BIONOMICS AND ECOLOGY OF THE FOUR-EYED SPRUCE BARK BEETLE, *POLYGRAPHUS RUFIPENNIS* (KIRBY) (COLEOPTERA: SCOLYTIDAE), IN NEWFOUNDLAND

by

Woodrow Wade Bowers

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Name: **W. WADE BOWERS**

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Examining Committee:

Chair: Dr. R. Nicholson, Associate Professor

Dr. J.H. Borden, Professor, Senior Supervisor,
Department of Biological Sciences, SFU

Dr. R.I. Alfaro, Research Scientist,
Pacific Forestry Centre, Forestry Canada,
Victoria, B.C.

Dr. M.L. Winston, Professor,
Department of Biological Sciences, SFU

Dr. B.S. Lindgren, Research Director,
Phero Tech Inc., Delta, B.C.
Public Examiner

Dr. L. Safranyik, Research Scientist,
Pacific Forestry Centre, Forestry Canada,
Victoria, B.C.
External Examiner

Date Approved 13 August, 1992

ABSTRACT

In Newfoundland, the four-eyed spruce bark beetle, *Polygraphus rufipennis* (Kirby), had 1 generation and produced a spring and summer brood. Both larvae and adults overwintered, and brood adults emerged during a discrete period in June. Four weeks after establishing a first brood, the beetles re-emerged to establish a second brood. Two peaks of flight activity corresponded strongly with peaks of emergence and re-emergence. Development from egg to adult took approximately 2 months. *P. rufipennis* of either sex initiated attack at mean densities per 100 cm^2 of 8.1 and 9.3 on felled and standing-severed trees, respectively. Densities were significantly lower at 4.7 per 100 cm^2 on standing unsevered trees. Following copulation, males stayed with the females. Trees attacked by *P. rufipennis* were often secondarily attacked by *Dryocoetes affaber* (Mannerheim) and *Crypturgus borealis* Swaine. The highest incidence of *P. rufipennis* attack on black spruces occurred in stands severely damaged by the eastern spruce budworm, *Choristoneura fumiferana* (Clem.), with 32.6, 16.6 and 6.0% of the trees successfully attacked in 1983-1985, respectively. Successful attack percentages in 1983-1985 in stands of moderate budworm damage were 13.5, 6.7 and 5.1%, respectively. There were significant trends between attacked trees and year, and between beetle attack and stand damage level. Significantly more beetles were attracted to male-infested logs than to logs infested by females, males and females, or uninfested logs. Male-produced frass elicited a response by both sexes in the laboratory. Porapak Q-captured volatiles of male *P. rufipennis* boring in black and white spruce, as well as extracts of male-produced frass, contained 3-methyl-3-buten-1-ol. *P. rufipennis* of both sexes responded strongly in the field to traps baited

with 3-methyl-3- buten-1-ol released at 4.4 mg per day. Nine of 20 black spruce trees baited with 3-methyl-3-buten-1-ol were attacked, compared to 2 of 10 unbaited control trees. The cylindrical bark beetle, *Lasconotus intricatus* Kraus., a predator of *P. rufipennis*, was also attracted to 3-methyl-3-buten-1-ol. Pheromone-based mass-trapping, as well as manipulation of populations in pheromone-baited trap trees, have considerable potential for the management of *P. rufipennis* outbreaks.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Bark and timber beetles (Coleoptera: Scolytidae) have long been the principal pest enemies of the coniferous forests of North America and Europe. Total forest losses to members of this Family are difficult to estimate but are more than to all other insects, pathogens, and fire combined (Massey 1974; Wood 1982). With the exception of *Ips typographus* L., research has been conducted largely on tree-killing bark beetles of the genus *Dendroctonus*. Development of theory concerning the importance of less aggressive bark beetles has been slow to emerge, and little effort has been made to integrate the role of secondary bark beetles into either conceptual or mathematical models describing beetle-conifer systems. The term 'aggressive' is used to denote the relative degree of vigor characterizing beetles that can colonize a tree species (Raffa and Berryman 1987). As efforts to manage forests intensify, there is a growing appreciation for the role played by less aggressive bark beetles, notably species of *Ips*, *Scolytus*, *Dryocoetes*, and *Polygraphus*, all of which have tree-killing potential when populations reach high levels, or when host trees are weakened by other agents. One species of the latter genus, the four-eyed spruce bark beetle, *Polygraphus rufipennis* (Kirby), is particularly prolific in the boreal forests of Newfoundland, especially in stands of black spruce, *Picea mariana* (Mill.) B.S.P., that have been weakened by eastern spruce budworm, *Choristoneura fumiferana* (Clem.).

