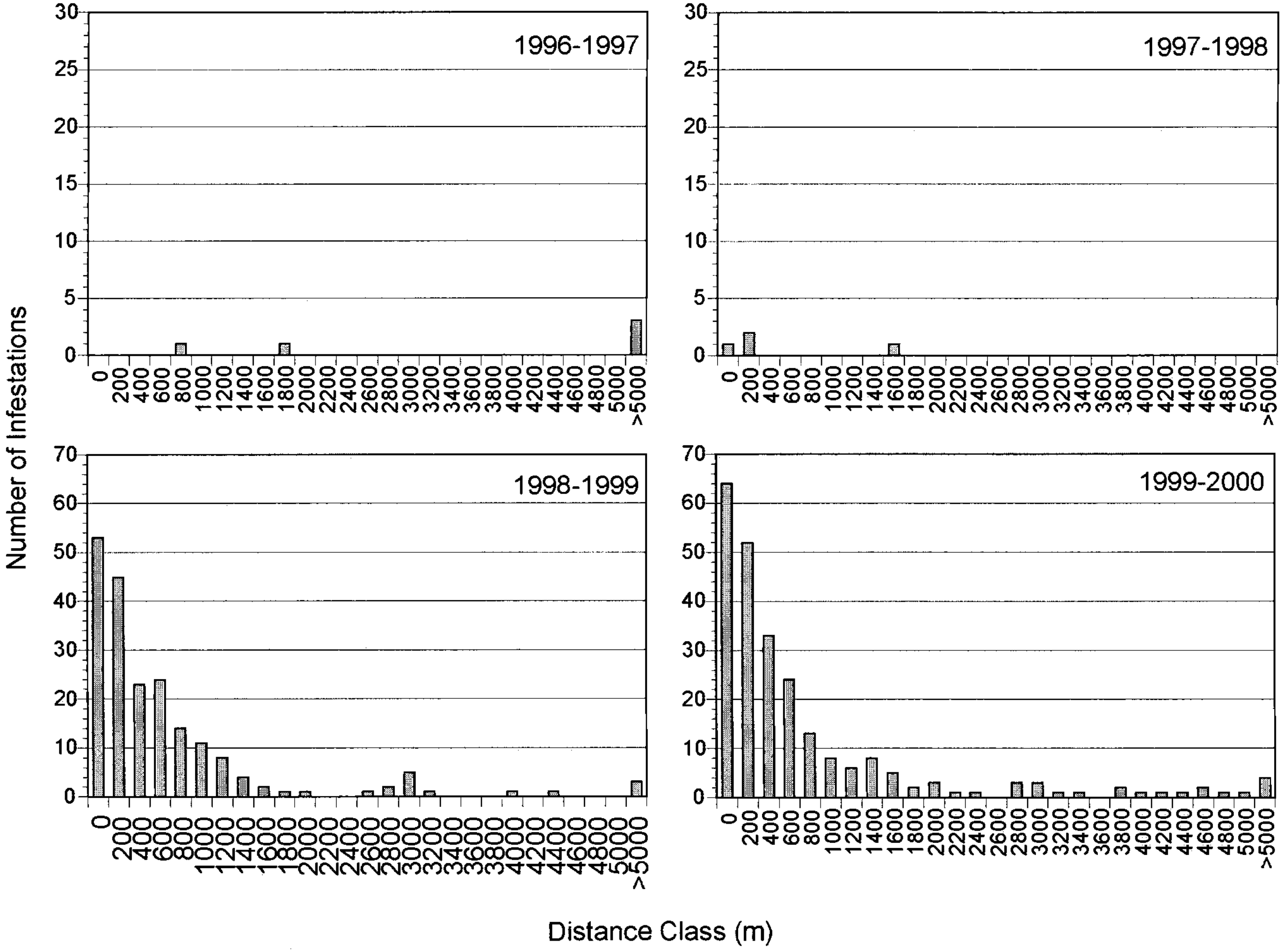

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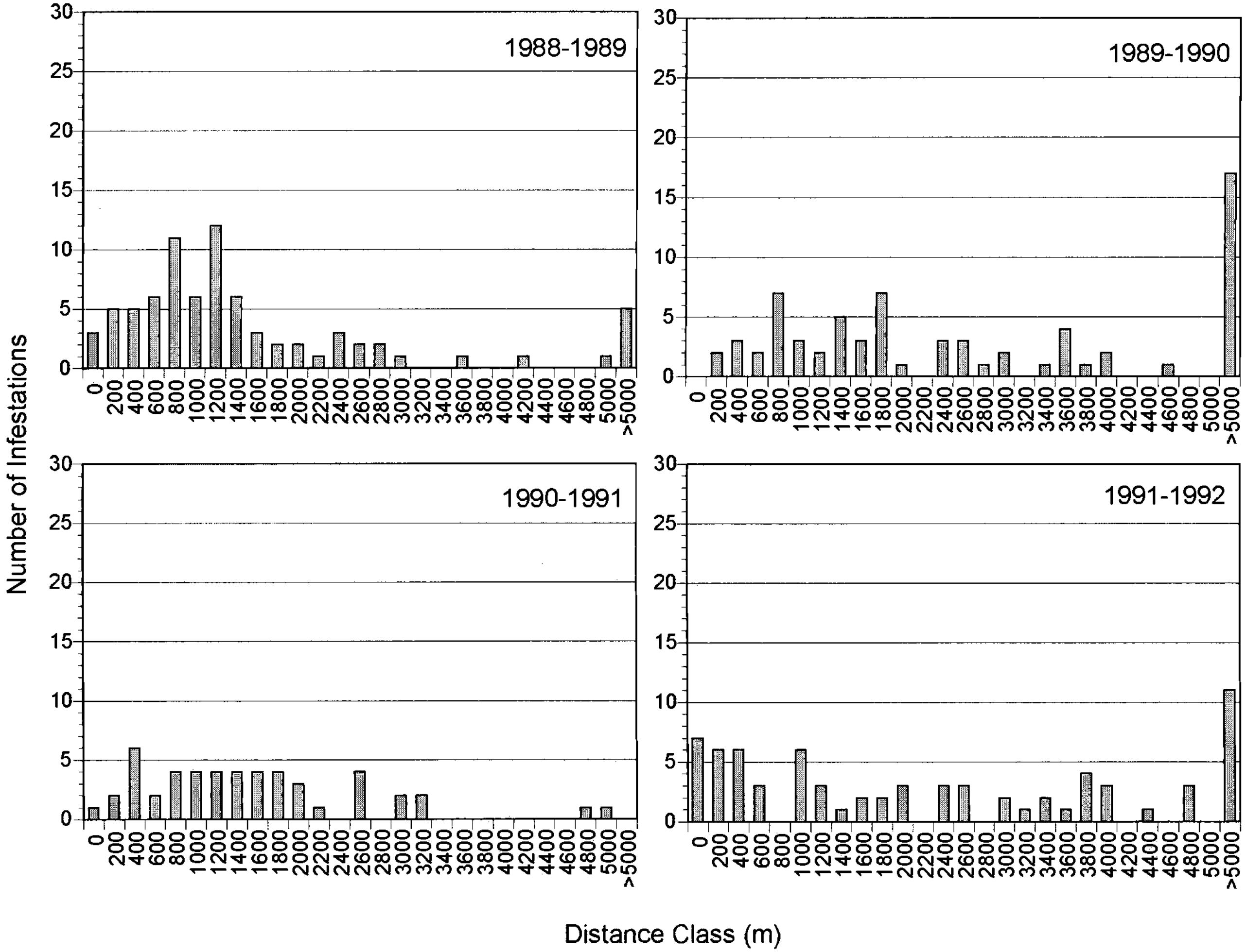
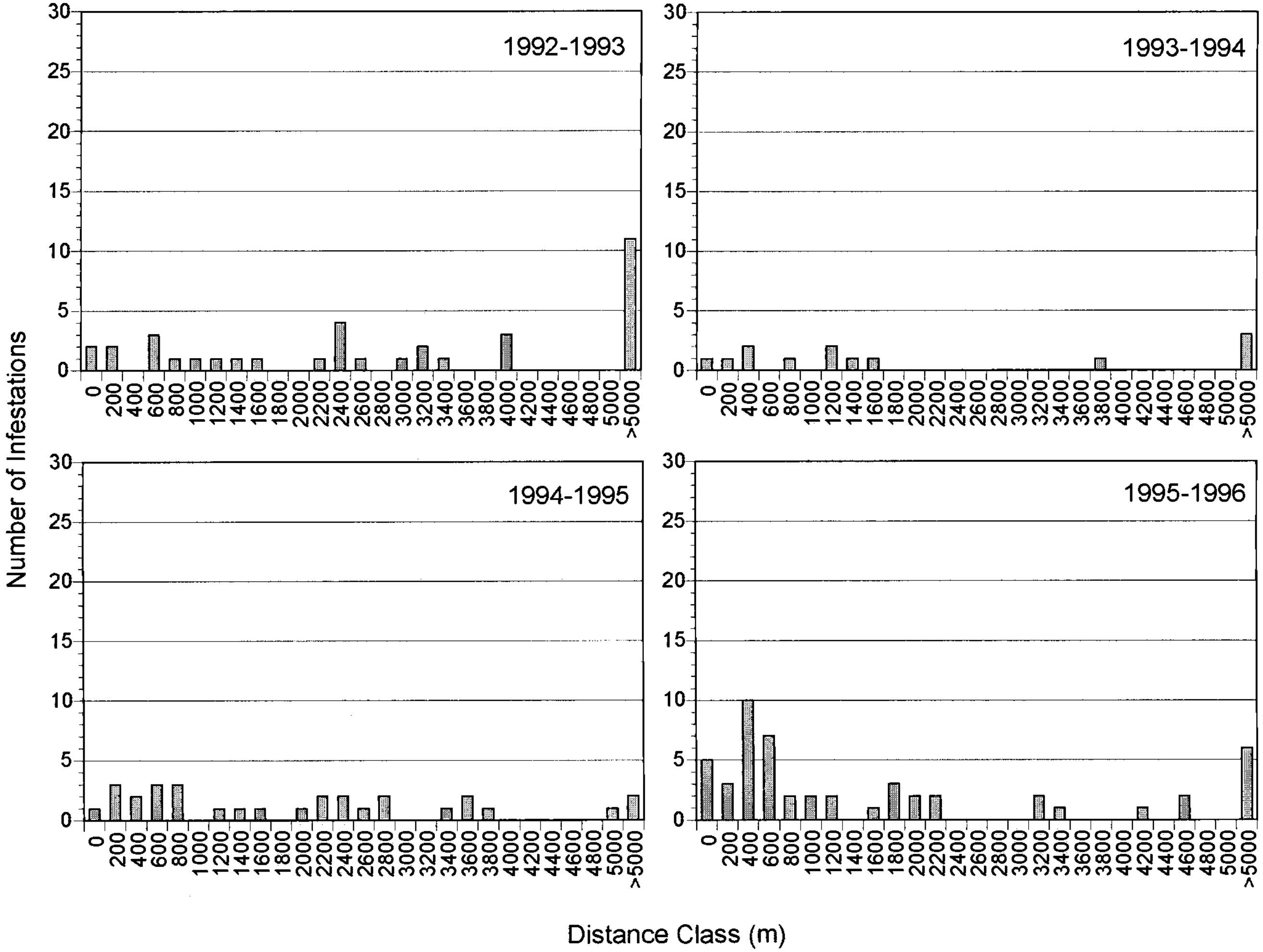


Figure 2.10. Number of infestations by nearest neighbor distance class for between-year infestations occurring on Salmon River Ranger District.



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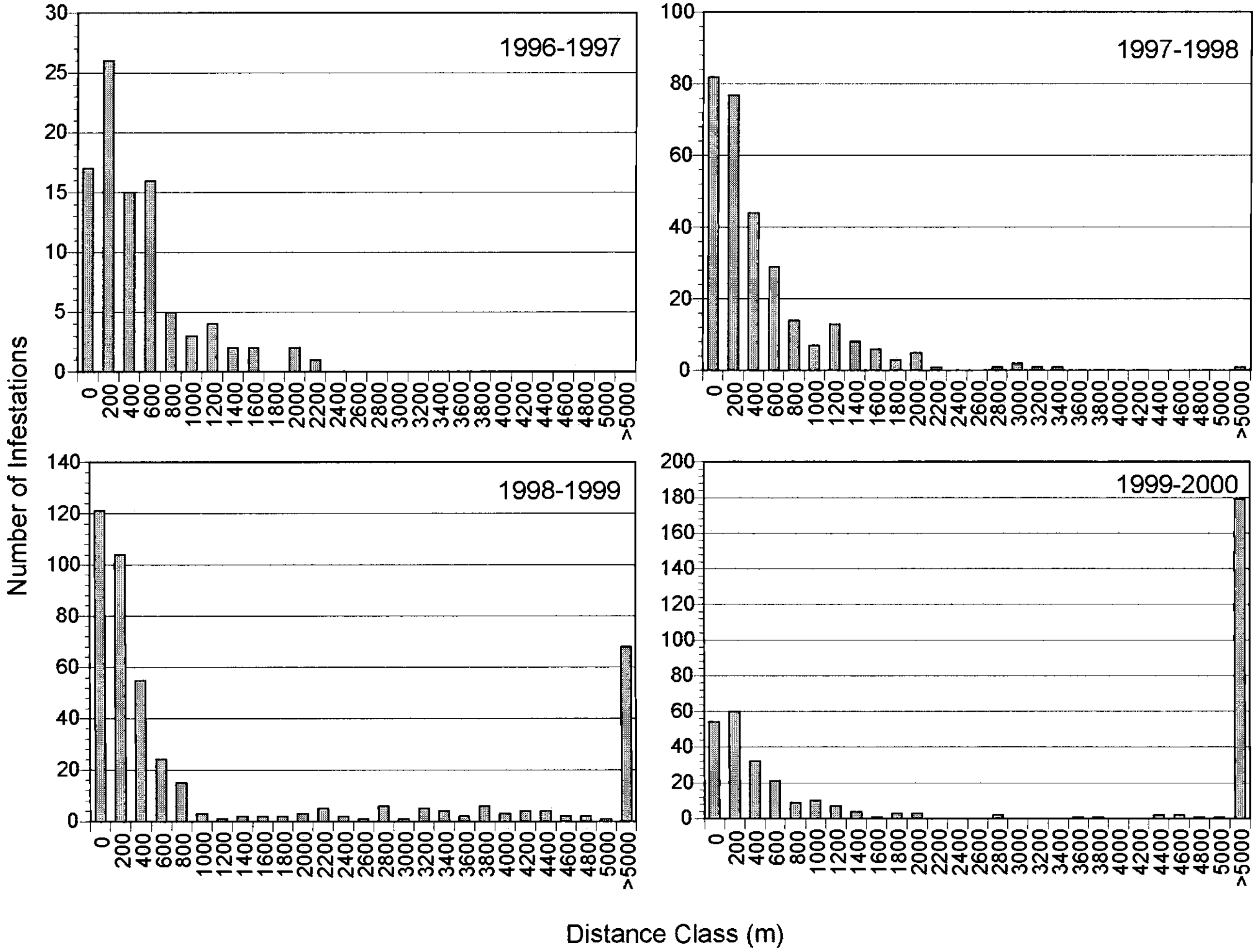

