FORESTRY

FRDA REPORT 019

Red Squirrel Population Dynamics and Feeding Damage in Juvenile Stands of Lodgepole Pine

ISSN 0835 0752

DECEMBER 1987

ECONOMIC & REGIONAL DEVELOPMENT AGREEMENT

Canada

BC

Red Squirrel Population Dynamics and Feeding Damage in Juvenile Stands of Lodgepole Pine

by
Thomas P. Sullivan

Applied Mammal Research Institute
23523 47th Avenue, R.R. 7
Langley, B.C., Canada
V3A 4R1

December 1987

ECONOMIC & REGIONAL DEVELOPMENT AGREEMENT

Canada BC

Funding for this research project was provided by the B.C. Ministry of Forests and Lands. The publishing costs were covered by the Canada/British Columbia Forest Resource Development Agreement — a five year (1985-90) $300 million program cost-shared equally by the federal and provincial governments.

Canadian Cataloguing in Publication Data

Sullivan, Thomas Priestlay, 1951-
Red squirrel population dynamics and feeding damage in juvenile stands of lodgepole pine

(FRDA report, ISSN 0835-0752 ; 019)

Co-published by B.C. Ministry of Forests and Lands.
On cover: Canada/B.C. Economic & Regional Development Agreement.
Issued under Forest Resource Development Agreement.
Bibliography: p.
ISBN 0-7718-8615-2

1. Lodge-pole pine - Wounds and injuries - British Columbia. 2. Tamiasciurus hudsonicus - Feeding and feeds. 3. Lodge-pole pine - Spacing. 4. Lodge-pole pine - Thinning. I. Canadian Forestry Service. II. British Columbia. Ministry of Forests and Lands. III. Canada/BC Economic & Regional Development Agreement. IV. Forest Resource Development Agreement (Canada) V. Title. VI. Series.

SB608.L6S96 1988 634.9'751 C88-092032-7

This is a joint publication of the Canadian Forestry Service and the British Columbia Ministry of Forests and Lands.

Produced and distributed by the Ministry of Forests and Lands, Research Branch.

For additional copies and/or further information about the Canada-British Columbia Forest Resource Development Agreement, contact:

Canadian Forestry Service
Pacific Forestry Centre
506 West Burnside Road
Victoria, B.C. V8Z 1M5
(604) 388-0600

or

B.C. Ministry of Forests and Lands
Research Branch
31 Bastion Square
Victoria, B.C. V8W 3E7
(604) 387-6719

ABSTRACT

This study measured the incidence of red squirrel (*Tamiasciurus hudsonicus* Erxleben) feeding injuries to thinned lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) during the first 7 years after spacing. Squirrel feeding damage in two manually spaced stands was monitored from 1979 to 1986 (Prince George) and 1980 to 1986 (Cariboo); squirrel populations were monitored from 1981 to 1986 in a juvenile (unspaced stand) and mature stand at each area. At Prince George, squirrel populations increased on two occasions (1980-1981 and 1984-1985) in association with substantial cone crops of interior spruce. Squirrel abundance in the mature stand peaked in the year after each cone crop, with a surplus of squirrels appearing in juvenile stands in subsequent years. In general, damage incidence and feeding intensity in the spaced stand tended to be associated with increased densities of squirrels, but exceptions to this pattern also occurred. This pattern was less evident in the Cariboo, where the absence of spruce stands presumably resulted in consistent squirrel densities over time. The inconsistent periodicity of cone crop and squirrel population cycles, as well as the preference by squirrels to attack large-diameter (> 60 mm) stems, negates the possibility of strategic timing of spacing operations. Several silvicultural recommendations are suggested to alleviate squirrel damage to spaced lodgepole pine.

Key Words: lodgepole pine, juvenile spacing, red squirrel, population dynamics, barking, girdling, British Columbia, intensive silviculture, feeding damage.

ACKNOWLEDGEMENTS

I thank the Research Branch of the B.C. Ministry of Forests and Lands for financial support. D.S. Sullivan provided invaluable assistance in the establishment and conduct of this study. I am most grateful to L. Herring and H. Coates of the Ministry at Prince George for providing logistical support and conducting the damage assessments; and to A. Vyse and W. Mitchell of the Ministry in the Cariboo for logistical support. I thank J. Gareau, B. Jones, W. Kaiser, F. Keitsch, M. Keitsch, W. Klenner, R. Kossman, J. Krebs, R. Moses, G. Mowat, C. Robinson, and J. Robinson for help with the fieldwork.

TABLE OF CONTENTS

TABLES

FIGURES

INTRODUCTION

Juvenile stands of lodgepole pine (*Pinus contorta* Dougl. var. *latifolia* Engelm.) form an integral part of the future forest resource of central British Columbia. The Prince George and Cariboo Forest Regions have an abundance of overstocked stands of lodgepole pine suitable for juvenile spacing. This practice concentrates growth on a prescribed number of stems that have been selected for superior growth and form at an early age in the life of the stand. However, rapidly growing crop trees within managed stands of lodgepole pine are particularly susceptible to feeding attacks by small mammals.

The red squirrel (*Tamiasciurus hudsonicus* Erxleben) and the snowshoe hare (*Lepus americanus* Erxleben) feed on young lodgepole pine (Sullivan and Sullivan 1982a). These animals remove the bark and vascular tissues from stems during their feeding activities. This damage may completely girdle the tree, resulting in mortality. Even semi-girdling (sublethal) damage by snowshoe hares has been found to suppress diameter and height growth of lodgepole pine (Sullivan and Sullivan 1986). As well, red squirrels preferentially attack vigorous stems, and the lost growth of these trees may be substantial (Sullivan and Vyse 1987).

In the Prince George Region, both hares and squirrels feed on lodgepole pine. Feeding damage by the red squirrel is most common in stands with average diameters > 60 mm (Sullivan and Sullivan 1982a). In addition, squirrel damage is the major type of mammal attack in the southern Interior (Cariboo and Kamloops Forest Regions), where the snowshoe hare is less abundant than further north (Dolbeer and Clark 1975; Wolff 1981; Brockley and Elmes 1987; Sullivan and Vyse 1987). Because hares prefer small-diameter stems (< 60 mm), crop trees in managed stands outgrow their susceptibility to attack. Thus, damage can be avoided if spacing is delayed until average tree diameter is > 60 mm (Sullivan 1984).

Squirrels prefer to attack large-diameter stems (> 60 mm), and therefore crop trees in managed stands remain at risk to squirrel damage for several years. The variable pattern of population fluctuation in red squirrels suggests that they could create a damage problem every year. If so, strategic timing of spacing operations may not help to reduce or eliminate the damage.

To address the problem, a long-term study of squirrel population dynamics and feeding injuries in stands of juvenile lodgepole pine (and of populations in adjacent mature stands) was initiated in 1981. This study was designed to determine the incidence of feeding injuries by squirrels in treated (spaced) and untreated (control) stands of lodgepole pine near Prince George and in the Cariboo, B.C. The major objective was to relate tree damage to squirrel populations in juvenile stands and in nearby mature stands. Information about population fluctuations of squirrels is important for predicting the incidence of damage to crop trees in spaced stands.

METHODS

Stand Selection and Site Description

The Prince George study was located at Bowes Creek on the Grove Burn (1961), 20 km southeast of Prince George in the Sub-Boreal Spruce (SBS) Biogeoclimatic Zone (Krajina 1969). This area (32 400 ha) was covered by a mixture of young lodgepole pine stands and several deciduous species: willow (*Salix* spp. L.), aspen (*Populus tremuloides* Michx.), black cottonwood (*P. trichocarpa* T. & G.), paper birch (*Betula papyrifera* Marsh.), and Sitka alder (*Alnus sinuata* (Regel) Rydb.). The site is sandy loam gleyed gray luvisol on a level valley floor at 760 m elevation.

The average density of lodgepole pine in the control stand in 1979 was 34 778 stems per hectare (range: 4000 to 140 000; n=18). The average density of lodgepole pine in the treatment stand before spacing was 40 000 stems per hectare (range: 2000 to 100 000; n=27), and after spacing was 2304 stems per hectare. The number of crop trees, by diameter classes, for the control and treatment stands (before spacing) is illustrated in Figure 1A. In general, there were significantly more large-diameter crop trees (but fewer small-diameter ones) in the control (average 56.5 ± 1.2 mm) than in the treatment (average 49.9 ± 0.8 mm) stand.