Damage assessment surveys in 1982 by the Forest Insect and Disease Survey (FIDS) of Forestry Canada recorded a general deterioration and increased tree mortality in stands infested with *P. rufipennis*. High-density beetle populations were reported in black spruce stands in the northwest Gander River Valley, and north of Twin Lakes. The possibility that the beetle was enhancing black spruce mortality in Newfoundland was cause for concern among forest

managers, given the importance and condition of softwood (conifer) stands. There are an estimated 544 million m^3 of merchantable timber in the province, 91% of which is softwood. Black spruce is the second most important tree species, covering 34% of the productive forest land base. In central and eastern regions, black spruce forms the most important part of the merchantable wood volume and is a major contributor to the annual production of industrial and nonindustrial wood fibre. Black spruce also is the major species used in reforestation.

Throughout the province, 71 establishments utilize softwoods in logging and the manufacture of wood products and newsprint. Forest industries contribute significantly to the provincial manufacturing sector, accounting for ca. 29% of the wages and salaries paid and 20% of the employees in Newfoundland manufacturing industries (Hudak and Raske 1982). The productive forest land area in Newfoundland and Labrador is 93,000 km^2, or 25% of the province's total land area. Maintaining or enhancing black spruce productivity is therefore a major concern of forest land managers.

Because of the alarming degree of mortality apparently caused by *P. rufipennis* in insular Newfoundland, I initiated my research with three principal objectives: (1) to elucidate the bionomics of the beetle to provide a base of biological information for future research and management efforts; (2) to evaluate the impact of the beetle as a mortality agent, so that management decisions in the future can be based on realistic estimates of potential damage; and (3) to characterize semiochemical-based communication by *P. rufipennis* as a basis for future pest management applications.

CHAPTER 1

The four-eyed spruce bark beetle is found throughout the northern coniferous forest from Alaska to Newfoundland and the northern and mountainous parts of the United States (Bright 1976; Wood 1982). The insect is reported to attack all conifers in its range, but prefers *Picea* spp. (Hilton 1968). In New Brunswick, the beetle occurs more frequently on red spruce, *Picea rubens* Sarg., than on black spruce and white spruce, *Picea glauca* (Moench) Voss. (Price 1966). Engelmann spruce, *Picea engelmanii* (Parry) Engelm., and white spruce are the preferred hosts in Alberta (Hilton 1968).

Under non-outbreak conditions, *P. rufipennis* feeds on recently broken, cut, or fallen trees, and is of minor economic importance. However, the presence of abundant breeding material in the form of weakened trees can result in outbreak populations that kill large quantities of timber, especially black spruce (Swaine 1918). Historically most *P. rufipennis* outbreaks have been innocuous, and as a result, the beetle was not considered a serious pest. However, from 1882 to 1893 in West Virginia and in New York state, widespread red spruce mortality occurred following attack by *P. rufipennis* (Hopkins 1899; Blackman and Stage 1919). More recently, Mielke *et al.* (1986) reported large numbers of dead and dying red spruce attacked by *P. rufipennis* in the Monongahela National Forest of West Virginia. Similarly, the closely related European species, *Polygraphus poligraphus* L., also is known to reach outbreak levels following disturbance of spruce stands (Chrystal 1949). Next to the spruce bark beetle, *Ips typographus*, it is considered the most economically important species in Sweden (Lekander 1959).