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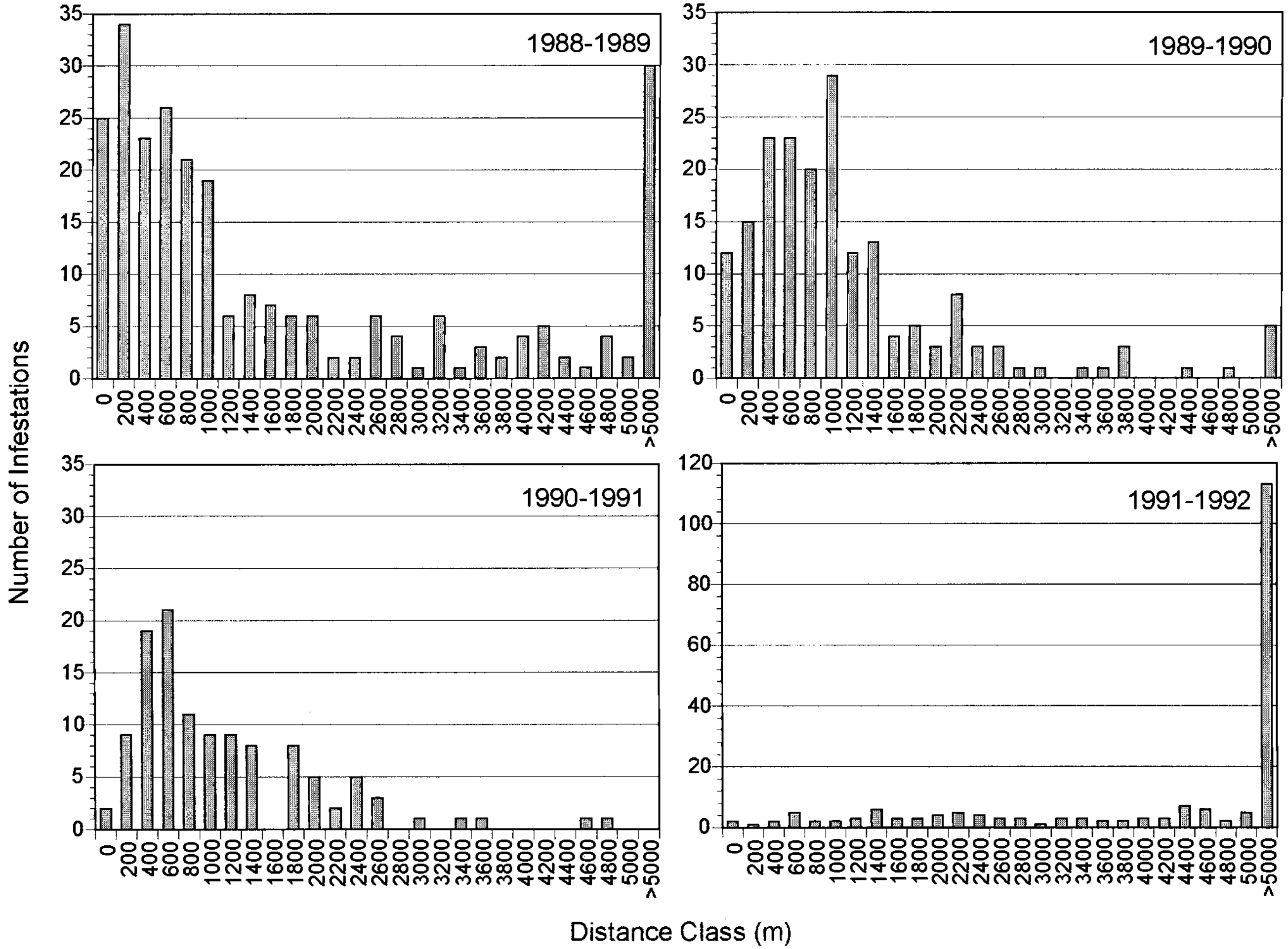
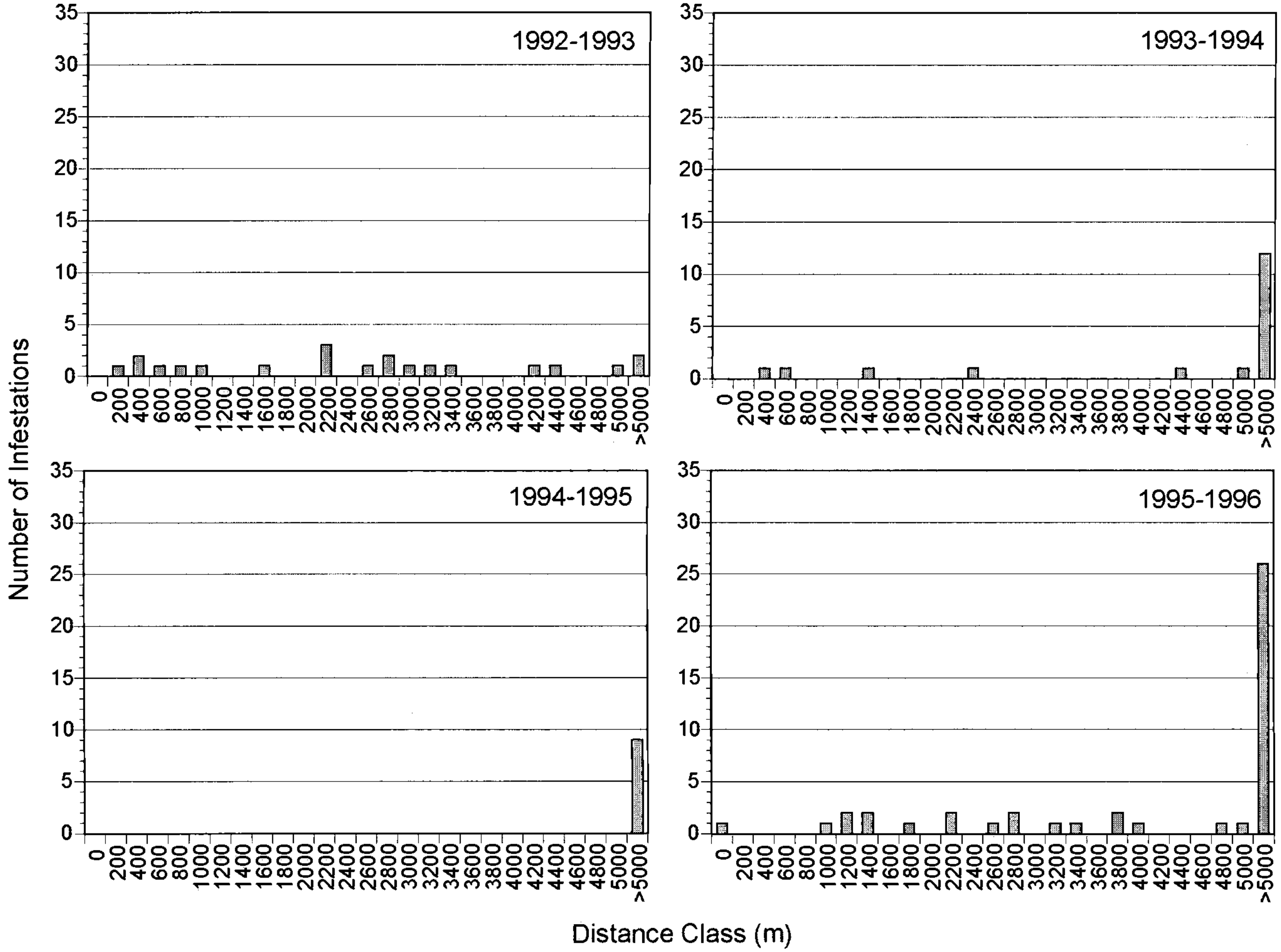


Figure 2.11. Number of infestations by nearest neighbor distance class for between-year infestations occurring on St. Joe Ranger District.



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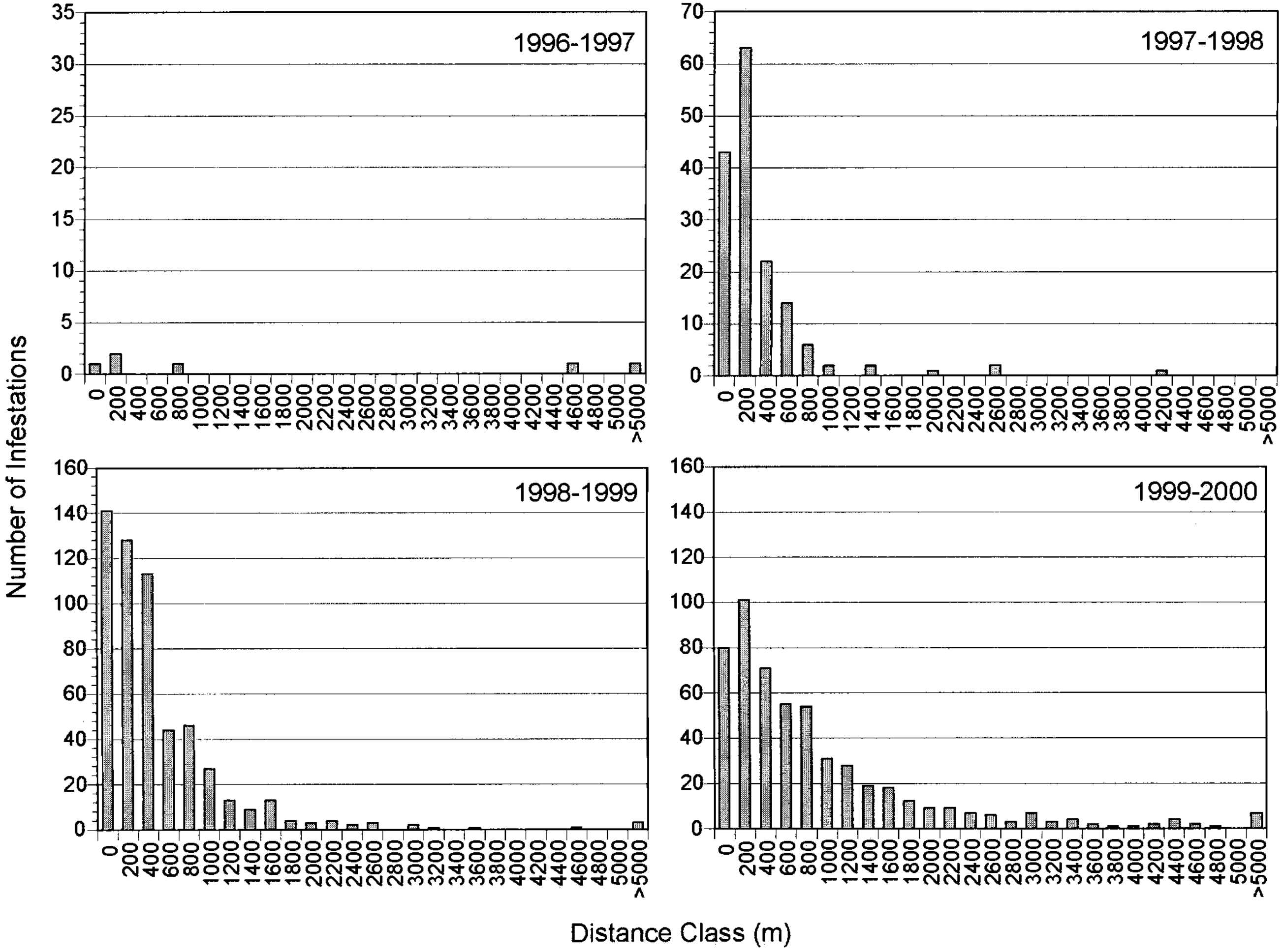

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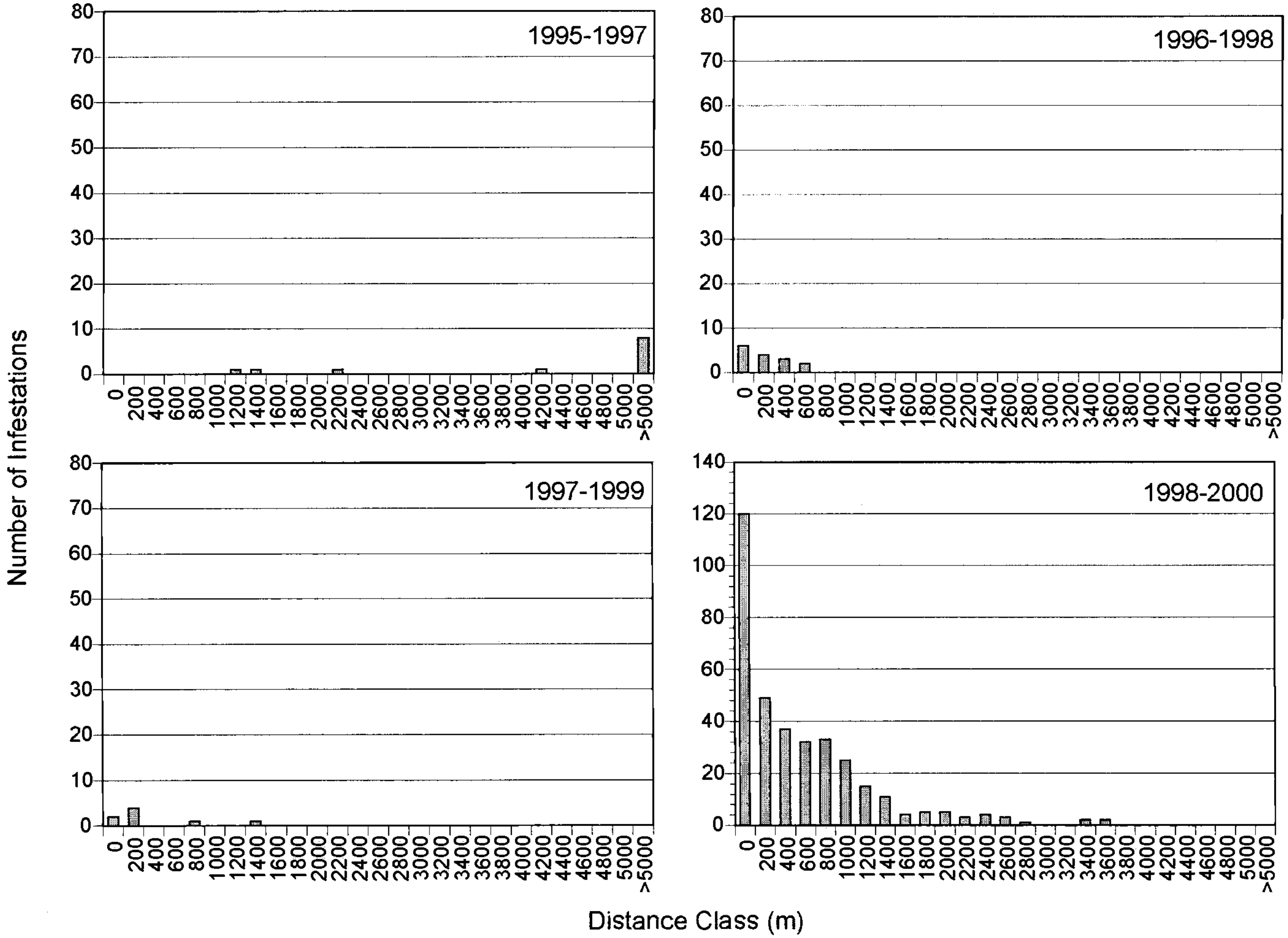


Figure 2.12. Number of infestations by nearest neighbor distance class for between 2-year infestations occurring on Priest Lake Ranger District.