The mature stand of white spruce (*Picea glauca* (Moench) Voss) and lodgepole pine was located approximately 0.5 km east of the Willow River (30 km from Prince George) and 1 km south of Highway 16. The stand was dominated by a mixture of spruce and pine, with subalpine fir (*Abies lasiocarpa* Hook. (Nutt.)) and Douglas fir (*Pseudotsuga menziesii* Mirb. (Franco)) in minor abundance. The understory was dominated by subalpine fir, and included some alder and spruce (Table 1).

The Cariboo study area was established at Mile 15-Palmer Lake Road, 88 km west of Williams Lake. This site was located in the SBSa (Chilcotin pine) subzone (Krajina 1969; Annas and Coupé 1979). Lodgepole pine forests in this subzone are very extensive and form a patchwork of different-aged pure stands which have developed from frequent wildfires. Most young stands are overstocked and require some degree of thinning to maximize productivity. This site produced a natural stand of lodgepole pine following a fire in 1961. The site was flat, with little discernible aspect.

The understory vegetation was dominated by pinegrass (*Calamogrostis rubescens* Buckl.), soapberry (*Sheperdia canadensis* (L.) Nutt.), kinnikinnick (*Arctostaphylos uva-ursi* (L.) Spreng), common juniper (*Juniperus communis* L.), blue leaf strawberry (*Fragaria virginiana* Duchesne), and several species of lichens. Scattered regeneration of white spruce was common. The average dbh of 20-year-old lodgepole pine was 50.3 ± 1.4 mm for the control stand and 53.2 ± 1.2 mm for the thinned stand (Figure 1B). The average density of pine in the control stand was 20 000 stems per hectare, and in the treatment stand, before thinning, 17 000 stems per hectare (reduced to 850 stems per hectare after thinning).

The mature stand of lodgepole pine (with some white spruce) was located 1 km west of Mile 14, Palmer Lake Road. The stand and understory were dominated by pine, with Sitka alder as a minor component (Table 1).

Sampling Design and Tree Measurement

At Prince George, two 9-ha matrix grids (one control and one treatment) were established during March 1979 in natural stands of lodgepole pine at Bowes Creek. Each grid had 18 permanent tree-sampling plots as described by Sullivan (1984). Two circular sampling plots (50 m^2) were systematically located within each of the 1-ha segments of each grid area. The size of these plots allowed for sampling of up to 15 crop trees per plot. All potential crop trees in the 50-m^2 plots on control and treatment grids were permanently tagged. Crop trees in the control area were chosen on the basis that these trees would be left as the future crop if the stand was spaced. Measurement of the height, diameter, and damage for all trees was done at the initial sampling period: May 29 - June 28, 1979. Height and diameter measurements were taken again in October 1982 and October 1984, 3 and 5 years after initial sampling (see Sullivan and Sullivan 1986). The 50-m^2 plots on the treatment grid were manually spaced (2 x 2 m) on August 7-9, 1979. The entire treatment area (11.7 ha) was manually spaced (2 x 2 m) between August 27 and September 26, 1979.

TABLE 1. Characteristics of mature forest stands at the Prince George and Cariboo study areas.

Study area and stand age	Species (relative %)	Average dbh ± S.E. (cm) 5.1-15.0	Average dbh ± S.E. (cm) >15.0	Ht (m)	Overstory density (stems/ha)	Understory density (stems/ha)
Prince George (100-120 yr)	Sw (53.2)	10.5±0.8	30.5±1.2	19.5-28.4	295	180
	Pl (40.5)	0.0	36.0±1.1		225	0
	Ab (3.6)	0.0	19.1±2.8		20	2,215
	F (2.7)	0.0	23.7±1.1		15	0
Cariboo (150-250 yr)	Sw (23.3)	8.6±0.4	23.9±1.9	19.5-28.4	300	400
	Pl (76.7)	10.1±0.4	21.9±0.4		995	3,395

Sw - white spruce, Pl - lodgepole pine, Ab - subalpine fir, F - Douglas-fir

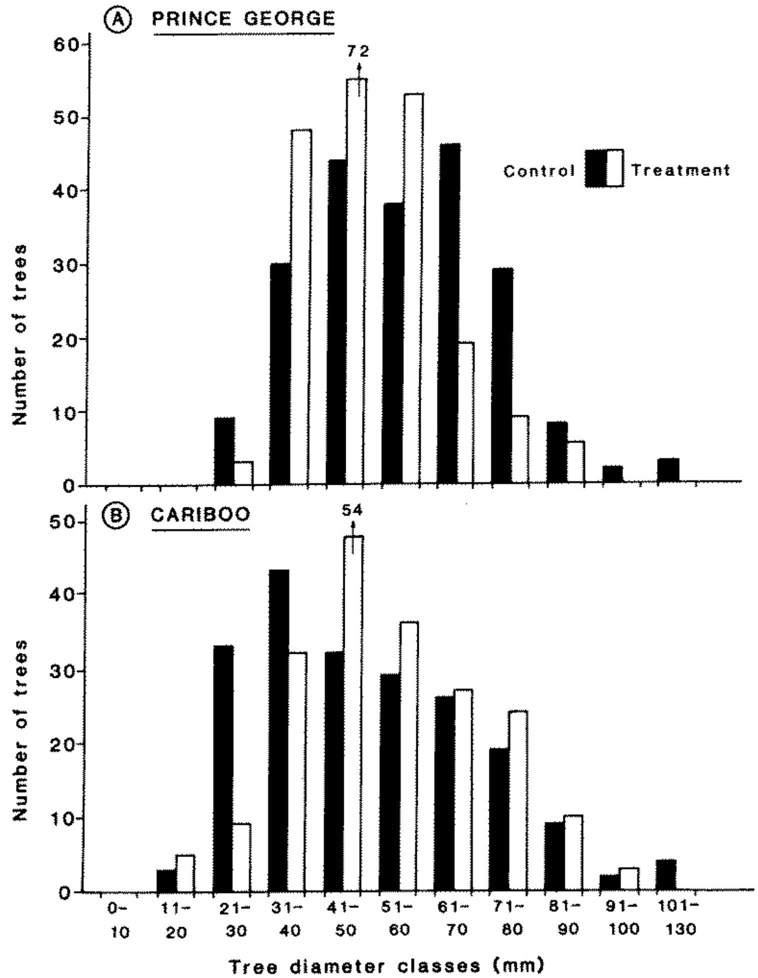

FIGURE 1. Crop tree diameter classes of lodgepole pine in control and spaced stands, (A) Prince George (1979) and (B) Cariboo (1980).

At the Cariboo study area, crop trees in twenty 50-m^2 circular plots, located every 50 m on a 9-ha grid system in each of the control and treatment stands, were marked and dbh recorded in October 1980. Diameter measurements were taken again in October 1985, a 5-year interval after the initial sampling (see Sullivan and Vyse 1987). The treatment stand was manually spaced (3.5 x 3.5 m) in the fall of 1978.

Lodgepole Pine Damage Assessment

Red squirrel damage to crop trees in control and spaced stands at Prince George was assessed annually in July or August from 1979 to 1986. In the Cariboo, damage was assessed annually in July or August from 1980 to 1986. The height (mm) and width (mm) of each new damage wound was recorded and marked with a different colour tack. The location of the centre of each damage wound was recorded with respect to the diameter of a given tree at that point. This allowed each wound to be identified and remeasured (if necessary) at subsequent sampling times. All new wounds were marked and recorded at each sampling time.

Girdling injuries to crop trees were assessed by calculating the width of each wound as a percentage of the circumference of a stem at that point. Trees having wounds with a damaged circumference ≥ 50% (semi-girdled) were considered likely to experience reduced growth and yield, or even to die. Trees completely girdled would, unquestionably, die. The surface area of each wound, and hence the amount of bark and vascular tissues removed per tree, was also calculated to assess the wound's effect on growth and yield, as well as its susceptibility to fungal attack. The impact of damage on tree diameter and height growth in these stands was reported in Sullivan and Sullivan (1986) and Sullivan and Vyse (1987).