In 1981, populations of the four-eyed spruce bark beetle began to increase throughout much of Newfoundland's productive forests, particularly in stands of pure black spruce damaged by eastern spruce budworm. The recent population increase in Newfoundland was detected at a time when black spruce stands recovering from budworm attack showed sudden partial crown mortality followed by widespread tree mortality. The outbreak of the spruce budworm in Newfoundland began in 1972 and collapsed in most stands by 1984. Sudden spruce mortality was first detected in the Fall of 1982 and occurred over 81,000 ha with a loss of 2,002,000 m^3 of black spruce (Table 1.1). By the end of 1983 the area affected had increased to 95,700 ha with dead volume of 3,194,000 m^3. The awareness that these stands may be predisposed to attack by *P. rufipennis* as a result of repeated defoliation has stimulated research to provide more detailed information concerning the beetle's bionomics.

The biology of *P. rufipennis* has been investigated by Hopkins (1899), Blackman and Stage (1918), Simpson (1929) and Hilton (1968), but there remains a paucity of information on the bionomics and life history of the species. Thus, a primary objective of the present work was to determine the pattern of host colonization by *P. rufipennis*. Discrete phases of the host colonization sequence (Borden 1982; Wood 1982), notably host selection, attack, and establishment were examined to understand better the behaviour and reproductive success of *P. rufipennis*, and to provide a basis for understanding the distribution of the beetle in time and space. One prerequisite to elucidating the seasonal life history of *P. rufipennis* is knowledge of its overwintering strategy. Thus the overwintering sites of the beetle were investigated to determine the overwintering stage(s) and to obtain estimates of brood survival under Newfoundland conditions.

Table 1.1. Cumulative areas and volumes of dead and severely damaged black spruce in areas of more than 10% tree mortality in Newfoundland from 1977 to 1983.

Year	Area (ha)	Volume (m^3)		
		Severely damaged	Dead	Total stand
1977	12,000	600	18,000	-
1978	19,000	7,000	57,000	-
1979	49,000	26,000	216,000	-
1980	66,000	150,000	420,000	-
1981	67,000	78,000	507,000	-
1982	81,000	464,000	2,002,000	8,233,000
1983	95,700	915,000	3,194,000	10,322,000

Brood adult emergence patterns for *P. rufipennis* are unknown, and despite the importance of parent adult re-emergence in contributing to bark beetle population increases, no studies have considered the re-emergence process for the beetle. A greater knowledge of bark beetle emergence would increase the understanding of dispersal and host selection processes, and would facilitate an accurate prediction of the course of an infestation (Borden 1982, Wood 1982). Because the re-emergence process may result in a second and possibly a third brood in Newfoundland, experiments were designed to investigate parent adult re-emergence as a function of season, as well as the number of days between the peak period of attack and the peak period of re-emergence (i.e. time spent on gallery construction, mating, and egg laying).

Apart from the work of Price (1966), no attempt has been made to provide information concerning the role of sunlight and shade in tree colonization. This information is vital to a full understanding of the beetle's breeding habits and behaviour and to implementation of forest management practices that could preclude or reduce the intensity of infestations. For example, such knowledge is required for maximal effectiveness of trap log techniques in the management of beetle populations. Consequently, a study was initiated to determine attack success in felled trees exposed to sunlight and to shade.

Because there is a paucity of information on organisms associated with *P. rufipennis* on black spruce, a final objective was to record the occurrence and to describe aspects of the biology and behaviour of several important insect and fungal associates of the four-eyed spruce bark beetle.

MATERIALS AND METHODS

Research on *P. rufipennis* bionomics was conducted at a study site near Miguels Lake in the northwestern part of the Gander River watershed, ca. 50 km south of the Trans Canada Highway and Bay D'Espoir junction (55°32'30"W longitude, 48°41'35"N latitude) (Fig. 1.1). The watershed is dominated by 7-14 m high, 120-year-old black spruce, which had been severely defoliated by eastern spruce budworm. White birch, *Betula papyrifera* Marsh., trembling aspen, *Populus tremuloides* Michx., and balsam fir, *Abies balsamea* (L.) Mill., occurred sporadically in forest stands at the study site. Understory vegetation was dominated by northern sheep laurel, *Kalmia angustifolia* L.