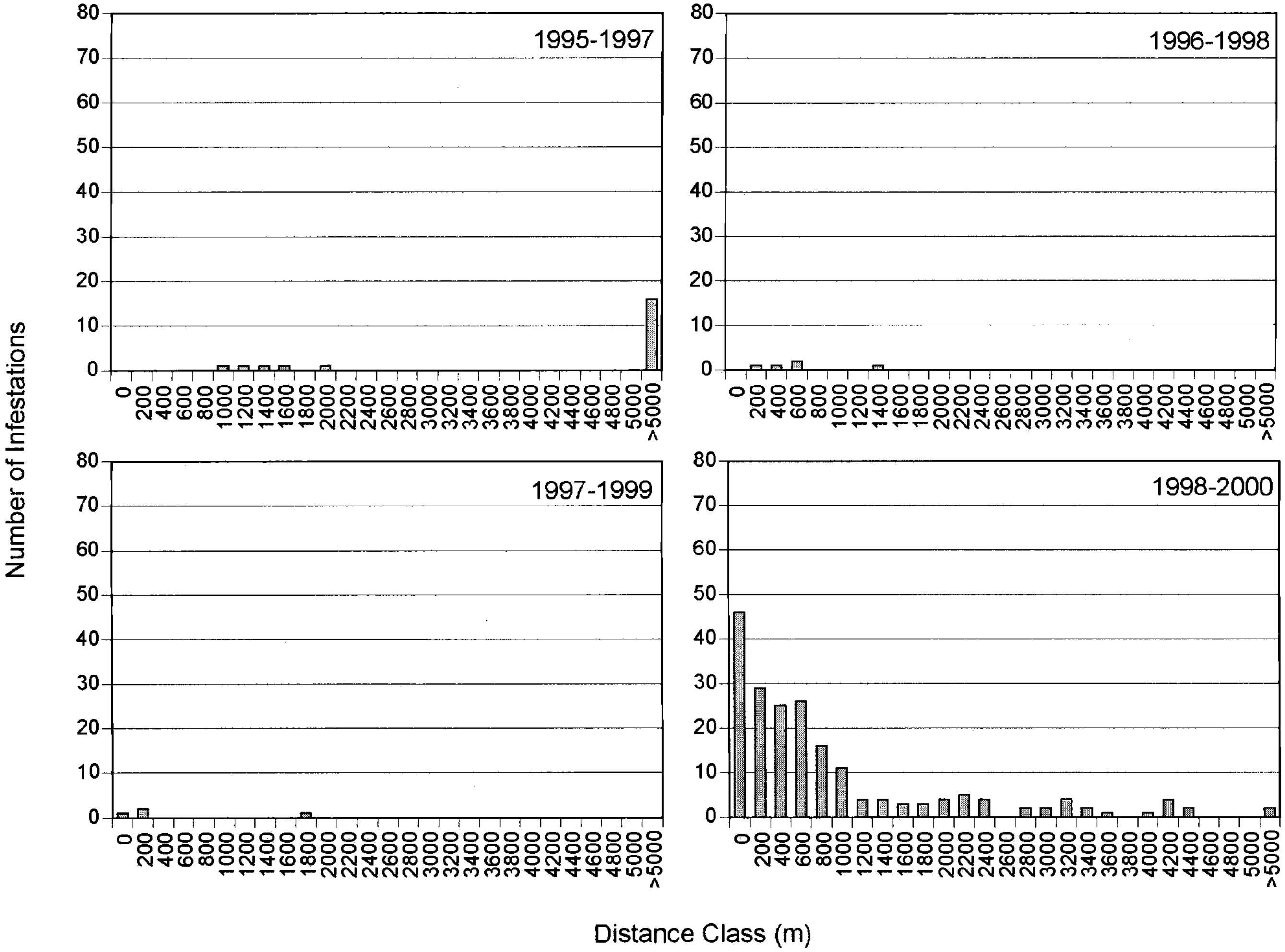


Figure 2.13. Number of infestations by nearest neighbor distance class for between 2-year infestations occurring on Bonners Ferry Ranger District.

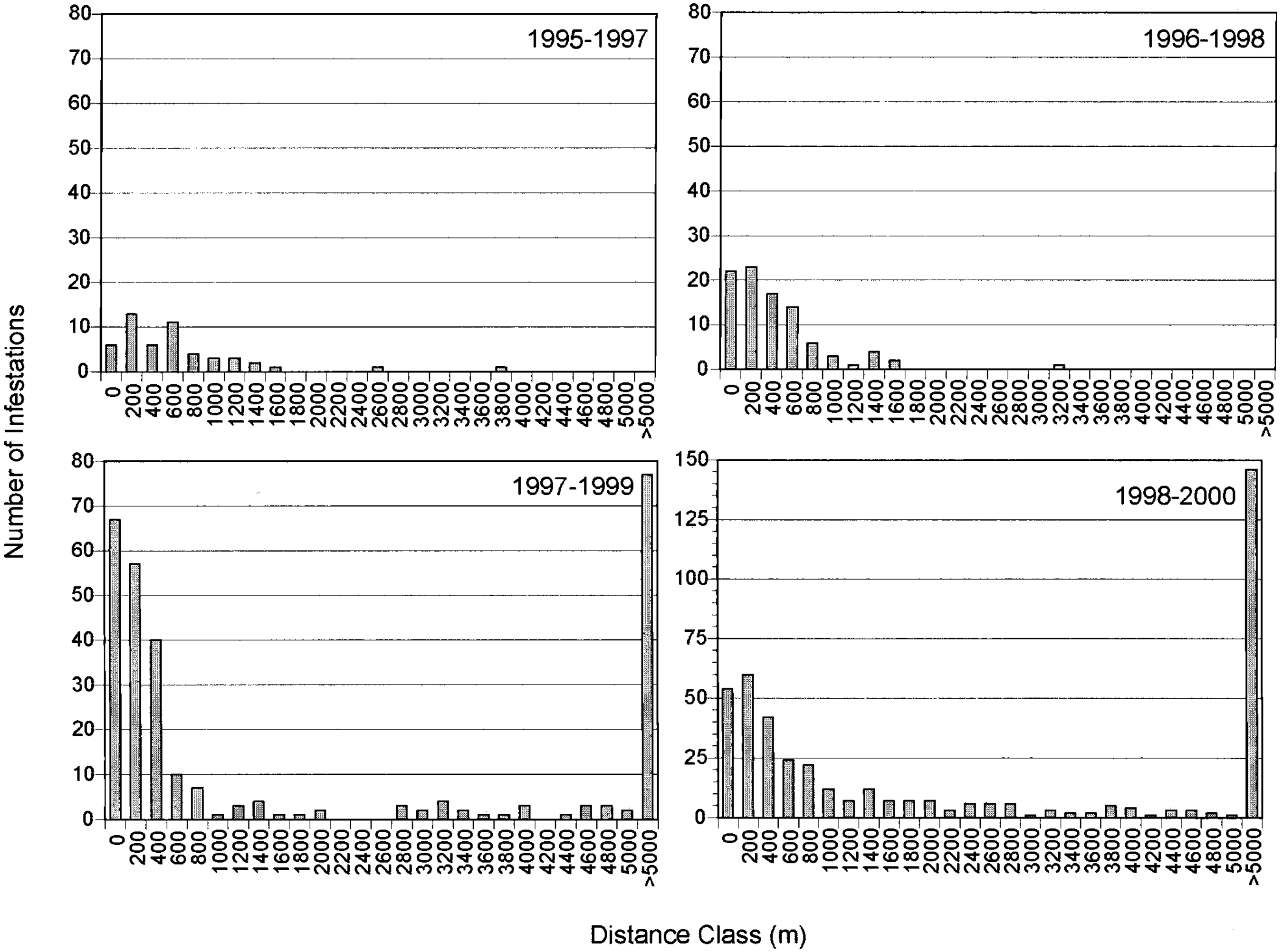


Figure 2.14. Number of infestations by nearest neighbor distance class for between 2-year infestations occurring on Salmon River Ranger District.

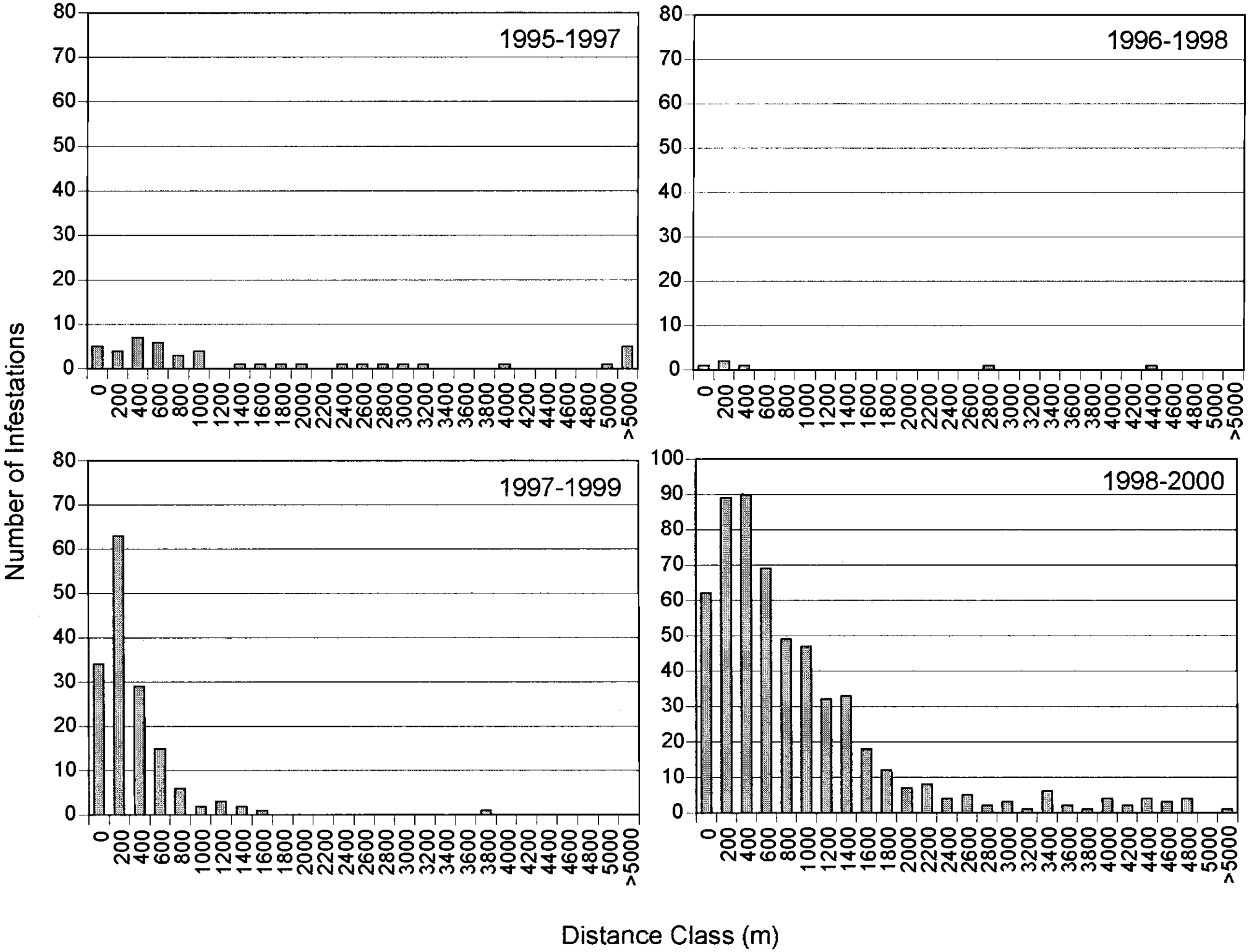


Figure 2.15. Number of infestations by nearest neighbor distance class for between 2-year infestations occurring on St. Joe Ranger District

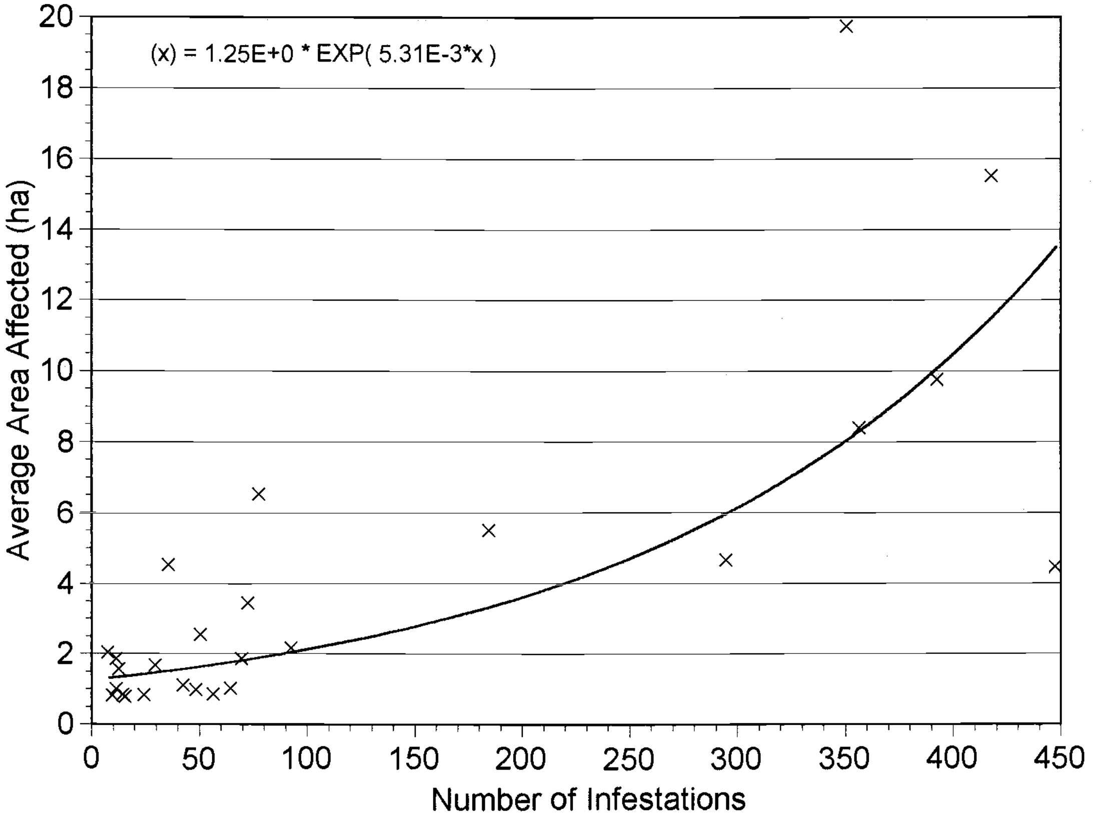


Figure 2.16. Relationship between number of infestations occurring on Priest Lake and Salmon River Ranger Districts and average hectares affected per infestation by Douglas-fir beetle.

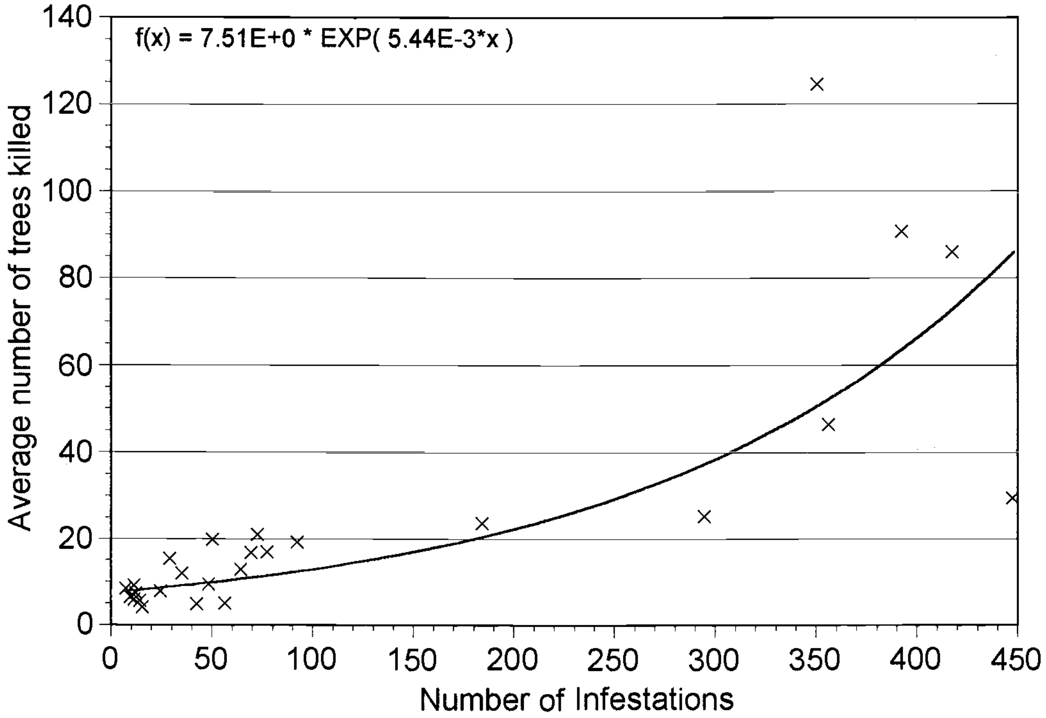


Figure 2.17. Relationship between number of infestations occurring on Priest Lake and Salmon River Ranger Districts and average numbers of trees killed per infestation by Douglas-fir beetle.