Red Squirrel Populations

At Prince George, populations of squirrels were intensively monitored at approximately 4-week (2-week in 1981) intervals during spring, summer and fall, and at irregular intervals during the winters of 1981/1982, 1983/1984, 1984/1985, and 1985/1986. Grid systems with 100 trap stations (10 X 10) and one live-trap (40 X 12.5 X 12.5 cm) at every other station were operated in each of the juvenile pine and mature spruce/pine stands. In the Cariboo, squirrel populations were similarly monitored, with overwinter trapping conducted during 1983/1984, 1984/1985, and 1985/1986. The grid in the mature pine stand included 100 trap stations (10 X 10), with one squirrel trap at every other station. The juvenile pine grid included 96 trap stations (6 X 16) with the same trap configuration. Traps were baited with sunflower seeds and a slice of apple. For 2 days during each trapping period, traps were set at dawn and checked 4-6 hours later. All squirrels were ear tagged, their reproductive condition noted, and weight and point of capture recorded.

Complete enumeration using minimum number alive (MNA) (Krebs 1966) provided the density values for each trapping period. Enumeration techniques provide sufficiently accurate estimates for a trapping design in which 80% or more of the animals are caught at each sampling time (Hilborn *et al.* 1976). However, at lower trappability levels, and for those reasons outlined by Jolly and Dickson (1983), population estimates were also calculated using the Jolly-Seber model (Jolly 1965; Seber 1982).

Statistical Analysis

Statistical analyses were conducted on parameters measured in control and spaced stands at each study area. Analysis of variance was used to compare tree diameters between control and treatment stands. Linear regression analysis was used to determine the effect of tree diameter on frequency of attack. Regression analyses for 1979-1981 regressed the proportion of crop trees attacked on 1979 (Prince George) or 1980 (Cariboo) diameter classes. Analyses of 1985 and 1986 damage frequencies used 1984 (Prince George) or 1985 (Cariboo) diameter classes to accommodate growth changes over the 5-year period. Chi-square tests were conducted to detect significant differences in the proportion of crop trees attacked in control and spaced stands; and on an annual basis within each stand. Average spring and fall densities (with 95% confidence limits) were used to compare squirrel populations from year to year and between stands. Percentage data were transformed by arcsin square root before analysis. In all analyses, the level of significance was at least $p \leq 0.05$.

RESULTS AND DISCUSSION

Lodgepole Pine Damage - Prince George

The percentages of crop trees damaged each year by squirrels in control and spaced stands at Prince George are listed in Table 2. Comparable levels of damage were recorded for control trees during 1979 to 1981. However, the intensity of damage declined to 1.6% in 1982 and 0.5% in 1983, before increasing slightly in 1984 (6.0%), 1985 (2.7%), and 1986 (3.3%). After no damage to spaced crop trees was observed in 1980, the incidence of squirrel feeding attacks in the spaced stand in 1981 increased three times (31.9%) from the pre-spacing level of 9.5%. The lack of damage in 1980 might be attributed to the spacing operation altering the habitat for residency of red squirrels. These rodents occupied the control stand during 1980, when they damaged 19.2% of the crop trees. However, some squirrels (one or two per 9 ha) were present in the spaced stand, at least during the damage period (May-June) in 1981 (Sullivan and Moses 1986), and caused considerable damage. Damage intensity in the spaced stand declined significantly to 5.8% in 1982 and 0% in 1983, before increasing again to 5.3% in 1984. Red squirrel attack of crop trees continued to increase in 1985 (11.1%) and 1986 (16.9%), with these levels being significantly higher than those in the control stand. In general, squirrels tended to prefer large-diameter stems in their feeding attacks (Table 3).

The surface area of damage is the amount (cm^2) of bark and vascular tissues removed from a given wound by squirrel feeding, and may be considered as a measure of feeding intensity. Total and average amounts of bark and vascular tissues removed from crop trees by squirrels in control and spaced stands at Prince George are given in Table 4. Squirrels removed nearly twice as much bark and tissues from the control than from the treatment (pre-spacing) stand in 1979. However, after spacing, only the control stand had bark removed in 1980. Thereafter, 2.2 and 6.1 times as much bark and tissues were removed from spaced than from control crop trees in 1981 and 1982, respectively. There was little difference in feeding intensity between control and spaced stands in 1983 and 1984. However, squirrels removed 6.6 and 9.1 times as much bark and tissues from spaced than from control stems in 1985 and 1986, respectively.

Lodgepole Pine Damage - Cariboo

The percentages of crop trees damaged each year in control and spaced stands at the Cariboo study area are listed in Table 2. More spaced than control crop trees were attacked during 1980; in 1981 this was reversed. However, there was a general decline in the proportion of trees wounded from 1981 to 1985 in both stands. The rate of attack did increase significantly in the spaced stand in 1986. In terms of feeding intensity, the total and average amounts of damage reflect the attack rates in 1980 and 1981 (Table 5) and the decline in damage during 1982 to 1985. Again, the frequency of squirrel attack was significantly greater among large- than small-diameter stems (Table 3). Further results regarding squirrel damage at this study area are discussed in Sullivan and Vyse (1987).

Red Squirrel Populations

Initially during the summer of 1981, squirrel populations were monitored in control and spaced stands of juvenile lodgepole pine at each study area. Squirrel densities in spaced stands, averaging 0.22 per hectare at Prince George and 0.54 per hectare at Cariboo (Sullivan and Moses 1986), were significantly lower than those in control stands. These densities were comparable to the lowest density estimates (0.12-1.24 per hectare for hardwood forest) reported for any of the major habitat types in North America (Rusch and Reeder 1978).

Because most squirrels captured in spaced stands actually lived in the adjoining unspaced control areas (Sullivan and Moses 1986), additional study areas in stands of mature lodgepole pine and white spruce were started in the summer of 1981 so that red squirrel populations could be monitored more accurately. Thus, the population changes monitored in the control stand represent the spaced stand as well. In addition, the very low sample sizes (number of squirrels captured) in the spaced stands did not allow rigorous comparison of squirrel densities between years (Sullivan and Moses 1986).

TABLE 2. Percentage of crop trees damaged each year by red squirrels in control and treatment stands at the Prince George and Cariboo study areas. Sample size in parentheses. Values followed by the same letter are significantly different by chi-square where sample size is appropriate.

	Prince George		Cariboo	
	Control	Treatment	Control	Treatment
1979	13.0(209)	9.5(210)[c]	-	-
1980	19.2(204)[a]	0.0(210)[acd]	17.0(200)[h]	32.0(200)[hi]
1981	14.3(194)[b]	31.9(191)[bde]	22.2(198)[l]	14.5(193)[ijl]
1982	1.6(184)	5.8(189)[e]	0.0(196)	2.6(190)[j]
1983	0.5(184)	0.0(189)	7.1(196)	1.1(190)
1984	6.0(184)	5.3(189)[k]	4.1(196)	2.1(190)
1985	2.7(184)[f]	11.1(189)[fk]	1.0(191)	0.5(190)
1986	3.3(184)[g]	16.9(189)[g]	3.1(191)[m]	8.9(190)[m]

a-a, b-b, c-c, d-d, e-e, f-f, g-g, h-h, i-i, j-j, $p < 0.01$; k-k, l-l, m-m, $p < 0.05$

TABLE 3. Summary of regression analyses (proportion of crop trees attacked, regressed on diameter class) as reported in text. Levels of significance indicated by * $p < 0.05$; ** $p < 0.01$; NS $p > 0.05$.

Study area and stand	Year: r values	Significance
Prince George		
Control	1979: 0.48	NS
	1980: 0.36	NS
	1981: 0.96	**
Spaced	1979: 0.89	*
	1981: 0.85	*
	1985: 0.82	*
	1986: 0.59	NS
Cariboo		
Control	1980: 0.94	**
	1981: 0.95	**
Spaced	1980: 0.97	**
	1981: 0.95	**
	1986: 0.91	**

TABLE 4. Total and average amounts (cm^2) of bark and vascular tissues removed from lodgepole pine crop trees by red squirrels, Prince George study area. Sample size in parentheses.

Stand and year	Number of sample crop trees	Total	Average per damaged tree	Average per wound
1979				
Control	209	2201.1	81.5(27)	48.9(45)
Treatment (pre-spacing)	210	1160.8	58.0(20)	32.2(36)
1980				
Control	204	2308.9	59.2(39)	42.0(55)
Spaced	210	0.0	0.0	0.0
1981				
Control	194	1956.8	67.5(29)	40.8(48)
Spaced	191	4345.1	71.2(61)	45.7(95)
1982				
Control	184	99.0	33.0(3)	33.0(3)
Spaced	189	608.0	55.3(11)	40.5(15)
1983				
Control	184	2.9	2.9(1)	2.9(1)
Spaced	189	0.0	0.0	0.0
1984				
Control	184	420.0	38.2(11)	26.3(16)
Spaced	189	570.0	57.0(10)	35.6(16)
1985				
Control	184	114.0	22.8(5)	19.0(6)
Spaced	189	754.6	35.9(21)	22.9(33)
1986				
Control	184	204.0	34.0(6)	22.7(9)
Spaced	189	1853.0	57.9(32)	34.3(54)

TABLE 5. Total and average amounts (cm^2) of bark and vascular tissues removed from lodgepole pine crop trees by red squirrels, Cariboo study area. Sample size in parentheses.

Stand and year	Number of sample crop trees	Total	Average per damaged tree	Average per wound
1980				
Control	200	1811.9	53.3(34)	36.9(49)
Spaced	200	5579.5	87.2(64)	66.4(84)
1981				
Control	198	5438.4	123.6(44)	56.1(97)
Spaced	193	774.1	27.6(28)	18.4(42)
1982				
Control	196	0.0	0.0	0.0
Spaced	190	85.7	17.1(5)	17.1(5)
1983				
Control	196	1013.0	72.4(14)	59.6(17)
Spaced	190	66.3	33.1(2)	33.1(2)
1984				
Control	196	371.1	46.4(8)	33.7(11)
Spaced	190	40.5	10.1(4)	10.1(4)
1985				
Control	191	34.8	17.4(2)	6.9(5)
Spaced	190	6.4	6.4(1)	6.4(1)
1986				
Control	191	105.9	17.6(6)	8.8(12)
Spaced	190	414.4	24.4(17)	12.6(33)

Minimum unweighted trappability (Krebs and Boonstra 1984) of squirrels averaged 62% in mature forest and 69% in juvenile pine at Prince George, and 59% and 52%, respectively, at the Cariboo study area. Population changes were similar for both MNA and Jolly-Seber density estimates. Subsequent analysis and discussion of squirrel populations will use MNA values.

Population densities of red squirrels in mature white spruce-lodgepole pine forest and in juvenile lodgepole pine at Prince George are shown in Figure 2. The squirrel population in mature spruce/pine was initially 50% higher (summer 1981) than that in the juvenile stand, before declining throughout the rest of 1981 and much of 1982. There were approximately 50% more squirrels in the juvenile than mature stand throughout 1982. This pattern contrasts sharply with that reported in the literature where stands of mature lodgepole pine, white spruce, or Douglas-fir (or any combination) are considered to be optimum squirrel habitat (Brink and Dean 1966; C. Smith 1968; M. Smith 1968; Rusch and Reeder 1978). Although the squirrel population in the juvenile pine was declining in 1982, comparable densities of squirrels (approximately 10-13 per 9 ha) occupied the stand during the early summer damage periods (May to July) in both 1981 and 1982.

The juvenile pine population declined further to just three squirrels during the overwinter of 1983/1984. The mature forest population stabilized at 6 to 8 squirrels on the study area in 1983, before increasing to a peak of 14 animals in the late fall. This lack of squirrels in the young pine and increased density in the mature stand is a predictable response to the heavy spruce cone crop in the Prince George Region in 1983. Squirrel populations increased dramatically in 1984 with higher reproduction and survival than in previous years. Density (up to 23 squirrels per 9 ha) was comparable to the high population recorded in 1981. The previous heavy cone crop in 1979 presumably resulted in abundant squirrel populations through 1981. The high density on our mature spruce/pine grid declined somewhat in 1985, whereas squirrel numbers increased sharply in the juvenile pine stand to a peak of 18 animals. Comparable densities were recorded on both grids in 1986.

The cyclic nature of the population fluctuation of squirrels at Prince George is shown in Figure 3A. Average spring (May-June) and fall (September-October) densities clearly indicate the significant differences between years and stands. Peak populations occurred in 1980 (presumably) and 1984 in the mature stand, and in 1981 and 1985 in the juvenile stand.

Population densities of red squirrels in mature and juvenile stands of lodgepole pine in the Cariboo are shown in Figure 4. There was little variation in squirrel densities in the mature pine. Except for an increase in the fall of 1984 to 20 animals per grid, the population in the juvenile pine also maintained a relatively consistent density. This generally consistent average density is clearly shown in Figure 3B. This pattern may be attributed to a lack of spruce stands and their fluctuating cone crops on the Chilcotin Plateau.

Spruce Cone Crops, Squirrel Populations, and Damage

The relationship of interior spruce cone crops to populations of the red squirrel, and the incidence of damage to juvenile pine at Prince George, are illustrated in Figure 5. As outlined previously, heavy spruce cone crops were recorded in 1979 and 1983 in the central Interior (see Figure 7). Squirrel populations in mature forests that have a significant component of spruce will peak in the year after a substantial cone crop, because of increased reproduction, recruitment, and survival. The highest annual density occurs in the fall (usually September) when recruitment of juveniles reaches a maximum. This high density may persist for an additional year, depending on the size of cone crop, incidence of spruce trees, and several other factors. The resulting surplus of squirrels in the mature forest will eventually "spill over" into stands of juvenile lodgepole pine, which are presumably sub-optimal habitat. Therefore, 2-3 years after a heavy cone crop, squirrels will be abundant in juvenile pine stands and their density may equal that of mature stands (Sullivan and Moses 1986; Sullivan[1]).

---

[1] Sullivan, T.P. [1987]. Comparative demography of red squirrel populations in juvenile and mature stands of lodgepole pine. In preparation.