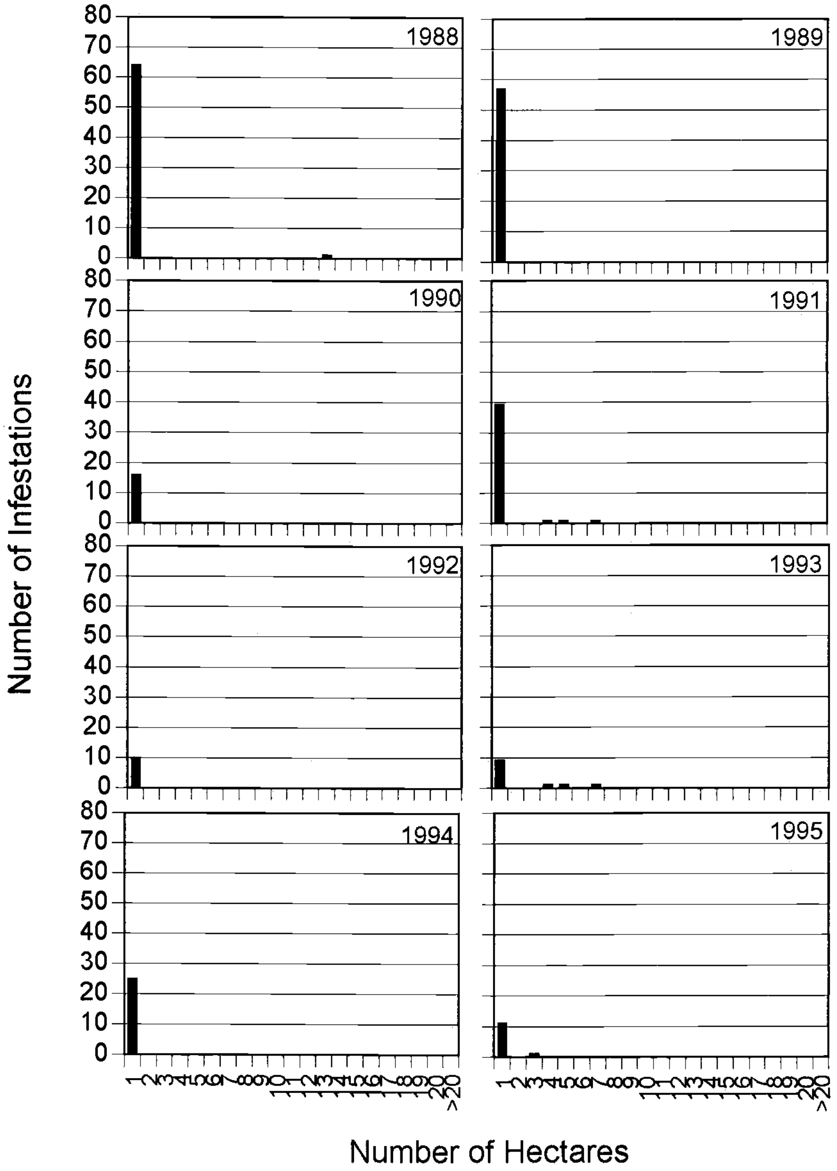
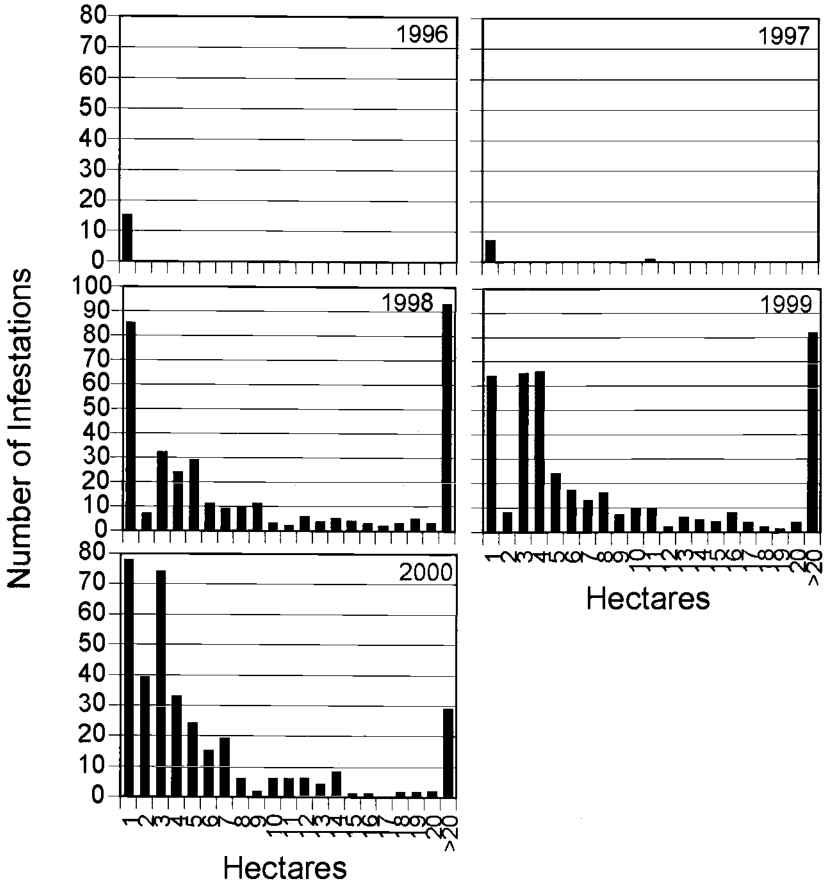


Figure 2.18. Frequency distributions of number of hectares affected by Douglas-fir beetle on Priest Lake Ranger District.



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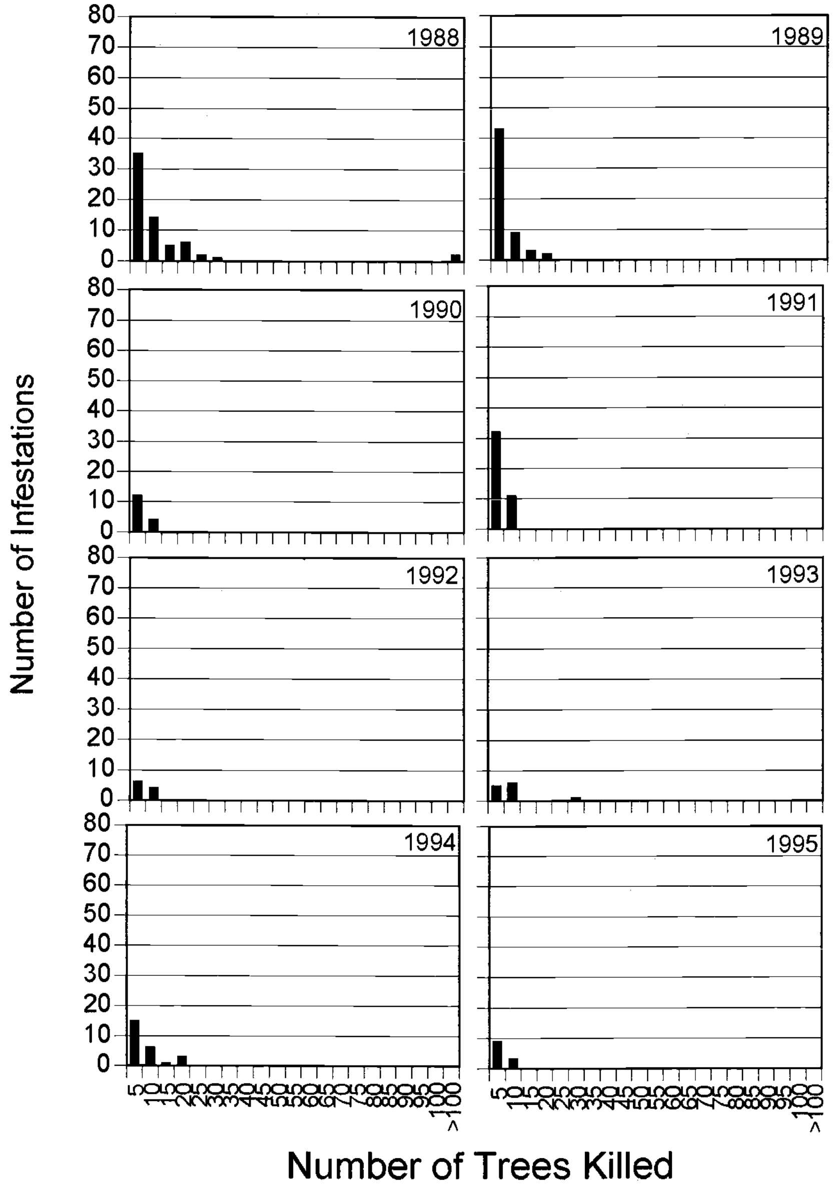
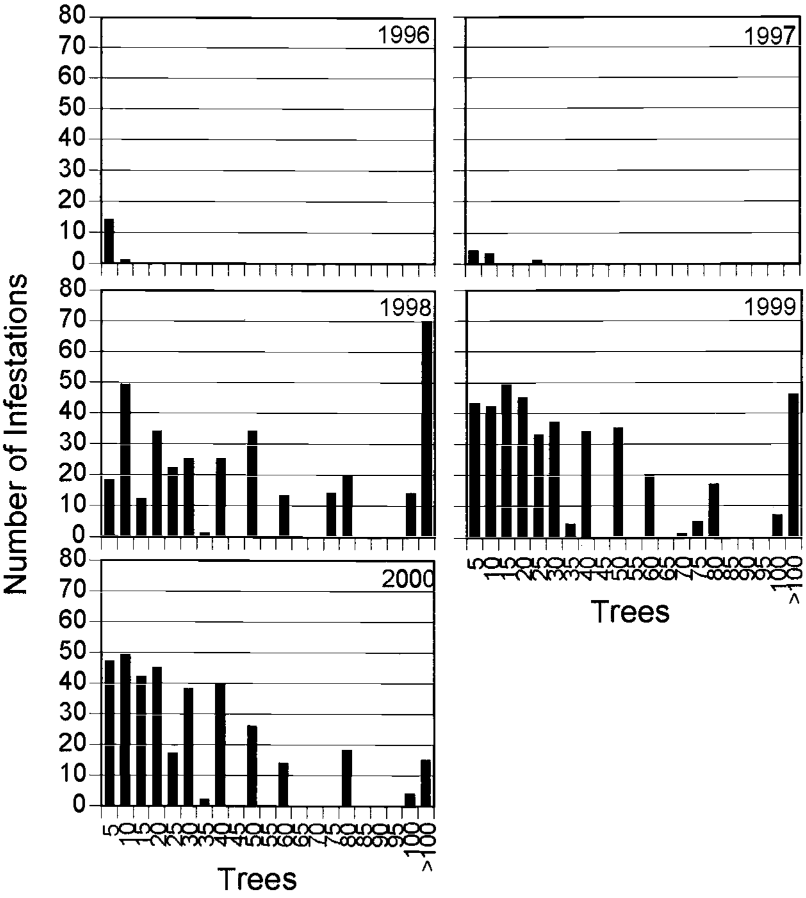


Figure 2.19. Frequency distributions of number of trees killed per infestation by Douglas-fir beetle on Priest Lake Ranger District.



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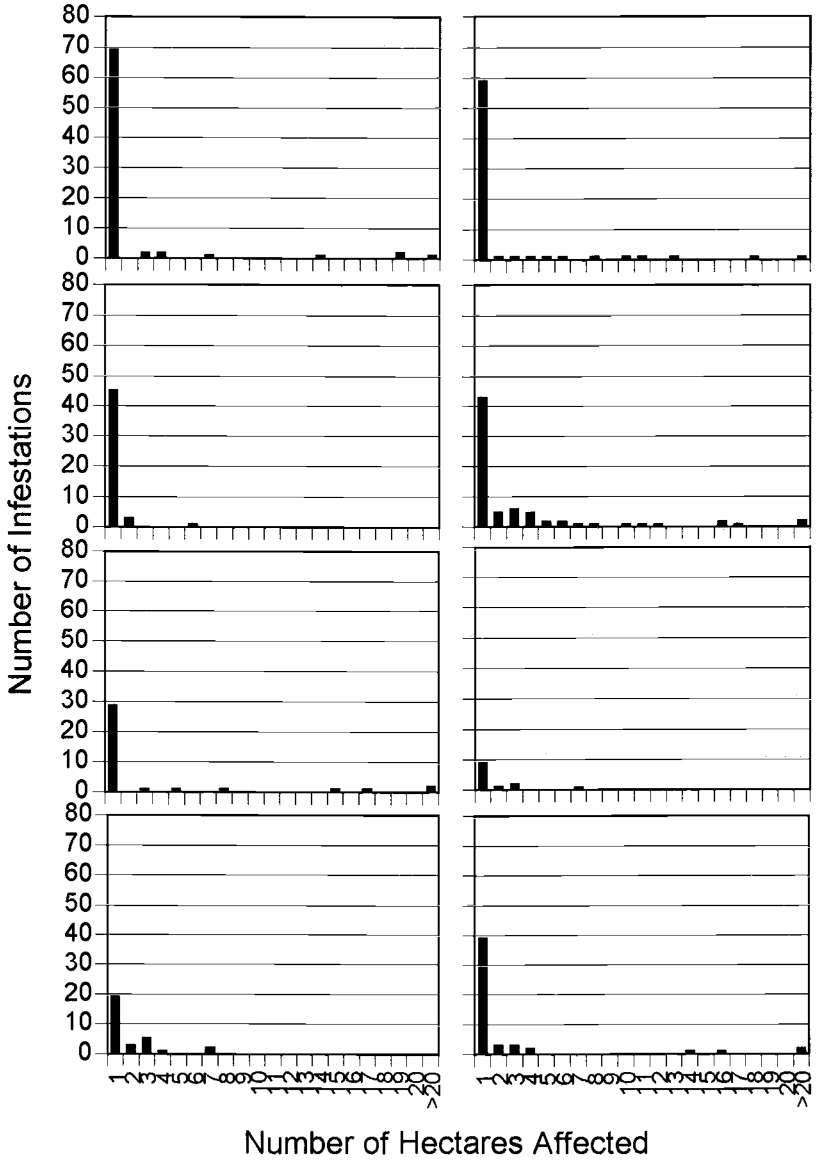
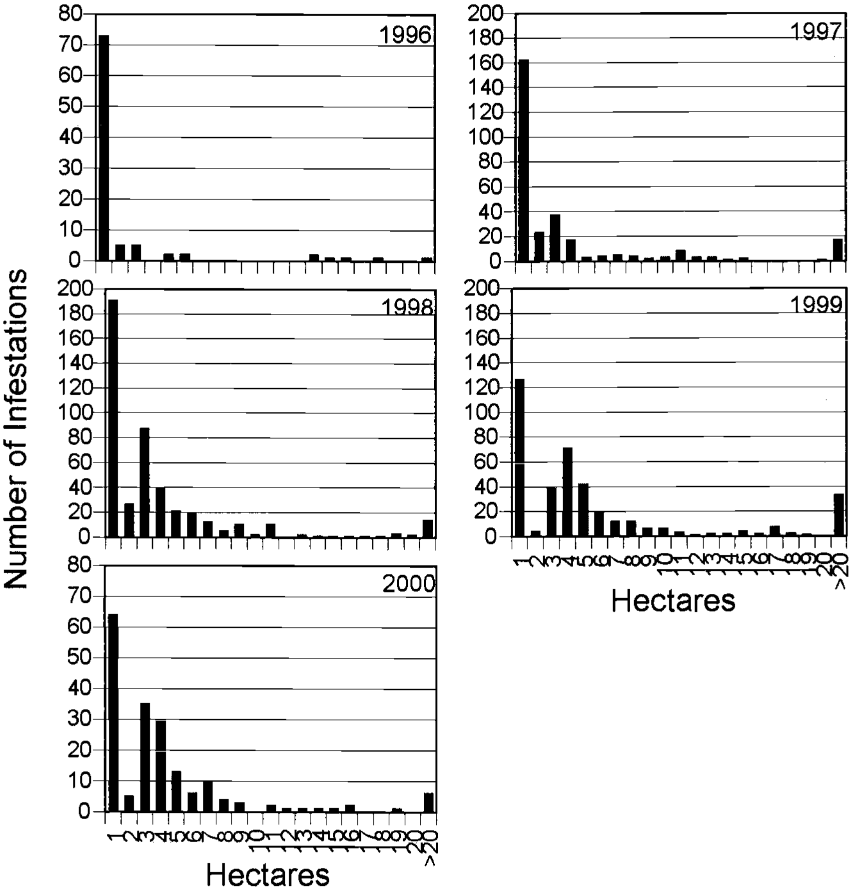


Figure 2.20. Frequency distributions of number of hectares affected by Douglas-fir beetle on Salmon River Ranger District.