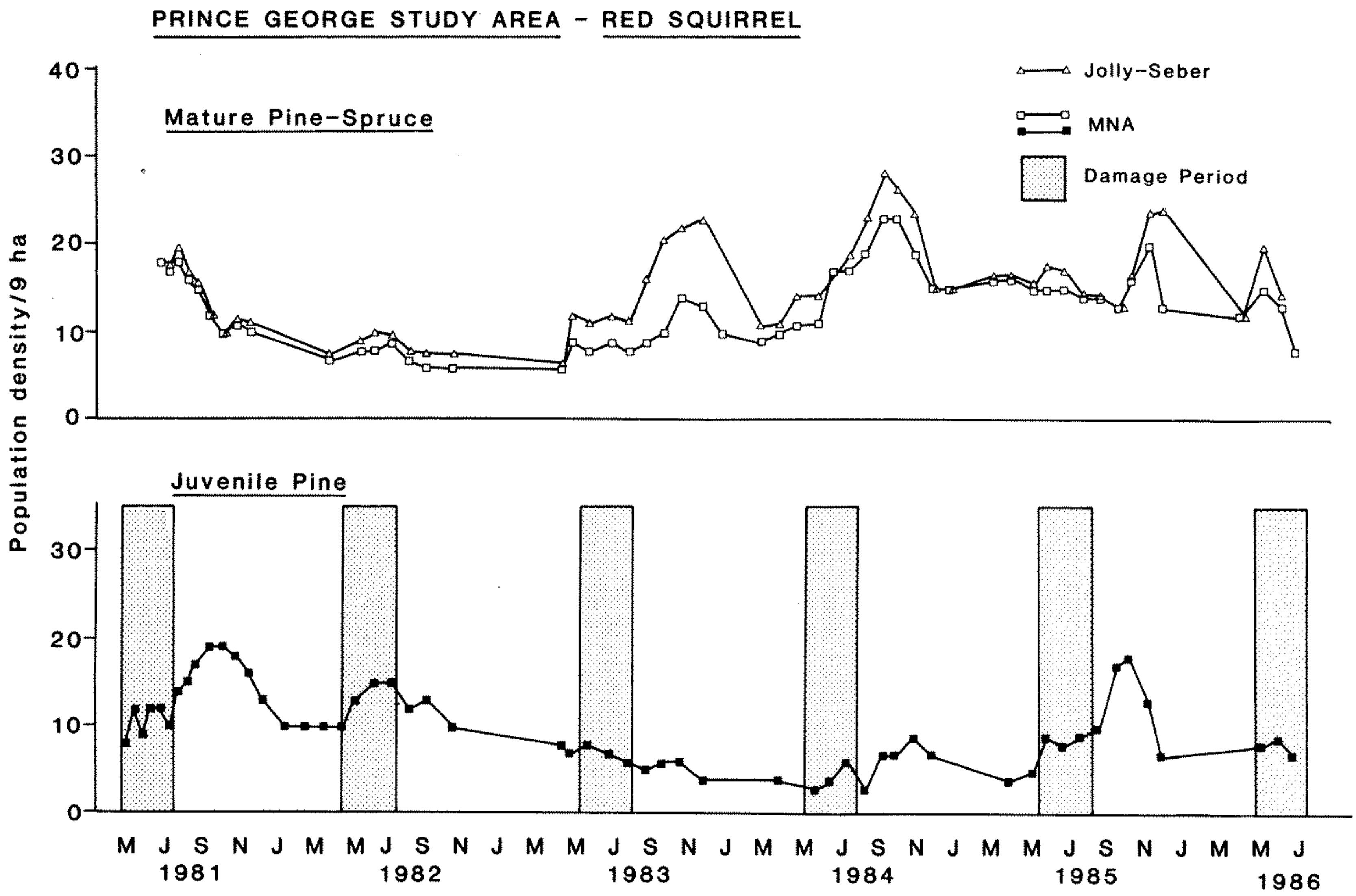

FIGURE 2. Red squirrel populations in mature spruce-pine and juvenile pine stands at the Prince George study area.

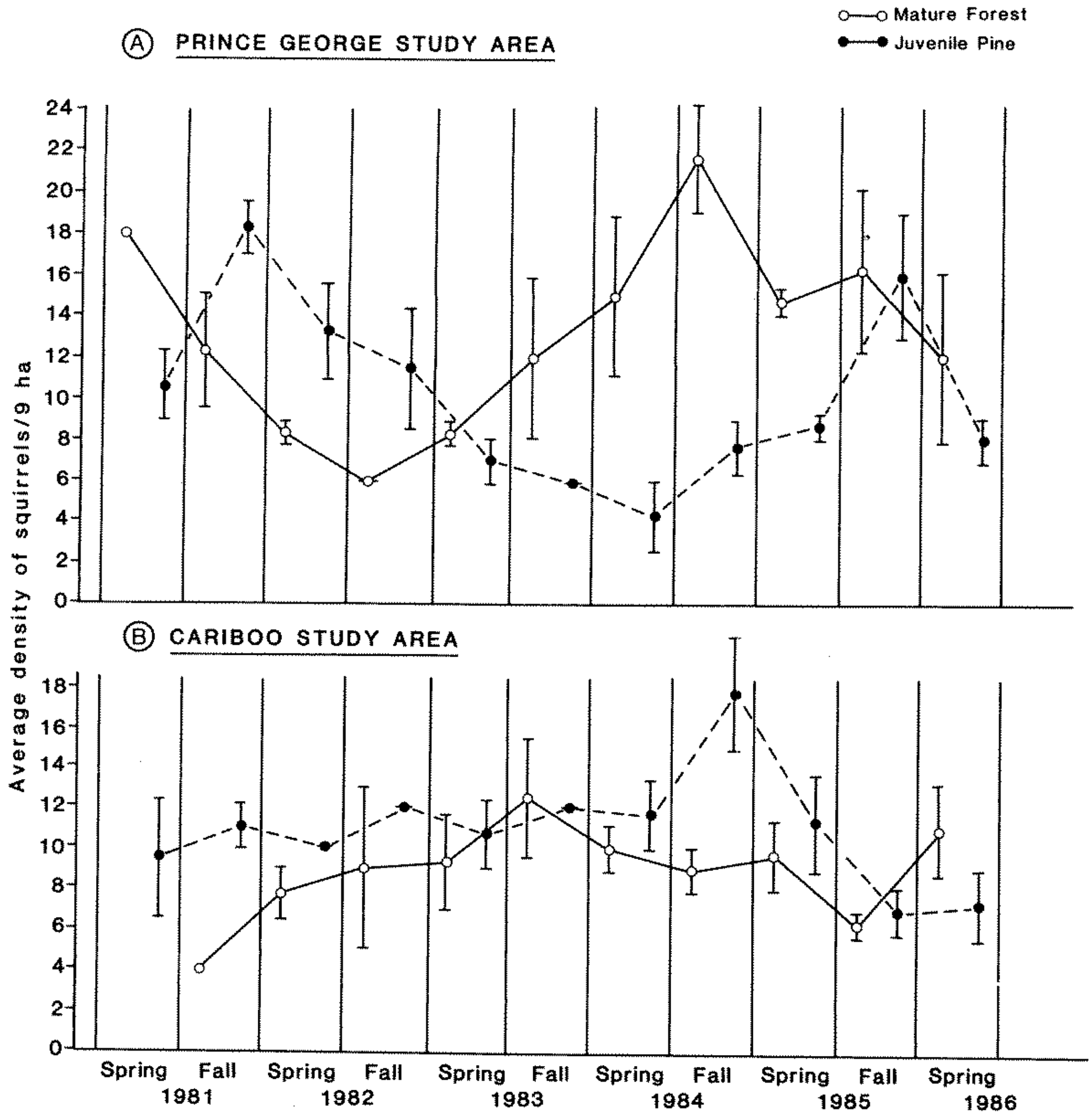

FIGURE 3. Average spring (May-June) and fall (September-October) densities (MNA) of squirrels (with 95% confidence limits) in mature and juvenile pine stands at (A) Prince George and (B) Cariboo.

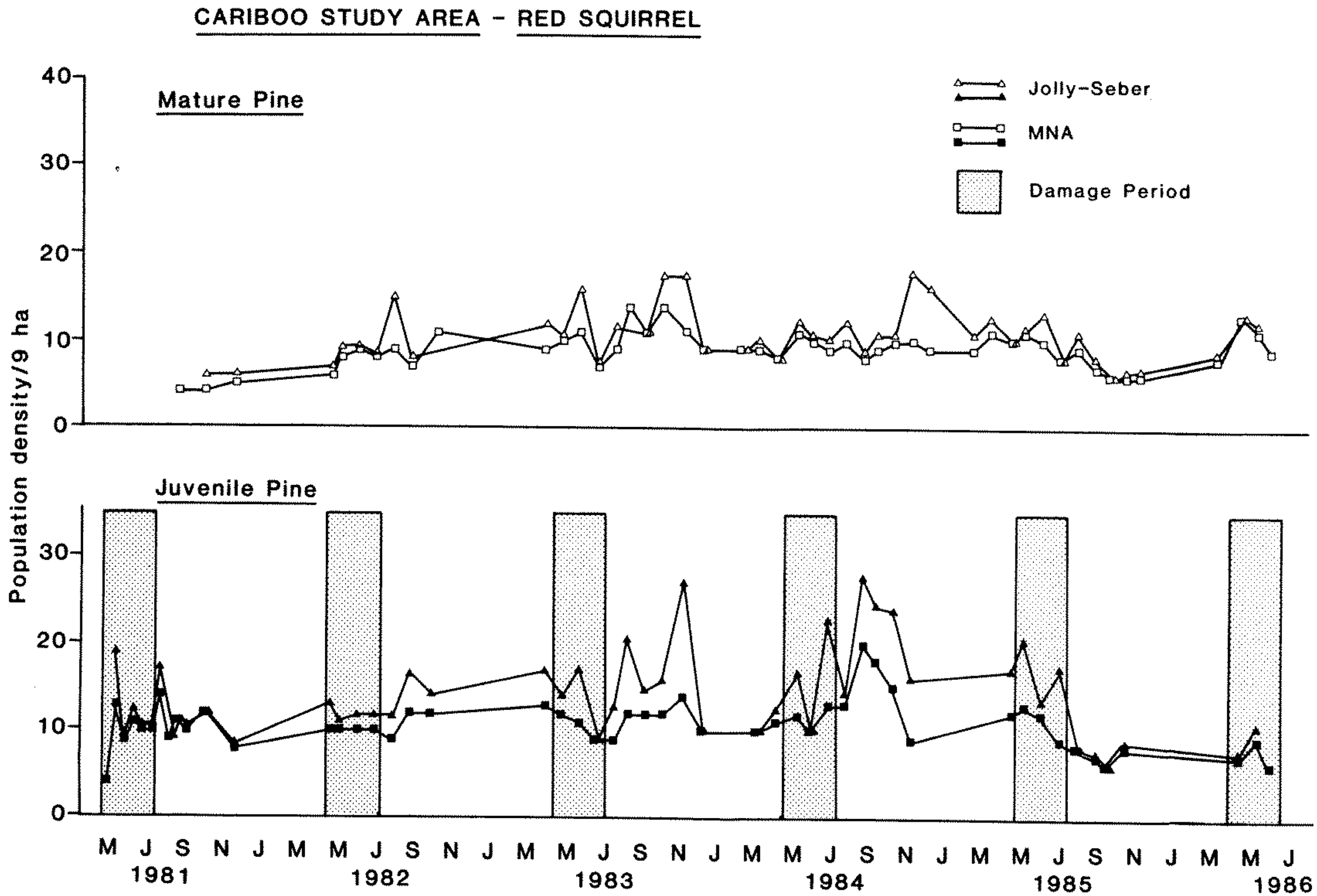

FIGURE 4. Red squirrel populations in mature and juvenile pine stands at the Cariboo study area.

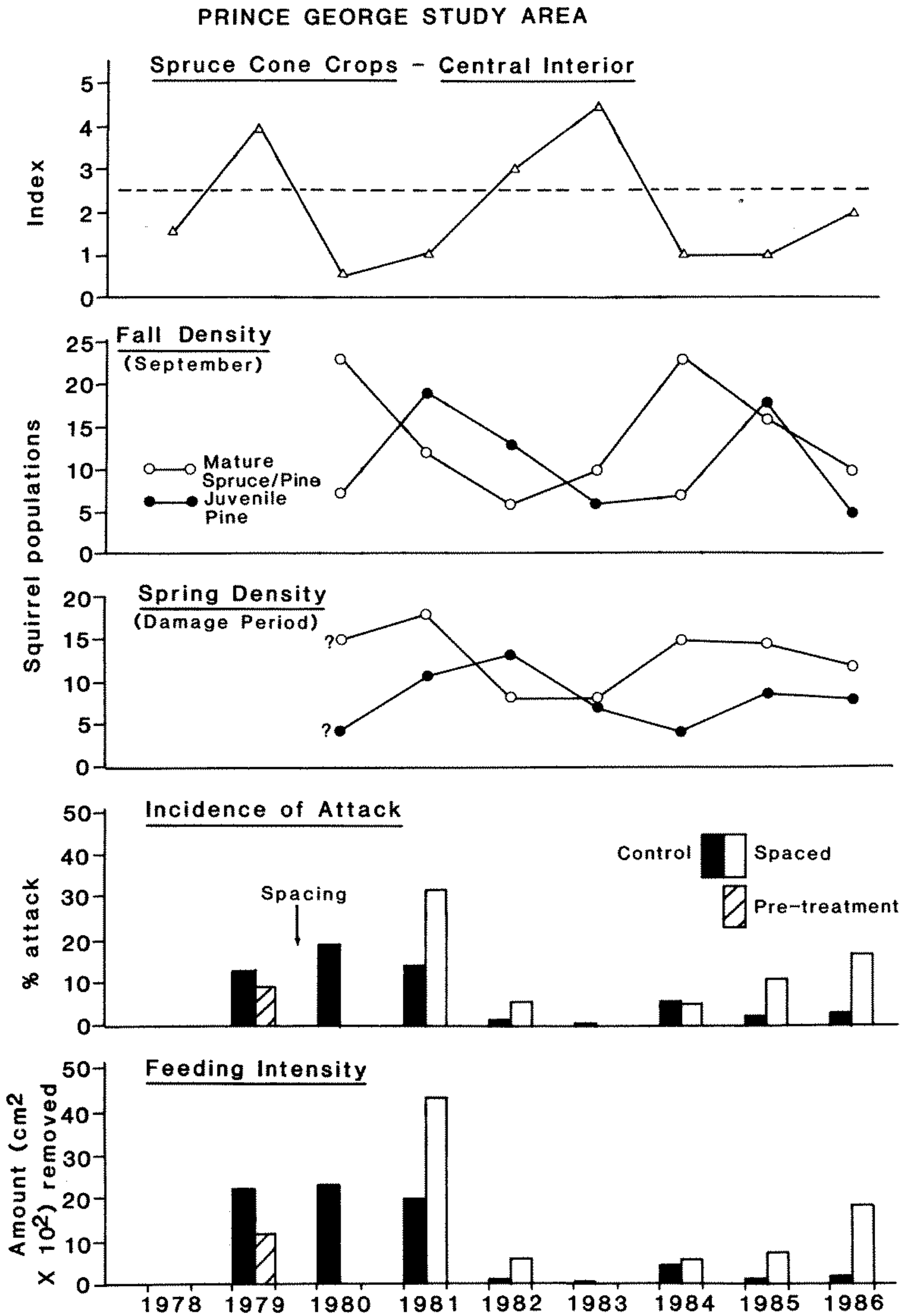

FIGURE 5. Interrelationship of spruce cone crops, squirrel population dentsity, incidence of attack, and feeding intensity at the Prince George study area.