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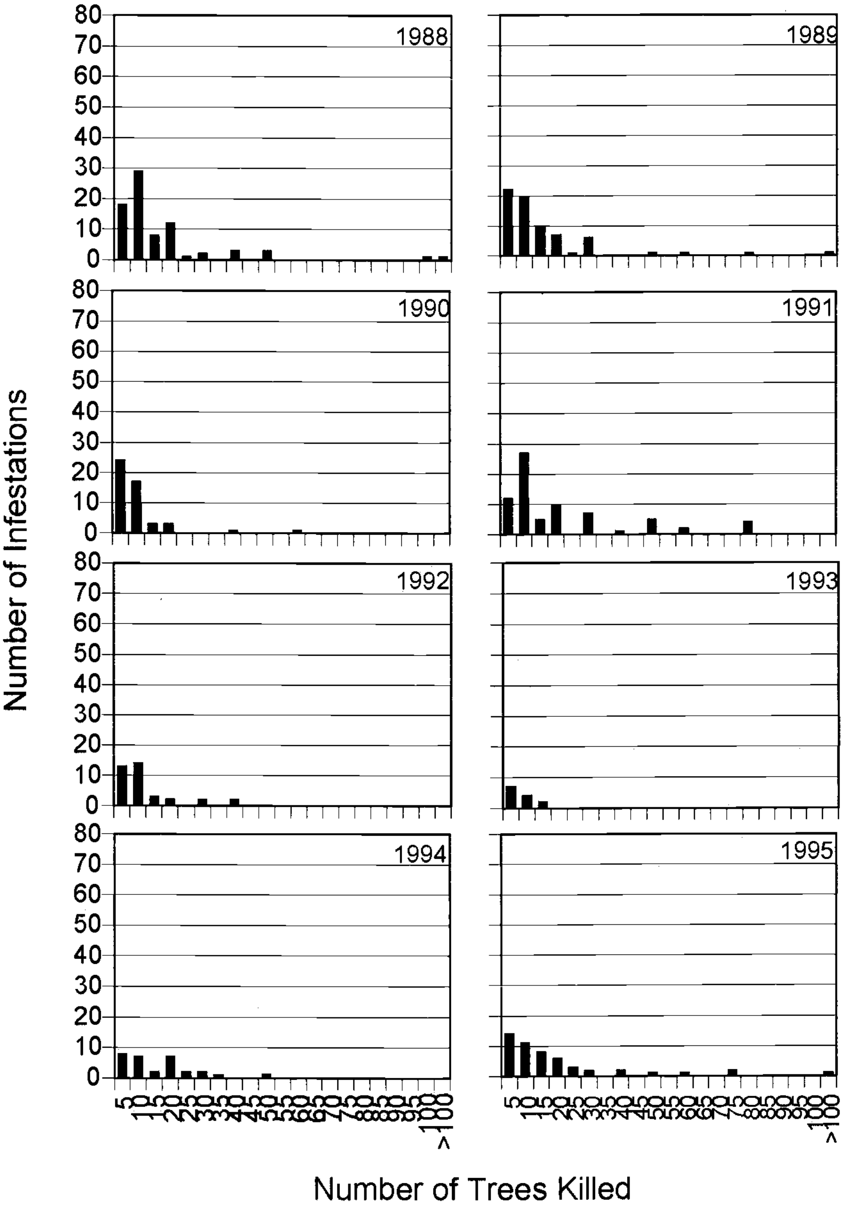

Figure 2.21. Frequency distributions of number of trees killed by Douglas-fir beetle on Salmon River Ranger District.

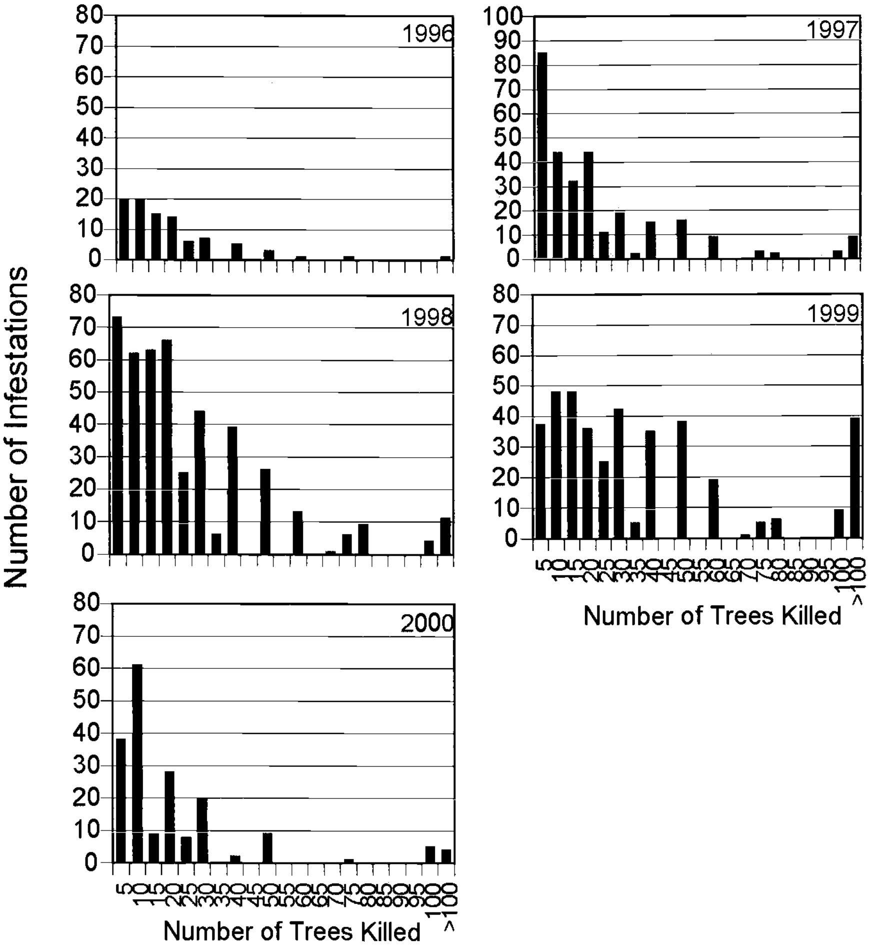

Figure 2.21 cont.

CHAPTER 3

DOUGLAS-FIR BEETLE LIPID LEVELS IN RELATION TO DEVELOPMENTAL POSITION ALONG THE LENGTH OF A TREE BOLE

Kevin J. Dodds and Darrell W. Ross

Abstract

The relationship of Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, brood adult lipid levels and position of development along infested tree boles was investigated. In addition, the effects of phloem and bark thickness on brood adult lipid levels were also tested. There were no significant differences ($P > 0.05$) in brood adult lipid levels in relation to bole position, phloem thickness, or bark thickness found in this study. Numbers of attacks, larval mines, brood adults, and parasitoid cocoons did not differ significantly by tree bole position. Results from this study suggest Douglas-fir beetle does not benefit, in the form of increased lipid levels, from oviposition at different bole positions.

Introduction

Bark beetles are economically important insects and knowledge of factors that affect their dispersal behavior could be useful for improving or developing new management techniques to reduce their negative impacts on forest resources. While aspects of bark beetle dispersal remain unclear, it is known that within a population beetles display varying degrees of flight capabilities. For example, some bark beetles can fly for extended periods of time, while others are incapable of flight or have limited capabilities (Atkins, 1966; Jactel, 1993).

Research on Douglas-fir beetle (DFB), *Dendroctonus pseudotsugae* Hopkins, has provided insight into the relationship of a beetle's physiological state and subsequent dispersal behavior. Atkins (1966) found that beetles with relatively high lipid levels were least likely to respond to pheromones and hence disperse, while beetles with low lipid levels responded immediately to pheromones. During a laboratory experiment, a flight of at least 90 minutes was required before DFB responded to pheromones (Bennett and Borden, 1971), thus suggesting the need to metabolize lipids in flight before pheromone arrestment occurred (Atkins, 1969). Relationships between lipid levels and pheromone arrestment or dispersal behavior have been found in other bark beetle species as well (Hagen and Atkins, 1975; Hedden and Billings 1977). In contrast, Botterweg (1982) found no relationship between lipid levels and flight capabilities or dispersal in *Ips typographus* L.

Several studies have investigated factors that influence bark beetle lipid levels. Atkins (1967) found temperature affected DFB lipid levels. Also, negative correlations have been found between bark beetle lipid levels and attack density, demonstrating the effect of intraspecific competition (Atkins, 1975; Botterweg, 1983; Anderbrandt et al. 1985). Mycangial fungi (Coppedge et al. 1995) and phloem width (Slansky and Haack, 1986) have also been correlated with lipid levels in bark beetles.

With the exception of *Ips calligraphus* (Germar), it is unknown whether host tree characteristics affect lipid levels in bark beetle brood adults. Nutrient levels (N, P, Mg, Fe, Zn) vary by bole height on Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, tree boles and could influence patterns of insect colonization (Schowalter and Morrell, 2002). Because there are variations in host tree characteristics and nutrient levels at different bole heights, it is possible colonizing bark beetles have evolved a mechanism for exploiting areas that are optimal habitat for developing brood. For example, in several *Dendroctonus* species, initial attacks occur at or near mid-bole (Miller and Keen, 1960; Safranyik et al. 1992; Fargo et al. 1978) and this might be attributed to optimal habitat selection. Consequently, brood developing at mid-bole could have higher lipid levels than developing brood elsewhere along the tree bole.

This research was initiated to determine if DFB brood development position along the length of tree boles and host tree characteristics (i.e., bark and phloem thickness) affected lipid levels in brood adults. Further, attack density, number of larval mines, brood adults, and parasitoids were also investigated to determine if there was any interaction with bole position.

Methods

Tree sampling

On April 27 to 29, 2002, prior to the flight period of DFB, Douglas-fir trees infested the previous year were felled and sampled from the Rock Creek Area (N 46°

34.619' W 113° 40.067'), 60 km southeast of Missoula, MT. The nine trees sampled ranged in diameter from 40.2 to 71.6 cm. All trees were removed from a small (< 1 ha), stand of pure Douglas-fir located on private land. An additional six trees were felled and sampled from one Douglas-fir stand on the Flathead National Forest (N 46° 25.316; W 114° 37.995) near Whitefish, MT on April 6, 2003. However, because DFB attacks were only successful on small portions of the tree boles, only two trees (41.1 and 53.3 cm dbh) were suitable for use in this study.

The portion of each tree bole infested by DFB was distinguished by the presence of successful egg galleries and brood adults. Total length of infested tree boles and dbh were recorded. Infested tree bole lengths ranged from 6.7 to 14.6 m ($\bar{x}$ = 9.7 m, SE ± 0.8). Bark samples were collected at three positions along the infested tree bole: 2 m from the bottom of the infestation, the mid-point of the infested tree bole, and 2 m down from the top of the infestation.

Four bark samples were collected from each bole position. Bark samples were taken randomly around the bole and were not based on cardinal direction. A 100-cm^2 hole saw attached to a power drill was used to remove bark samples from the infested tree bole. Bark samples were removed and placed individually in labeled plastic bags. Samples were transported to the laboratory on ice and stored in a freezer at -10° C until processed.

Bark Analysis

Brood adults were removed from bark samples and placed individually in numbered 7 ml glass vials with caps attached. Numbers of DFB entrance holes, larval mines, parasitoid cocoons, and bark and phloem thickness were recorded for each bark sample. Using micro-calipers, bark thickness was measured on four locations around the bark sample, while phloem thickness was measured in two locations making sure to account for any variability (i.e., fissures and ridges). To account for bark thickness variability, measurements were made so minimum and maximum thicknesses would be recorded.

Lipid Analysis

Beetles (N = 283 from 2002, 73 from 2003) removed from bark samples were placed in an oven to dry at 70° C for 48 hrs then weighed using a Mettler AE 240 balance. To determine the lipid levels of individual beetles, petroleum ether was used to remove lipids with methods modified from Langor et al. (1990). Five ml of petroleum ether was added to each vial, the vial was capped, then placed in a drying oven at 50° C for 24 hrs. Petroleum ether was removed and replaced with fresh solvent every 24 hrs for a total of 72 hrs. After the extraction was complete, beetles were oven dried for 48 hrs and reweighed. To ensure all lipids were extracted, dried beetles were again placed in petroleum ether for 24 hrs, oven dried for 48 hrs, and reweighed. Because there was no change in their extracted weights, it was assumed all extractable lipids were removed from the beetles during the initial 72-hour process. Lipid levels were calculated as percent loss in dry weight. Beetles that had 0% lipid levels were assumed dead at the time of sampling and discarded from the study.

After lipid extraction was complete, the gender of each DFB brood adult was determined (Jantz and Johnsey, 1964). In addition, pronotal width of each beetle was measured using microcalipers and a dissecting microscope.

Statistical Analysis

Analyses of variance (PROC MIXED, SAS 8.0) were conducted with trees as blocks and bark and beetle samples grouped by bole position to test for differences between bark and phloem thickness, numbers of entrance holes, brood adults, parasitoid cocoons, and larval galleries by height. Residual and normality plots were visually interpreted for homogenous variances and normality. Where necessary, data were log transformed to meet ANOVA assumptions. Differences between means were assessed using Tukey pairwise comparisons. In addition, relationships between bark and phloem thickness, and lipid levels and pronotal widths were investigated using analysis of covariance. Analysis of covariance was also used to investigate the relationship between parasitoid abundance and bark thickness. Differences in lipid levels and pronotal width by gender were assessed using ANOVA. All reported means and confidence limits were backtransformed from data used in the statistical analyses.

Results

There were no significant differences between brood adult lipid levels and bole position ($F_{2,20} = 0.75$, $P = 0.48$) (Table 3.1). Overall lipid levels ranged from 3.12% to 43.08%. Frequency distributions of all DFB lipid levels from the two years of sampling are shown in Figure 3.1. Frequency distributions of DFB lipid levels by bole position are shown in Figure 3.2. Analysis of covariance indicated there was no significant relationship between phloem thickness ($F_{2,20} = 0.87$, $P = 0.43$) or bark thickness ($F_{2,20} = 0.73$, $P = 0.49$) and lipid levels. Phloem width ranged from 1.5 mm to 4.9 mm, while bark width ranged from 7.45 mm to 32.55 mm. There were no significant relationships between pronotal width and bole position ($F_{2,20}$= 2.02, $P = 0.16$) (Table 3.1), phloem width ($F_{2,20}$= 1.89, $P = 0.18$), or bark thickness ($F_{2,20}$= 0.34, $P = 0.72$).

Phloem width, numbers of entrance holes, larval mines, brood adults, and parasitoid cocoons were not significantly different among the three bole positions (Table 3.2). However, bark thickness was significantly different among the three heights ($F_{2,20}$= 32.74, $P < 0.0001$). Bark at the bottom was thicker than the middle ($t_{20} = 4.95$, $P =$ 0.0002) and top ($t_{20} = 8.02$, $P < 0.0001$) of tree boles, while the middle was also thicker than the top ($t_{20} = 3.07$, $P = 0.02$). Analysis of covariance indicated there was no relationship between number of parasitoids and bark thickness ($F_{2,20}$= 0.92, $P = 0.42$).