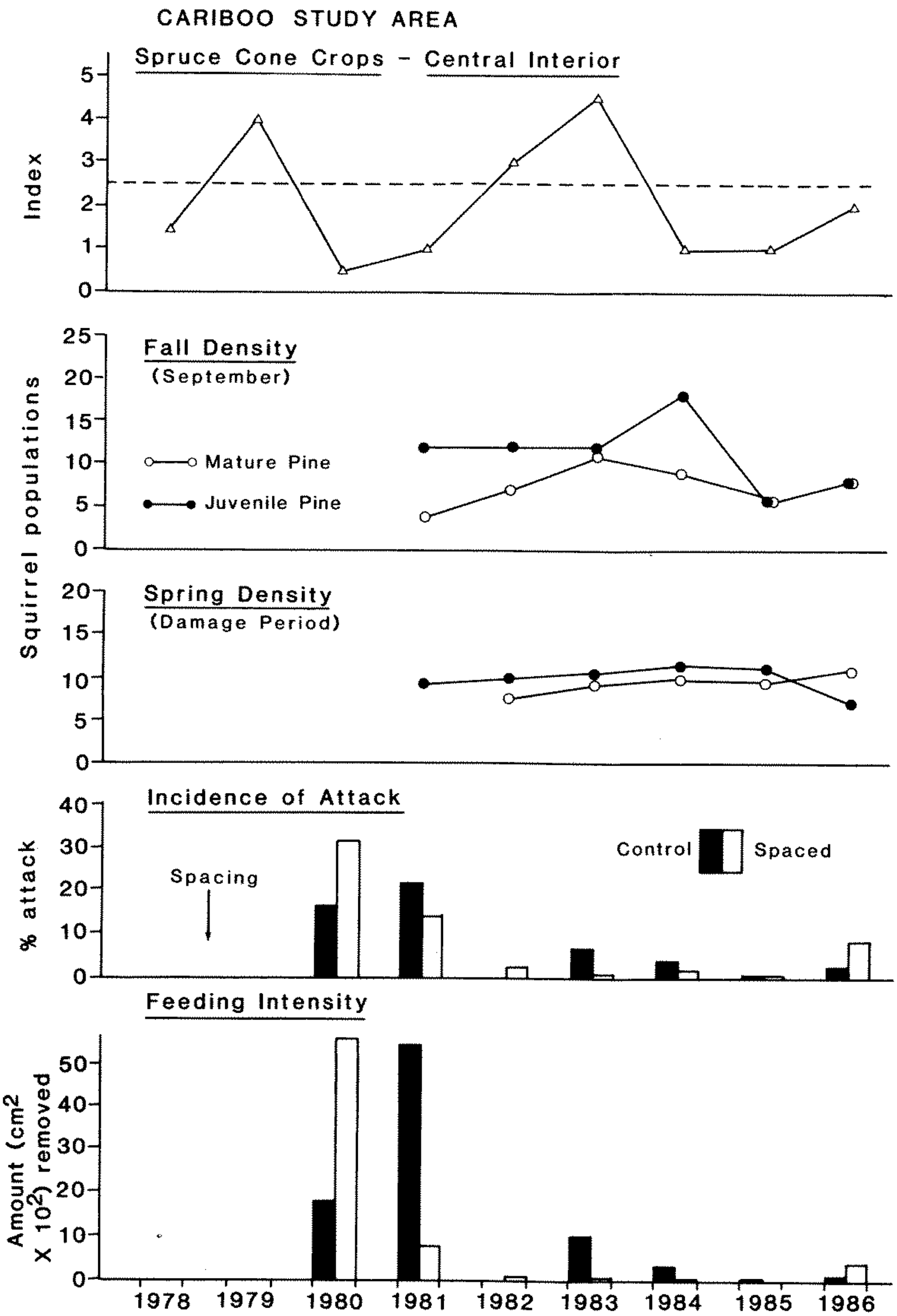

FIGURE 6. Interrelationship of spruce cone crops, squirrel population density, incidence of attack, and feeding intensity at the Cariboo study area.

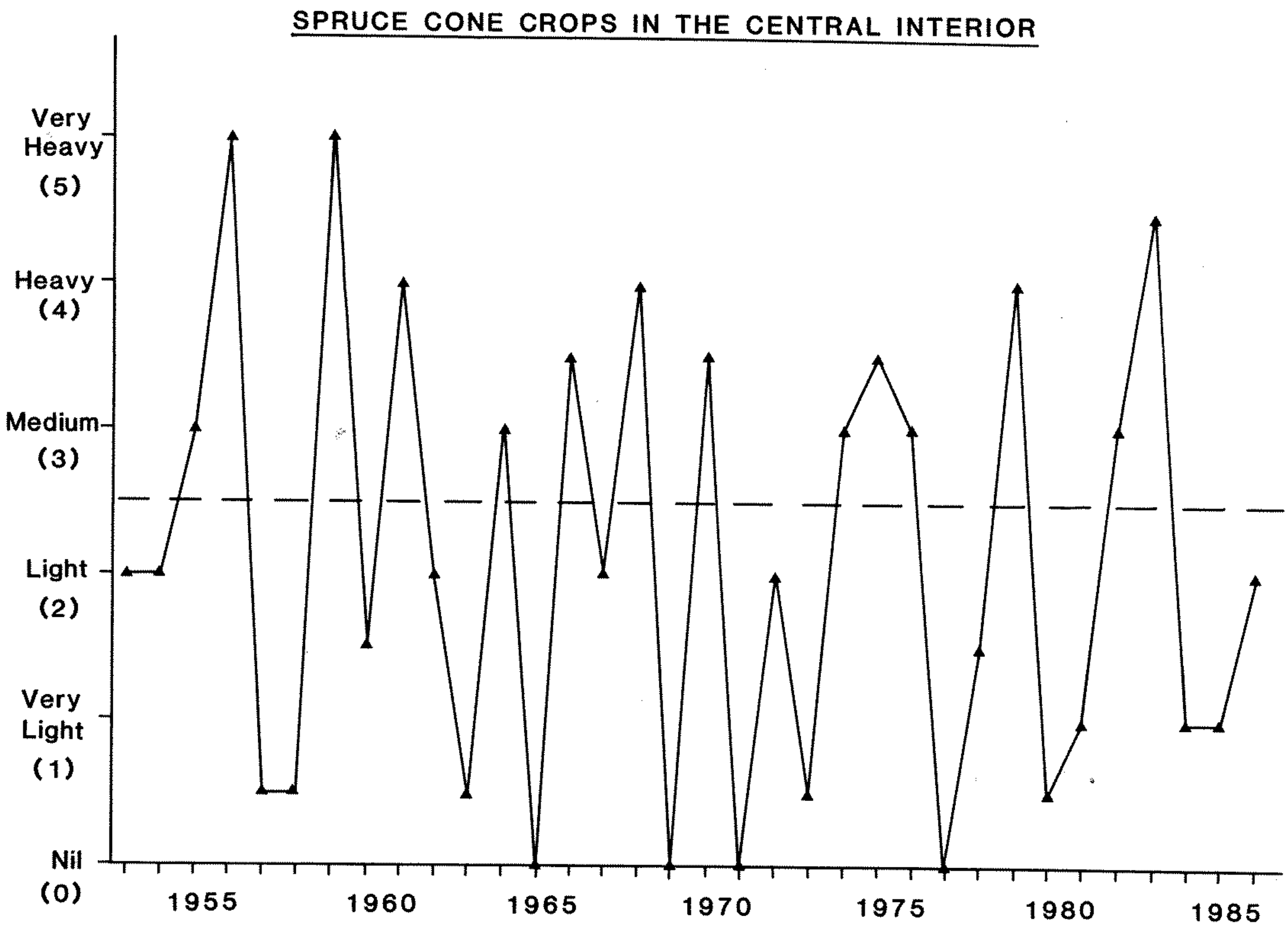

FIGURE 7. Spruce cone crop trends in the central Interior of British Columbia, 1953 to 1986. (Source: Silviculture Branch, Ministry of Forests and Lands).

This overall relationship is clearly outlined in Figures 3A and 5. Several studies have reported on red squirrel populations and the availability of cone crops in mature stands (C. Smith 1968; Kemp and Keith 1970; Rusch and Reeder 1978). A long-term (12-year) study by Halvorson (1984) clearly outlined the correlation between red squirrel population fluctuations and cone crops. Experimental evidence relating supplemental food to increased population size of squirrels has been recorded by Sullivan and Sullivan (1982b) and Sullivan[2].

In general, during years of squirrel abundance, the proportion of trees attacked and feeding intensity tended to increase in spaced stands at Prince George (Figure 5). An exception to this pattern was the lack of damage in 1982 even though squirrel density was high. Perhaps the lodgepole pine cambial tissues were not as attractive in 1982 as in previous years, or an alternative food source was available in the juvenile stands.

This general pattern was not evident in the Cariboo where the lack of spruce stands and cone crops did not generate any degree of consistent fluctuation in the squirrel populations (Figure 6). The increase in fall density in 1984 may have been related to the previous year's cone crop, but this trend was not evident in the mature pine stand relative to other years (see Figures 3B and 4). The lack of appreciable damage from 1982 to 1986 suggests that either the abundance of squirrels (which may be related to availability of alternative natural foods) was at a threshold below which spaced crop trees will sustain negligible feeding injuries; or the quality and quantity of nutrients in the vascular tissues varies from one year to another. The outbreak of damage in the Cariboo in 1980 and 1981 suggests that there may have been higher populations of squirrels during that period, possibly in response to a conifer cone crop. Alternatively, squirrels may have responded positively to the initial increase in growth of the recently thinned lodgepole pine. This latter explanation may also have contributed to the higher incidence of damage at Prince George in 1981 than in later years.

The general pattern provides a predictable population cycle for red squirrels in juvenile stands, at least in areas where cone crops in nearby mature stands could be accurately monitored. The historical trend in spruce cone crops in the central Interior indicates an average interval of 3.4 years between medium-heavy to heavy crops (Figure 7). This trend suggests that high squirrel populations and damage could be expected in susceptible stands of juvenile pine approximately every 3-4 years. There could certainly be local and geographic variation in the magnitude of the overall cone crop in a year, which should be considered when increases in squirrel abundance are predicted. However, as discussed by Sullivan and Sullivan (1982c) and Brockley and Sullivan (1987), prediction of damage potential may be only partially successful for fertilized stands, where even low densities of squirrels attack the high quality vascular tissues associated with vigorously growing stems.