Overall, the gender of brood adults was 55% female and 45% male. Average brood adult lipid levels were significantly higher in female (25.3%, CL = 22.4%, 28.2%) than in male (23.0%, CL = 20.1%, 26.0%) DFB ($F_{1,322}$= 6.88, $P = 0.009$). There was no difference in pronotal width between male and female DFB ($F_{1,318}$= 0.16, $P = 0.70$).

Discussion

Lipids are a source of energy for insect flight (Canavosa et al., 2001) and have been correlated with flight capabilities in bark beetles (Atkins, 1966; Slansky and Haack, 1986; Jactel, 1993). Because of their association with bark beetle dispersal potential, a better understanding of factors that influence lipid levels is important for understanding population movements. While lipid levels have been studied in several species of bark beetles, including DFB, there have been few previous studies on how host tree characteristics affect lipid levels in brood adults. This research investigated position of DFB development along a tree bole and how this related to lipid levels found in brood adults. In addition, colonization characteristics were investigated by height along the tree bole.

Before a discussion of lipid levels and host tree characteristics can be undertaken, it is important to note that there were no differences in intraspecific competition among bole positions. Intraspecific competition has been correlated with lipid levels in DFB and other bark beetle species, (Atkins, 1975; Botterweg, 1983; Anderbrant et al., 1985), and must be considered when evaluating factors that influence brood adult lipid levels among sample trees. Because entrance holes, larval mines, and brood adult densities were equal at the three bole positions, it was assumed developing brood encountered similar intraspecific competition levels at each position. Therefore, intraspecific competition should not have been responsible for any variations in lipid levels among bole positions.

No significant differences in lipid levels were found among the three bole positions. Within tree phloem width did not differ significantly among bole positions. Previous studies have also shown little variation in phloem width along the length of Douglas-fir boles below the live crown, with phloem becoming thinner within the live crown area (Gartner, 2002). The combination of equivalent lipid levels and consistent phloem thickness at the three bole positions could suggest a possible relationship between phloem width and brood adult lipid levels (Slansky and Haack, 1986). However, there was no significant relationship between phloem width and lipid levels found. Other factors, such as phloem nutrient level, could be more important at influencing lipid levels. Ayres et al. (2000) found a positive relationship between *Dendroctonus frontalis* Zimmermann size and phloem nitrogen levels of infested trees.

Atkins (1966) determined that DFB adults with lipid levels of less than 10% were unlikely to fly, those with 11-20% lipid content can fly and respond to pheromones, and brood adults with over 20% lipid content disperse but are less likely to respond to pheromones. In the current study, large numbers of beetles from both sample years had between 25 and 35% lipids (Figure 3.1). Based on Atkins (1966) data for potential to disperse, 67.7% of beetles sampled in this study, regardless of the bole position where they developed, would be capable of long distance dispersal.

As with phloem width, there was no relationship between bark thickness and lipid content of DFB. Bark thickness imparts some level of insulation on host tree phloem (Graham, 1924; Beal, 1934; Powell, 1967) and influences bark beetle brood survival during cold periods (Miller and Keen, 1960). Consequently, bark thickness may have influenced lipid levels in this study. Bark samples were not partitioned by cardinal direction, thus aspect-related differences in lipid levels could not be analyzed. Also, within sample bark thickness was not considered, so it was possible for a beetle developing in a thick bark portion of a tree to actually be experiencing habitat similar to that found in a thin bark section of tree.

Nutritional levels of phloem at the three bole positions were not sampled in this study. This was because sampled trees were already colonized and extensively fed upon by bark beetle brood and associated insects (e.g., Cerambycidae and Buprestidae) at the time of sampling. Although there is little variation in nutrient levels within the bole area (Schowalter and Morrell, 2002) infested by DFB, there is likely nutritional variation among trees within forest stands (Ayres et al., 2000), especially those of multiple age/size classes.

Female brood adults had higher lipid levels than males in sample trees, while pronotal widths were equal between the sexes. In *Dendroctonus* species, females locate and initiate attacks on host trees. Higher energy levels benefit dispersing females that must locate, begin colonization, and release aggregation pheromones that attract conspecifics to overwhelm host tree defenses. In comparison, Anderbrant et al. (1985) found higher lipid levels in male *Ips typographus* (L.) and attributed this to males being the colonizing sex, and therefore benefiting from increased energy reserves.

Studies investigating the relationship between parasitoid density and tree height have produced mixed results. Several studies found relationships between parasitoid density and height on tree boles (Ryan and Rudinsky, 1962; Mills 1986; Wermelinger 2002), while others have not (Gargiullo and Berisford, 1981). In the current study, there were no differences between parasitoid densities at each bole position. Although bark was significantly thinner at the upper bole position, an attribute commonly associated with higher parasitism levels, there was not a higher level of parasitoid abundance found there. Likely, parasitoids are exploiting thinned bark portions or crevices at all positions.

Bark beetles attacking host trees are affected by natural predators (Reeve, 1997; Aukema and Raffa, 2002), competitors (Schroeder and Weslien, 1994; Dodds et al., 2001), and host tree defenses (Raffa and Berryman, 1983). In addition to minimizing interactions with these mortality factors, bark beetles must also locate areas that are suitable for brood development and reproductive success. If lipid levels are viewed as a relative fitness measure, there seems to be no benefit to oviposition on different bole positions for developing DFB brood. Consequently, it is unlikely that the colonization behavior of attacking the mid-bole first, is a fitness response to seeking out and exploiting optimal habitat for developing brood. While no relationship between lipids and bole position were found, other factors (e.g., avoidance of predators or host tree defenses) might make oviposition at the mid-bole first beneficial.

Results from this study also suggest DFB brood adult lipid levels are not influenced by tree phloem or bark thickness. However, beetles emerging from different host trees within or between forest stands could explain the population level variations in brood adult lipid levels and subsequent flight behaviors found in wild populations. Further studies into the direct relationship of phloem characteristics and lipid levels may help explain landscape level dispersal behaviors of DFB and mortality patterns attributed to this beetle.

Acknowledgements

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Table 3.1. Mean (95% confidence limits) percent lipid content and pronotal width for Douglas-fir beetles collected at three bole positions.

	Bole Position			
Variable	Bottom	Middle	Top	*P*-value
Lipids content (%)	21.3 (17.8-25.5)	23.6 (19.5-28.2)	21.8 (18.0-26.3)	0.48
Pronotal width (mm)	1.9 (1.9-2.0)	1.9 (1.9-2.0)	1.9 (1.9-2.0)	0.16

Table 3.2. Mean bark and phloem thickness and Douglas-fir beetle and parasitoid population parameters from 100-cm^2 bark samples taken at three bole positions. 95% confidence limits are reported in parentheses.

	Bole Position			
Variable	**Bottom**	**Middle**	**Top**	***P*-value**
Bark (mm)	16.28 (13.87-18.91)	13.74 (11.82-16.12)	12.43 (10.69-14.44)	<.0001
Phloem (mm)	3.49 (3.22-3.82)	3.39 (3.1-3.71)	3.39 (3.1-3.71)	0.54
No. entrance holes	0.73 (0.55-0.92)	0.91 (0.72-1.09)	0.8 (0.62-0.98)	0.40
No. brood	3.49 (2.56-4.81)	2.64 (1.95-3.6)	2.77 (2.03-3.78)	0.29
No. parasitoid cocoons	1.36 (1.08-1.7)	1.32 (1.06-1.65)	1.58 (1.27-1.97)	0.41
No. larval galleries	24.95 (17.31-32.6)	31.14 (23.49-38.78)	27.36 (19.72-35.01)	0.11

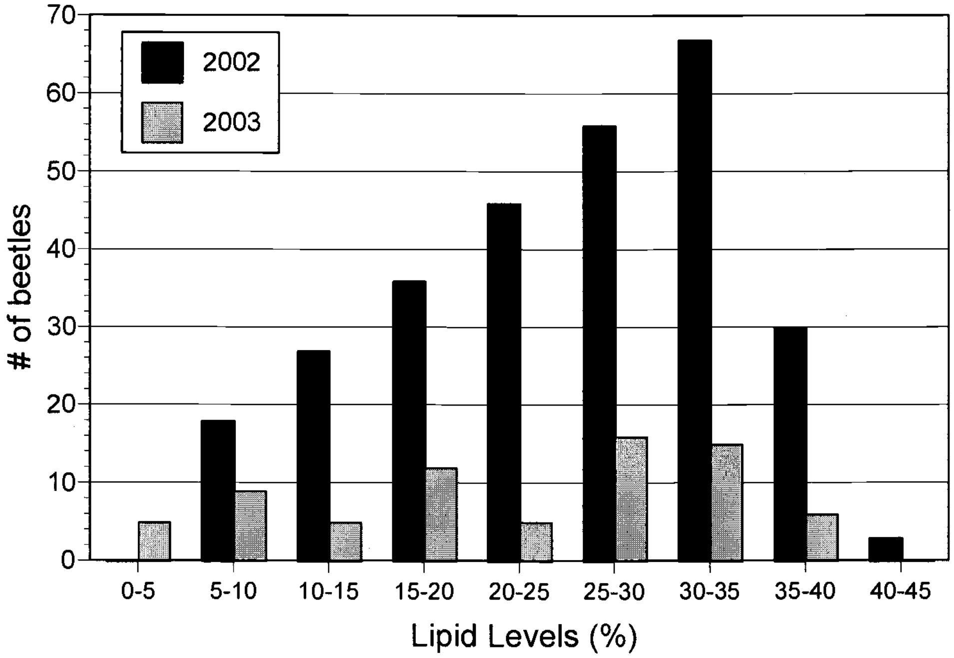

Figure 3.1. Frequency distribution of Douglas-fir beetle brood adult lipid levels (%) found in two years of sampling.

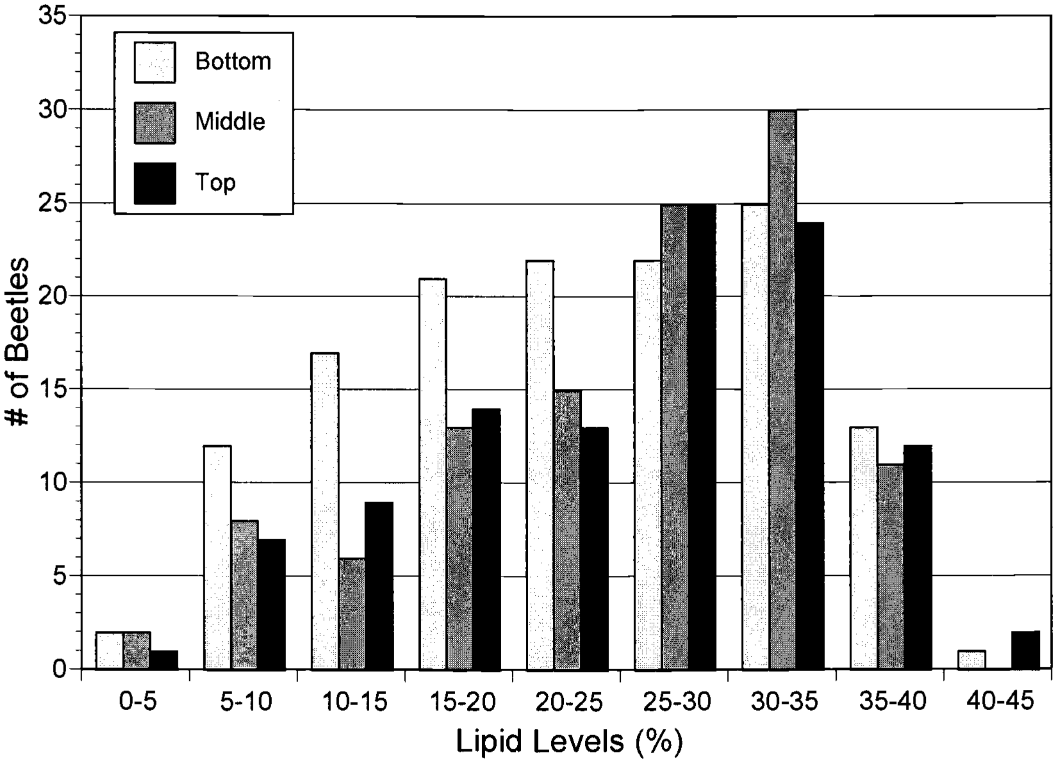

Figure 3.2. Frequency distribution of Douglas-fir beetle brood adult lipid levels (%) by bole position.

CHAPTER 4

SAMPLING RANGE AND RANGE OF ATTRACTION OF *DENDROCTONUS PSEUDOTSUGAE* PHEROMONE-BAITED TRAPS

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Abstract

Two mark-recapture experiments and a trap interference experiment were conducted to determine, respectively, the sampling range and range of attraction of *Dendroctonus pseudotsugae* (Coleoptera: Scolytidae) pheromone-baited traps in northern Idaho. To determine the sampling range, either live beetles or logs containing brood were marked with one of four colors of fluorescent powders. Colored beetles or logs were placed along transects oriented away from a central pheromone-baited trap at distances of 50, 100, 200, and 300 m. A release distance of 400 m was added to one mark-recapture experiment during the second year. To determine the range of attraction, a trap interference study was conducted. For this experiment, groups of three traps were oriented in equilateral triangles with distances of 50, 100, 200, and 300 m between the three traps. Distances between traps were changed daily to allow for adequate replication.

Mark-recapture studies indicated that most *D. pseudotsugae* were recaptured from distances ≤ 200 m from the pheromone-baited trap. On average, 95% of beetles recaptured were males. Results of the trap interference experiment provided no insight into the range of attraction of *D. pseudotsugae* pheromones.

Natural resource managers should attempt to place pheromone-baited suppression traps within 200 m of target *D. pseudotsugae* populations. Also, to minimize undesirable beetle-caused tree mortality, traps should be placed as far as possible from live trees that managers wish to protect.

Introduction

Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins (Coleoptera: Scolytidae), is an economically important bark beetle affecting Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Pinaceae), in North America. Although endemic *D. pseudotsugae* populations primarily breed in damaged and recently downed trees, epidemic populations may attack and kill many healthy live trees, sometimes causing severe economic losses. Silvicultural practices are often used to decrease or prevent the risk of infestation (Furniss 1959; Schmitz and Gibson 1996) and regional hazard rating systems have been developed to aid land managers in reducing susceptibility of stands to *D. pseudotsugae* outbreaks (Furniss *et al.* 1981; Negron 1998; Randall and Tensmeyer 1999; Shore *et al.* 1999). In addition, techniques employing anti-aggregation and aggregation pheromones are used as part of integrated *D. pseudotsugae* management programs (Ross and Daterman 1997*a*).

Douglas-fir beetle aggregation and anti-aggregation pheromones have been extensively studied (Pitman and Vité 1970; Kinzer *et al.* 1971; Furniss *et al.* 1972; Rudinsky *et al.* 1974; Libbey *et al.* 1983). Several of these pheromones have been used in the management of local *D. pseudotsugae* populations in the western United States. The anti-aggregation pheromone, 3-methylcyclohex-2-en-1-one (MCH), has been used to prevent infestation of windthrown timber (McGregor *et al.* 1984) and to protect high-risk stands and individual trees (Ross and Daterman 1994, 1995*a*, unpublished data). In contrast, the aggregation pheromones, frontalin (1,5-dimethyl-6,8-dioxabicyclo [3.2.1] octane) and seudenol (3-methylcyclohex-2-en-1-ol), are effective at attracting and capturing large numbers of *D. pseudotsugae* from local populations (Ross and Daterman 1994). Traps baited with these aggregation pheromones plus ethanol removed more beetles from a local population than trap trees, demonstrating their potential efficacy in management programs (Dodds *et al.* 2000).

A combination of frontalin, seudenol, and ethanol was determined to be the most attractive bait for *D. pseudotsugae* among all possible combinations of frontalin and three alcohols, seudenol, ethanol, and 1-methylcyclohex-2-en-1-ol (MCOL) (Ross and Daterman 1995*b*). Further, Ross and Daterman (1998) identified the pheromone blend and release rate that were optimal for trapping *D. pseudotsugae.* This release rate is high compared to other synthetic pheromone blends and is designed for use in suppression programs. Although optimal pheromone blends and release rates for trapping *D. pseudotsugae* have been identified, the attraction distances of these pheromones are unknown. To develop more efficient trapping programs for *D. pseudotsugae*, knowledge of attraction distances of pheromone-baited traps would be helpful.