---

2 Sullivan, T.P. [1987]. Demographic responses of red squirrel (*Tamiasciurus hudsonicus*) populations to supplemental food. In preparation.

SUMMARY AND CONCLUSIONS

This study assessed the incidence of red squirrel feeding injuries to thinned lodgepole pine during the first 7 years after spacing. During this period at Prince George, squirrel populations increased on two occasions in association with heavy cone crops of interior spruce. Squirrel abundance in a mature stand peaked in the year after a substantial cone crop, with a surplus of squirrels appearing in juvenile stands in subsequent years. Incidence of damage and feeding intensity tended to be associated with high densities of squirrels. This pattern was not evident in the Cariboo where the absence of spruce, in essentially pure stands of lodgepole pine on the Chilcotin Plateau, resulted in consistent squirrel densities over time. Thus, this lack of both cone crops and population fluctuations in the Cariboo provided a "control" situation for the dynamic interaction of cone crops and squirrel populations at Prince George. The two population peaks in juvenile pine in 1981 and 1985 at Prince George provided temporal replication for this relationship. Even though in 1 year (1982) of high squirrel density there was little damage to lodgepole pine, it may be generally concluded that the two periods (1980-1981 and 1985-1986) of damage incidence at Prince George have clearly been associated with substantial cone crops and increased abundance of red squirrels.

Unfortunately, the red squirrel population cycle does not have the consistent long-term periodicity of the snowshoe hare 10-year cycle. This factor, and the preference by squirrels to attack large-diameter stems (>60 mm) negates any possibility of timing spacing operations with population cycles, as recommended for snowshoe hares (Sullivan 1984). In addition, as discussed by Brockley and Sullivan (1987), delaying spacing until crop trees are large enough to withstand damage is not a "realistic" option in dense stands that require density control. However, the ability to predict outbreaks of squirrel damage from periodicity of conifer cone crops would allow application of direct damage control techniques, such as encapsulated predator odour repellents or systemic repellents, at the appropriate times. Predator odour repellents and systemic repellents (to be applied with fertilizer) may be developed in the future.

Juvenile pine stands appear to act as marginal habitat for the surplus of squirrels from population increases in mature forests. Since spaced stands had significantly fewer squirrels than unspaced, it is possible that stand thinning over a large area (e.g., > 100 ha) may reduce immigration from surrounding areas, which would help alleviate damage (Sullivan and Moses 1986). However, it must be noted that even low numbers of squirrels evidently can cause high levels of damage to juvenile trees, particularly in fertilized stands. As discussed by Sullivan and Moses (1986), a population reduction program with toxicants or trapping would likely be ineffective because of the difficulty in achieving complete removal of all animals. In addition, the resiliency of squirrels to depopulation would result in a rapid filling of available habitat.

RECOMMENDATIONS TO ALLEVIATE DAMAGE

1. Spacing stands with an apparent low hazard rating (based on a pre-spacing damage survey), and leaving a greater number of trees than is currently done, are presently the best methods for preventing or minimizing damage. A two-step spacing program is the most conservative and flexible approach.
2. Spacing operations should cover as large an area as possible (at least > 50 ha and preferably > 100 ha) to make the managed stand less attractive to squirrel populations.
3. In general, conifer (interior spruce and Douglas-fir) cone crops should be closely monitored to predict future outbreaks of squirrel populations and damage. There is up to a 2- to 3-year delay after a substantial cone crop before squirrel populations increase in juvenile stands.
4. Examination of timber harvest options (such as preservation of some mature stands within a matrix of juvenile stands, wherever possible) might prevent or reduce post-spacing damage.

INFORMATION AND RESEARCH NEEDS

The results of this study point to several information and research needs:

1. Development of a diagnostic system and forecast model to identify those stands susceptible to squirrel attack. This should be done on a region-wide basis by assessing damage in managed stands in various conditions.
2. Testing of control methods, such as predator odour repellents (and perhaps systemic repellents) and supplemented alternative foods, in susceptible stands.
3. A need to understand further the year-to-year variability in damage, e.g., why there is little damage in some years with high populations of squirrels.

LITERATURE CITED

Annas, R.M. and R. Coupé (editors). 1979. Biogeoclimatic zones and subzones of the Cariboo Forest Region. Cariboo Region Research Advisory Committee, B.C. Min. For., Victoria, B.C.

Brink, C.H. and F.C. Dean. 1966. Spruce seed as a food of red squirrels and flying squirrels in interior Alaska. J. Wildl. Manage. 30:503-512.

Brockley, R.P. and E. Elmes. 1987. Barking damage by red squirrels in juvenile-spaced lodgepole pine stands in south-central British Columbia. For. Chron. 63: 28-31.

Brockley, R.P. and T.P. Sullivan. [1987]. Impact of feeding damage by small mammals on cultural treatments in young stands of lodgepole pine. *In* Proc. Future Forests of the Mountain West: A Stand Culture Symp. U.S. Dept. Agric. For. Serv., Int. For. Range Exp. Stn. Tech. Pap. In Press.

Dolbeer, R.A. and W.R. Clark. 1975. Population ecology of snowshoe hares in the central Rocky Mountains. J. Wildl. Manage. 39:535-549.

Halvorson, C.H. 1984. Long-term monitoring of vertebrates: A review with suggestions. *In*: Proc. of Research Natural Areas: baseline monitoring and management. J.L. Johnson and others (editors). U.S. Dep. Agric. For. Serv., Int. For. Range Exp. Stn. Tech. Rep. INT-173.

Hilborn, R., J.A. Redfield, and C.J. Krebs. 1976. On the reliability of enumeration for mark and recapture census of voles. Can. J. Zool. 54: 1019-1024.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. Biometrika 52: 225-247.

Jolly, G.M. and J.M. Dickson. 1983. The problem of unequal catchability in mark-recapture estimation of small mammal populations. Can. J. Zool. 61: 922-927.

Kemp, G.A. and L.B. Keith. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology 51: 763-779.

Krajina, V.J. 1969. Ecology of forest trees in British Columbia. Ecology of Western N. Am. 2: 1-147.

Krebs, C.J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. Ecol. Monogr. 36: 239-273.

Krebs, C.J. and R. Boonstra. 1984. Trappability estimates for mark-recapture data. Can. J. Zool. 62: 2440-2444.

Rusch, D.A. and W.G. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology 59: 400-420.

Seber, G.A.F. 1982. The estimation of animal abundance and related parameters. 2nd Ed. Charles Griffin and Company, London.

Smith, C.C. 1968. The adaptive nature of social organization in the genus of tree squirrels, *Tamiasciurus*. Ecol. Monogr. 39: 31-63.

Smith, M.C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. J. Wildl. Manage. 32: 305-317.

Sullivan, T.P. 1984. Effects of snowshoe hare damage on juvenile lodgepole pine — Implications for spacing natural stands. B.C. Min. For., Res. Branch, Res. Note 94. 27 p.

Sullivan, T.P. and R.A. Moses. 1986. Red squirrel populations in natural and managed stands of lodgepole pine. J. Wildl. Manage. 50: 595-601.

Sullivan, T.P. and D.S. Sullivan. 1982a. Barking damage by snowshoe hares and red squirrels in lodgepole pine stands in central British Columbia. Can. J. For. Res. 12: 443-448.

________.1982b. Population dynamics and regulation of the Douglas squirrel with supplemental food. Oecologia 53: 264-270.

________.1982c. Influence of fertilization on feeding attacks to lodgepole pine by snowshoe hares and red squirrels. For. Chron. 58: 263-266.

________.1986. Impact of feeding damage by snowshoe hares on growth rates of juvenile lodgepole pine in central British Columbia. Can. J. For. Res. 16: 1145-1149.

Sullivan, T.P. and A. Vyse. 1987. Impact of red squirrel feeding damage on juvenile spacing of lodgepole pine in the Cariboo Region of British Columbia. Can. J. For. Res. 17: 666-674.

Wolff, J.O. 1981. Refugia, dispersal, predation, and geographic variation in snowshoe hare cycles. *In* Proc. World Lagomorph Conf. K. Myers and C.D. MacInnes (editors). Univ. Guelph, Guelph, Ont., pp. 441-449.