Definitions of insect response to pheromone sources vary throughout the literature. Wall and Perry (1987) define two types of attraction distances that apply to the current study. The sampling range is the greatest distance that insects can be shown to move to a pheromone source in a given time period. This includes not only the distance from which insects exhibit directed movement toward the pheromone, but also includes the distance moved by the insect prior to contact with and response to the pheromone signal. In comparison, the range of attraction is the greatest distance over which insects can be shown to direct their movements to a pheromone source. The range of attraction consists of only the distance from which insects begin directed movement to the pheromone signal. Consequently, the range of attraction is always a shorter distance than the sampling range.

Mark-recapture studies are often used to determine the sampling range of insect pheromones. Mark-recapture studies have been commonly used to study scolytid behavioral patterns (Shore and McLean 1988; Salom and McLean 1991; Safranyik *et al.* 1992; Franklin and Grégoire 1999; Franklin et al. 2000). These mark-recapture studies incorporate fluorescent powder to mark either live beetles or breeding material from which beetles emerge and become contaminated with the powder prior to flight.

A common method used to determine the range of attraction of insect pheromones is a trap interference study (Wall and Perry 1978, 1980; Van Der Kraan and Van Deventer 1982; Dransfield 1984; Schlyter 1992). This type of study incorporates multiple traps in a set configuration replicated with different distances between traps (Schlyter *et al.* 1987; Schlyter 1992). Interference of pheromone sources occurs when pheromone-baited traps are close together, causing an overlap of pheromone plumes that results in trap competition and lower insect catches per trap. As greater distances separate pheromone sources, less interference and competition occurs between traps. Consequently, higher numbers of insects are captured in each trap. The distance at which traps begin to act independently and no longer interfere with one another is two times the range of attraction.

In the current study, we attempted both types of mark-recapture experiments (live beetles and marked breeding material) and a trap interference experiment, to determine, respectively, the sampling range and range of attraction, of the optimal blend of *D. pseudotsugae* pheromones (Ross and Daterman 1995*b*, 1998).

Methods

Experiment 1: Marked log study

Beetle-infested trees were located, felled and bucked into 50-70 cm long sections on 18-20 April 2000, before *D. pseudotsugae* flight began. Trees were cut from an area within the Wallace Ranger District, Idaho Panhandle National Forest, approximately 20 km east of Wallace, Idaho (N 47°37' W115°55'). Logs were transported to our study site (approximately 80 km) keeping them out of direct sunlight to prevent beetle emergence prior to initiating the experiment. Diameter at both ends and length of each log were recorded. End diameters were averaged and used along with length to estimate surface area of each log. Two 100-cm^2 bark samples were removed from opposite sides of each log for estimating brood adult densities prior to the start of the experiment and brood emergence. Bark samples were kept chilled until dissected in the lab. Brood density in each log was estimated from the average numbers of adult beetles in the two bark samples and the surface area of each log.

Three study sites were located within the Granite Plantation (N 47°59.398' W 116°43.602') on the Idaho Panhandle National Forest, approximately 40 km north of Coeur d'Alene, ID. The plantation was dominated by ponderosa pine, *Pinus ponderosa* Laws (Pinaceae), with few *P. menziesii* in the area. All study sites were located in areas that were generally flat, included a minimum component of *P. menziesii*, and were separated by at least 1 km. Because study sites covered a large area (28.3 ha), several stages of forest development and tree sizes were present at each site. Typically, clearings and areas of early regeneration (seedling to sapling stage) were intermixed with older stands (pole to small sawtimber stage). A few pole to small sawtimber sized *P. menziesii* were scattered throughout one study site.

At each site, four 300 m transects, one oriented in each cardinal direction, were delineated away from a central clearing (Fig. 4.1). At the center of transects, a 16-unit multiple-funnel trap (Lindgren 1983) was baited with *D. pseudotsugae* pheromones and ethanol. Traps were baited with 400 mg of frontalin and 200 mg of seudenol in polyvinyl chloride formulations, and 15 ml of ethanol in a plastic pouch formulation. Descriptions of chemicals and release rates can be found in Ross and Daterman (1998). A piece of dichlorovinyl dimethyl phosphate (DDVP)-impregnated plastic was added to each collection cup to kill recaptured insects.

Two logs standing upright were placed along each transect at distances of 50, 100, 200, and 300 m from the pheromone-baited trap. Fluorescent powder (Day-Glo® Color Corp., Cudahy, CA, USA) was applied to logs using a household ketchup dispenser. Approximately 6 g of powder was applied to cover each log thoroughly. All logs at the same distance from the trap (n = 8) were coated with the same color of fluorescent powder as follows: 50 m = Blaze Orange™; 100 m = Saturn Yellow™; 200 m = Horizon Blue™; 300 m = Signal Green™. Logs were coated with fluorescent powder twice, once at the beginning of the study on 24 April and again on 14 May.

Four logs separate from those used in the study were covered with fluorescent powder to determine the percent of emerging beetles accumulating a detectable amount of powder. Brood emergence traps with a surface area of about 700 cm^2 were placed on these logs and emerged beetles were recaptured and killed in Nalgene® bottles containing a piece of DDVP-impregnated plastic. Emerged beetles were inspected under UV light for the presence of fluorescent powder.

Traps were checked every 1-2 days and recaptured beetles were placed in plastic bags. The final trap collections of captured beetles occurred on 2 June. In the lab, beetles were separated by color under a UV light (Blak-Ray® Lamp, Model UVL-56) and examined under a microscope to determine the sex of each beetle (Jantz and Johnsey 1964).

Experiment 2: Marked beetle study

Beetles were collected in 16-unit multiple-funnel traps baited with *D. pseudotsugae* pheromones as in Experiment 1, but without DDVP. During spring 2000, flying beetles were captured at a site (N 47°34.691' W 116°42.496') on the Fernan Ranger District of the Idaho Panhandle National Forest, approximately 24 km southeast of Coeur d'Alene, Idaho. In spring 2001, beetles were captured from the Slate Creek Ranger District (N 45°41.626' W 116.051') of the Nez Perce National Forest, approximately 56 km south of Grangeville, Idaho. Traps were checked daily and all captured beetles were collected. Captured beetles were stored in cardboard cartons and kept chilled until further use in the experiment. Before release, collections were sorted and dead or injured beetles were discarded. Five subsets of 100 beetles from each year were stored separately for determination of sex ratio of pre-release beetles.

In the Granite Plantation, a 300 m transect was established leading away from a 16-unit multiple-funnel trap baited with *D. pseudotsugae* pheromones as previously described. Transect direction was selected randomly with certain limitations due to site characteristics (e.g., roads, private property boundaries). At distances of 50, 100, 200, and 300 m, 30 cm high milk crates were positioned on the ground to serve as beetle release platforms. Based on results obtained from the year 2000 releases, an additional distance of 400 m was added in 2001. Release platforms consisted of a 61 x 61 cm plywood platform with a smaller raised 41 x 41 cm plywood platform placed in the middle of the larger sheet of plywood. A sheet of plastic was placed under the platform to catch any beetles that fell off the release surface. For the 2001 releases, two transects with one pheromone-baited trap each, (approximately 1.75 km apart) were established to facilitate daily releases alternating between the two sites. Both transects were oriented in the same direction as the previous year.

Beetles were coated with fluorescent powder using the same color and distance combinations described for Experiment 1. In 2001, Aurora Pink™ was used to mark beetles released from 400m. In 2000, one hundred beetles were released from each distance and, in 2001, two hundred beetles were released from each distance. Beetles were gently shaken in cardboard cartons with a small amount of fluorescent powder to mark them. Beetles were placed each morning, on release platforms between 1000 and 1200 h, on 24 May, 4 and 6 June, 2000 and 26 – 30 June, 2001. After approximately 3 h, beetles remaining on the platforms were counted to determine the numbers that initiated flight. The pheromone-baited trap was checked for 2-d (at 1000 to 1200 hrs) following the release and all beetles recaptured were handled in the same way as Experiment 1. Beetles were returned to the lab, separated under a UV light, and examined under a microscope to determine sex.

Data for Experiments 1 and 2 were analyzed using a linear regression model. Before analysis, an arcsin square root transformation was performed on proportion mean recaptures of beetles to meet the assumptions of equal variances. Statistical analysis was conducted with SAS version 8.0.

Experiment 3: Trap interference study

Four sites were located on the Fernan Ranger District, approximately 32 km southeast of Coeur d'Alene, ID (Table 4.1). The study area was in a mixed conifer forest with an ongoing *D. pseudotsugae* outbreak. All sites were located in recently harvested stands with low brush and understory distributed throughout. The four sites were located from 0.75 to 1.0 km apart.

At each site, three 12-unit multiple-funnel traps were baited with *D. pseudotsugae* pheromones (see Experiment 1) and placed in an equilateral triangular configuration on 15 May. Beetles captured in these traps were collected daily from 16 May to 18 May, 22 May to 25 May, and 2 June to 6 June for a total of 12 sample days. During the periods of 18-21 May and 25 May to 1 June, traps were kept down due to cold rainy weather. On each sample day, every site had one of four intertrap distances (i.e., distance between traps) of 50, 100, 200, or 300 m, so that on a single trapping day all intertrap distances were represented (Table 4.2). The next sample day, traps were moved to another distance and this continued until the four sample distances occurred at each site. Initially, one intertrap distance was chosen randomly for each site. After the initial distances were determined, a systematic approach was used to designate subsequent intertrap distances. The study was replicated until each distance had occurred three times at each site. All intertrap distances were determined using a global positioning system (Garmin III+, Garmin Corp., Olathe, Kansas).

At the time intertrap distances were changed, all insects captured in the pheromone-baited traps were collected and placed individually in plastic bags. Insects were returned to the lab where they were sorted and all *D. pseudotsugae* were removed and counted. A subset of 100 beetles from five randomly selected sample days and traps was sexed and the percent male was calculated.

Daily beetle catches from the three traps at each site were averaged to determine the number of beetles caught per trap at each distance for every day. A log transformation was used to meet the assumptions of an ANOVA. These numbers were then analyzed using a 4 x 4 Latin square design with date and site as blocks and distances as treatments. To meet the requirements of the Latin Square design, data were divided into three separate series. Each series consisted of the four sites with each of the four distances occurring once on every site. Data reported are non-transformed. Statistical analysis was conducted with SAS version 8.0.

Results

Experiment 1: Marked log study

Surface area of logs ranged from 0.57 to 0.99 m^2 with an average ± SE of 0.74 ± 0.007 m^2. Brood density per log varied considerably from 0 to 250 with an average ± SE of 56.4 ± 6.1. On average, between 422 and 466 beetles were released from each distance, with between 2.9% and 7.2% average recaptures (Table 4.3). Ninety-six percent of beetles recaptured were male. The relationship between distance and beetle recaptures for Experiment 1 was not significant ($P = 0.15$; $r^2 = 0.19$; $n = 12$) (Fig. 4.2). However, most beetles were caught from release distances of 200 m or less: 29% of recaptures occurred from 50 m, 59% from ≤ 100 m, and 88% from ≤ 200 m. Total recapture rate for the experiment was 5.6%. Mean number ± SE of captured unmarked *D. pseudotsugae* per trap was 707.0 ± 470.5.

A total of 24 beetles emerged from sample logs dusted with fluorescent powder for determining the success rate for marking beetles. Of these, 23 (95.8%) were marked with fluorescent powder.

Experiment 2: Marked beetle study

On average, between 95 and 117 beetles were released from platforms in Experiment 2, with between 1% and 7% recaptured (Table 4.4). All recaptured beetles were caught on the first day after release. Before sorting, marking, and release, an average of 91% of beetles were male. Ninety-five percent of recaptured beetles were males. There was a negative relationship between beetle recapture and release distance ($P = 0.0004$; $r^2 = 0.30$; $n = 37$) (Fig. 4.3). Over 90% of beetles recaptured were released from distances $\leq$ 200 m. Total recapture rate for the experiment was 4.2%.

Experiment 3: Trap interference study

Mean number of beetles caught at each intertrap distance ranged from 112 to 1061 (Table 4.5). The trap catches at different distances did not differ in any of the three series ($0.21 < P < 0.40$ for the three series). Lowest average beetle catch per trap occurred at the 50 m distance in each series. Ninety-five percent of beetles captured were male.

Discussion

Attraction distances to pheromone sources have been well studied for Lepidoptera (see Wall and Perry 1987), but there have been fewer studies with

Coleoptera. Studies of beetle species responding to pheromones have found distances ranging from 15 to 500 m (Vité and Gara 1962; Mason *et al.* 1990; Barclay *et al.* 1998).

Of the three experiments conducted during this study, Experiments 1 and 2 provided similar results. In contrast, results from Experiment 3 were inconsistent and difficult to interpret. Considering the results from Experiments 1 and 2, *D. pseudotsugae* pheromone-baited traps appear to collect beetles from at least 200 m, with a marked decrease in captures at greater distances.

There was no significant relationship between distance from the pheromone-baited trap and beetle recaptures in Experiment 1. Similar numbers of beetles were recaptured at all distances. Results of Experiment 1 suggest that *D. pseudotsugae* pheromone-baited traps attract similar numbers of beetles up to distances of at least 300 m.

Previous laboratory studies concluded that *D. pseudotsugae* require an extended flight period before a response to pheromones is elicited (Bennett and Borden 1971). However, Atkins (1966) found that *D. pseudotsugae* arrestment to pheromones was dependent on lipid levels, with beetles having high levels being host negative (dispersing) and beetles with low levels responding immediately to pheromone sources. Wood (1982) hypothesized that a portion of beetles emerging from host material would respond directly to local pheromone sources, but others would disperse. Thus, we did not believe that placement of logs close to pheromone traps would negatively affect trap catches

Beetle recaptures were relatively low in this study, but were similar to those found in other studies where fluorescent powder was used to mark breeding material

(Linton *et al.* 1987; Werner and Holsten 1997). After the initial application of fluorescent powder to logs, intermittent, heavy rain occurred for several days. While fluorescent powder remained on logs, it changed consistency, became hardened and was unevenly distributed. An earlier study showed that marking efficacy is reduced when water is sprayed on logs coated with fluorescent powder (Cook and Hain 1992). Two of the areas used in this experiment had little or no *P. menziesii*, so local populations of *D. pseudotsugae* should have been low. However, numerous unmarked *D. pseudotsugae* were captured. Because of the rain, it is likely that some unmarked beetles captured during this study emerged from experimental logs and did not become marked with fluorescent powder or had the mark removed by rain. Consequently, numbers of captures may have been higher than suggested by the data.

Over 95% of beetles collected from logs with emergence traps were marked with fluorescent powder. Although our estimate is similar to numbers found for *D. ponderosae* Hopkins (McMullen *et al.* 1988) and *D. frontalis* Zimmermann (Cook and Hain 1992), it may not reflect the degree of marking on experimental logs. The logs with emergence traps were left under a mature forest canopy that provided some protection from direct rainfall. Also, the emergence traps themselves may have prevented wind and rain from removing or redistributing the powder. Furthermore, beetles emerging beneath a trap likely spent more time in contact with the bark surface and were more likely to become marked. As a result, a higher percentage of beetles emerging beneath traps were probably marked with fluorescent powder compared to those emerging from a log in the experimental area.

Percent recaptures in Experiment 2 were similar to estimates found for other bark beetle species (Shore and McLean 1988; Salom and McLean 1990). Average recaptures were similar among 50, 100, and 200 m release distances, but were at least four times lower from 300 or 400 m distances. Regression analysis indicated that beetles may be attracted to the pheromone-baited traps from as far away as almost 600 m, but extrapolation beyond the limits of the data can be misleading and should be interpreted cautiously. Traps caught high numbers of beetles from distances ≤ 200 m, with a marked drop from distances > 200 m.

While results from Experiments 1 and 2 were similar and provided information on the sampling range, results from Experiment 3 were variable and provided no clear insight into the range of attraction. There were no significant differences among the four intertrap distances studied. Intertrap distances were chosen based on preliminary studies with intertrap distances as close as 5 m, so it is unlikely that the insignificant results were due to using intertrap distances greater than the range of attraction. Instead, it is likely trap interference studies will not provide reliable results in a heterogeneous environment such as northern Idaho.

The trap interference method of determining attraction radius has been used for tsetse flies (Dransfield 1984), Lepidoptera (Wall and Perry 1978, 1980, 1981) and bark beetles (Schylter 1992). Although this experimental method has been successful in agricultural settings, there are several factors that may have limited the effectiveness of this type of experiment in the study areas. First, topography varied within and among sites and this likely influenced local wind patterns and thus, pheromone dispersion in these areas. Second, stand characteristics within and surrounding experimental sites also varied and may have influenced local air movements as well. Third, bark beetle populations are spatially variable over a landscape. Consequently, proximity to sources of beetles may have had a greater influence on individual trap catches than intertrap distance. Fourth, silvicultural activities, including firewood cutting and recent prescribed burning, varied among the sites. These activities may have reduced local beetle populations and provided competing sources of attraction in the form of slash and fire-stressed trees. Finally, exposure to wind varied among sites. Constant winds over 8 kph inhibits beetle flight (Rudinsky 1963). Two sites consistently experienced stronger winds than others (pers. obs.), likely affecting beetle catches at those sites. Although wind speed was not measured, it was clear that wind was impacting beetle catches at the more exposed sites (Salom and McLean 1991). Trap interference studies are probably more suitable for areas where the landscape is more homogenous (i.e. agricultural fields, flat areas) than encountered in our study area.

Over 90% of all beetles captured or recaptured were male. Sex ratio of *D. pseudotsugae* captured in pheromone-baited traps is heavily male biased during the early portion of their flight period (Ross and Daterman 1997*b*), a time corresponding to trapping in the current studies. All captures of beetles in these experiments were concluded by early June.

Knowledge of the sampling range and range of attraction of pheromone-baited traps is useful in the development of effective management programs that attempt to reduce insect populations through trapping. These distances are important when determining where to place traps relative to target insect populations, other traps, and potential host trees. However, although these terms are simple to define in theory, they are difficult to quantify precisely in the field. Sampling range and range of attraction are likely to be influenced by a variety of environmental factors such as topography and weather that may affect dispersion of pheromones from trap lures.

Although sampling range and range of attraction may be difficult to quantify precisely, important conclusions that are useful for natural resource managers can be gleaned from experiments that attempt to measure these distances. For example, in Experiment 2, beetles were collected from 400 m, which suggests a sampling range of at least this distance. However, because 88-90% of recaptured beetles were from distances ≤ 200 m in Experiments 1 and 2, this distance is more important to natural resource managers designing trapping programs for suppression. While some beetles were caught at greater distances, significantly reduced catches beyond 200 m suggest that for practical applications managers should consider this to be the limit from which traps will collect beetles. Consequently, natural resource managers who use pheromone-baited traps to monitor or manage local *D. pseudotsugae* populations should place traps within 200 m of a target population. Also, traps should be placed as far as possible from trees or stands managers wish to protect. These results are only applicable to multiple-funnel traps baited with the same lures that we used. Similar studies would be needed to determine critical trapping distances for different trap and lure combinations.

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Table 4.1. Location and site characteristics for the 4 sites used in Experiment 3. Plot locations were determined with a GPS.

Site #	*Plot Location*	**Slope (°)**	**Aspect**	**Stand conditions**
1	N 47° 33.219' W 116° 39.798'	34	SW	No residual overstory trees, open area, low brush
2	N 47° 34.072' W 116° 40.002	22	SW	No residual overstory trees, open area, low brush
3	N 47° 34.198 W 116° 40.911'	12	SW	Few residual overstory trees (Douglas-fir) present
4	N 47° 34.339' W 116° 41.596'	14	SE	Recently burned area, residual Douglas-fir and western larch

Table 4.2. Experimental design for the trap interference experiment (Experiment 3). On each date, one intertrap distance was represented at each site.

Date	**Site 1**	**Site 2**	**Site 3**	**Site 4**
		Intertrap Distance (m)		
16-May	300	200	100	50
17-May	200	100	50	300
18-May	100	50	300	200
22-May	50	300	200	100
23-May	50	300	200	100
24-May	100	50	300	200
25-May	200	100	50	300
2-June	300	200	100	50
3-June	300	200	100	50
4-June	200	100	50	300
5-June	100	50	300	200
6-June	50	300	200	100

Table 4.3. Mean number (± SE) of *Dendroctonus pseudotsugae* released from *Pseudotsugae menziesii* logs and percent recaptured for the marked log study. Mean numbers of beetles released and recaptured are based on totals for 8 logs at each distance for 3 replications.

Distance released from trap (m)	No. of beetles released	% beetles recaptured
50	449.3 ± 93.0	6.2 ± 3.6
100	422.7 ± 46.6	7.2 ± 1.9
200	457.0 ± 171.2	6.2 ± 1.4
300	466.0 ± 82.0	2.9 ± 0.5

Table 4.4. Mean number (± SE) of *Dendroctonus pseudotsugae* released and percent recapture for marked-beetle study.

Distance released from trap (m)	No. beetles released	% beetles recaptured
50	94.8 ± 16.5	6.2 ± 1.4
100	116.5 ± 19.6	6.0 ± 0.9
200	96.2 ± 20.4	7.0 ± 2.4
300	104.8 ± 18.0	1.3 ± 0.3
400	115.6 ± 19.5	1.0 ± 0.33

Table 4.5. Mean number (± SE) of *Dendroctonus pseudotsugae* caught per trap at each intertrap distance from the three Latin square series.

	Intertrap Distance			
Series	50 m	100 m	200 m	300 m
1	263.7 ± 105.7	732.8 ± 275.9	328.4 ± 50.6	707.3 ± 214.1
2	112.4 ± 46.8	171.3 ± 60.9	206.0 ± 49.2	286.2 ± 141.2
3	207.4 ± 77.4	672.7 ± 190.4	1061.0 ± 305.4	590.8 ± 121.8
Overall mean	**194.5 ± 44.2**	**607.0 ± 234.9**	**531.9 ± 266.9**	**528.1 ± 125.5**

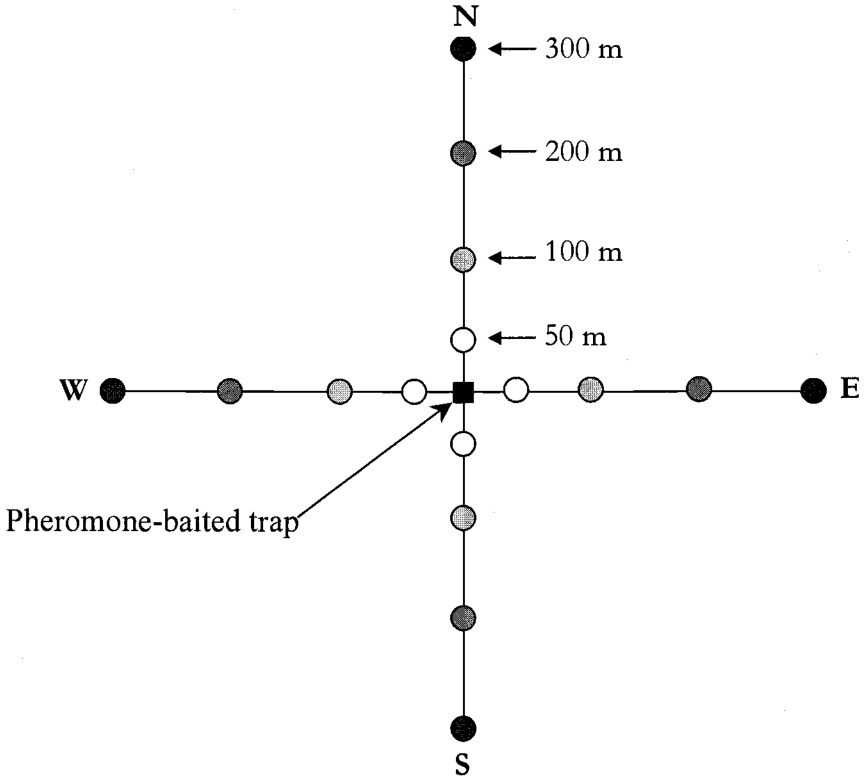

Figure 4.1. Schematic diagram of the experimental design used in Experiment 1. Two *Dendroctonus pseudotsugae*-infested logs were placed at each distance along all transects. A pheromone-baited trap was placed in the center of transects.

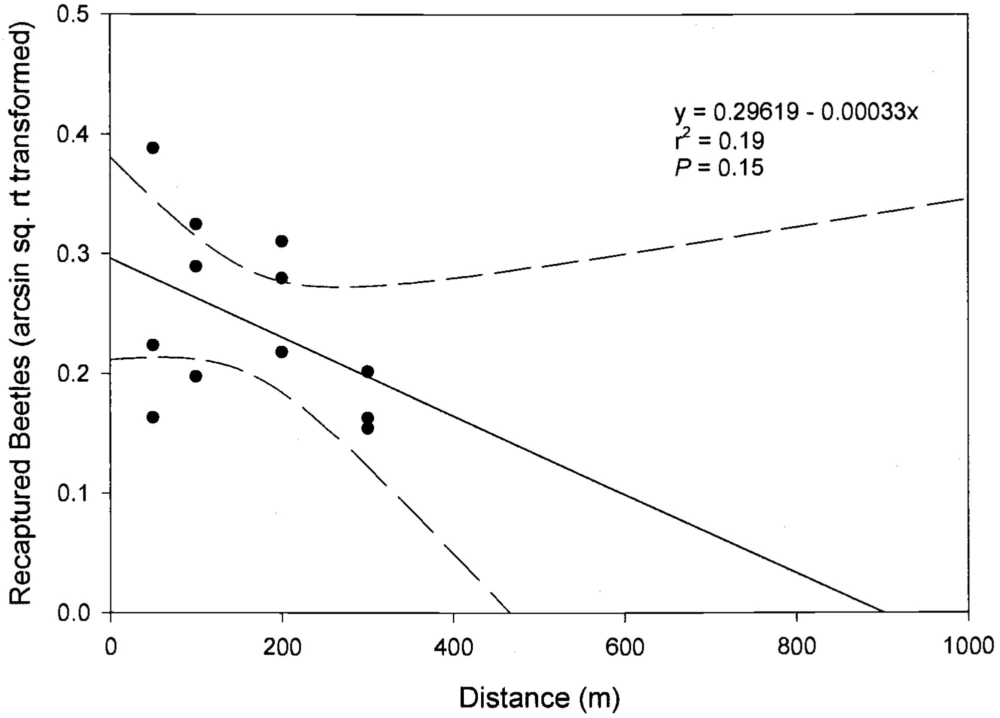

Figure 4.2. Relationship between the percent *Dendroctonus pseudotsugae* recaptured (arcsin √ transformed) and distance from the pheromone source in the marked log study (Experiment 1).

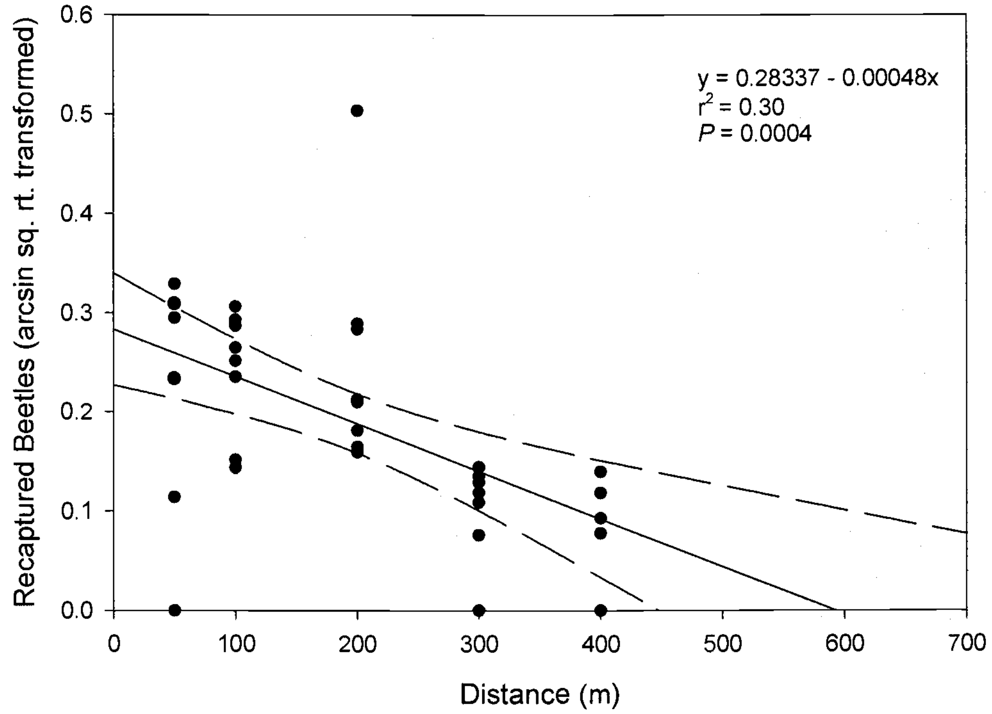

Figure 4.3. Relationship between the percent *Dendroctonus pseudotsugae* recaptured (arcsin √ transformed) and the distance from the pheromone-baited trap in the marked beetle study (Experiment 2).

CHAPTER 5

GENERAL CONCLUSIONS

Studies were conducted to gain a better understanding of the biology of Douglas-fir beetle (DFB), *Dendroctonus pseudotsugae*, and provide tools for the management of this species in the interior western US. Three studies were completed: (1) an investigation into the spatial relationship of DFB infestations over large landscapes and multiple years, (2) relationship between brood adult lipid levels and position of development along the length of tree boles and host tree characteristics, and (3) determination of distance at which DFB pheromone-baited traps attract beetles.

Spatial analysis of DFB infestations provided important insights into the relationship of infestations from one year to another, while also providing relevant information for natural resource managers. On three of the four ranger districts studied, highest number of infestations occurred directly adjacent to previous year infestations. All ranger districts had approximately 50% of infestations occurring ≤ 200 m from previous year infestations during epidemics. Risk rating models were developed for ranger districts and an overall risk model for northern Idaho. The knowledge gained from this research has important implications for biological and applied studies on DFB. The relationship between brood lipid levels and position of development along the length of a tree bole was undertaken to begin exploration into a mechanism responsible for population level variation in dispersal potentials and subsequent spatial patterns of DFB infestations found over landscapes. While it is important to understand and elucidate patterns like those found in the spatial analysis chapter, it is equally important to search for mechanisms/processes that underlie these patterns. Research into the relationship of brood adult lipid levels and position of development along the length of a tree bole and host tree characteristics is an attempt to identify such a mechanism. No relationship was found between brood adult lipid levels and position of development along the length of a tree bole or host tree characteristics. However, because this study had a limited scope of inference, more research is needed on how host tree characteristics affect the colonization and subsequent development of bark beetles. A more thorough understanding of these factors may uncover mechanisms responsible for beetle dispersal potential and subsequent patterns of tree mortality seen over landscapes.

The final study of this dissertation investigated the distance at which pheromone-baited traps attracted DFB. Knowledge of this distance is helpful to natural resource managers who desire to use pheromone-baited traps in a program to help manage local bark beetle populations. Although we attempted to estimate the sampling range and range of attraction of DFB pheromone-baited traps, we were unsuccessful at gaining any insight into the latter. However, two experiments focusing on the sampling range provided important information that should be incorporated into any use of DFB pheromone-baited traps. We concluded that DFB pheromone-baited traps attracted most beetles from less than or equal to 200 m. This distance can now be used when developing programs to use pheromone-baited traps to manage DFB. This distance can be used along with the increased knowledge of the spatial relationship of DFB infestations to optimize the placement of pheromone-baited traps over a landscape.

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