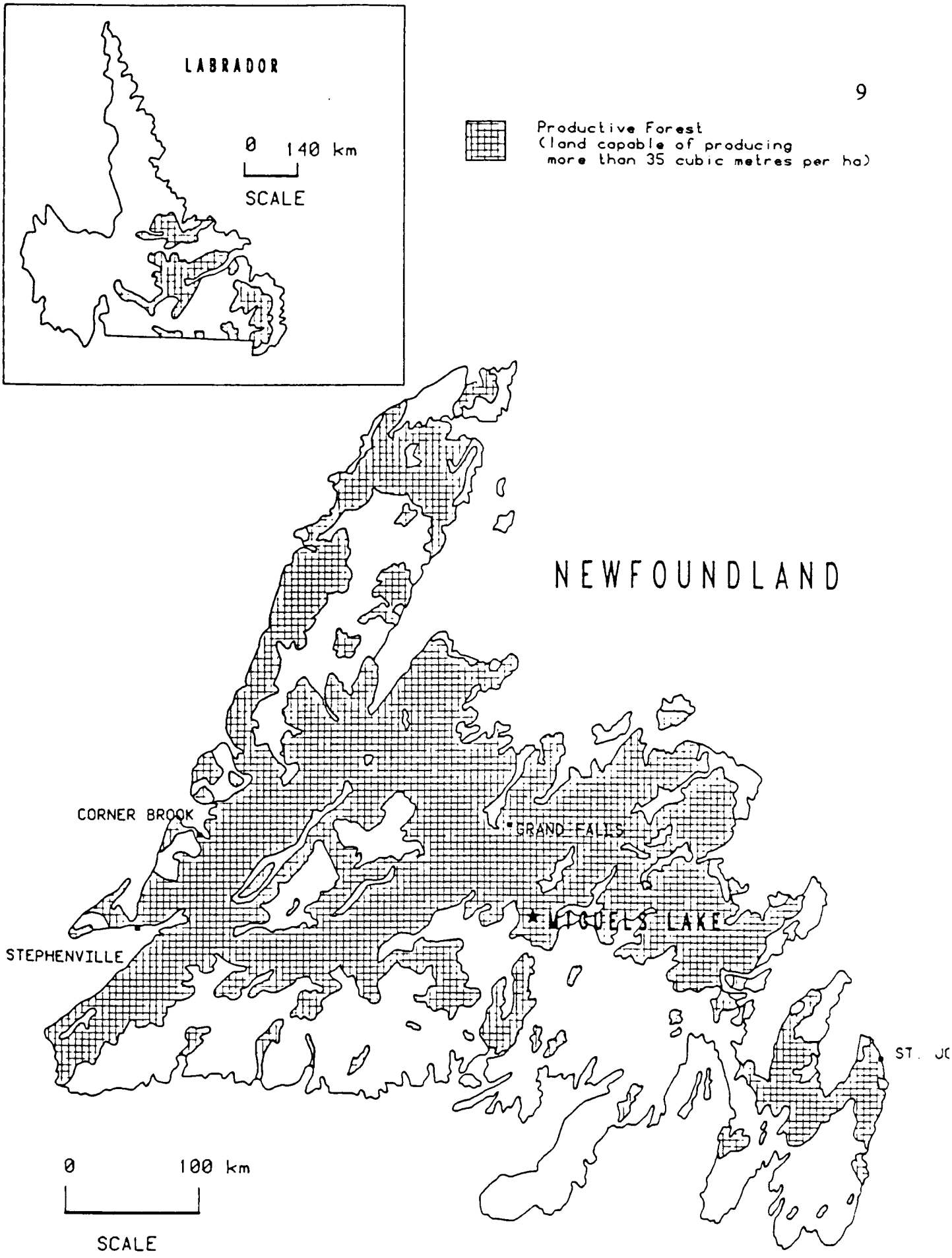
COLONIZATION SEQUENCE OF *P. RUFIPENNIS*

Overwintering Site and Stadia

On 26 May, 1983 six 5 L duff samples were collected from the base of each of 6 black spruce trees killed in 1982 by *P. rufipennis*. Samples were maintained indoors at room temperature in Styrofoam^{R} emergence containers until 1 July. Each container measured 30.5 x 35.6 x 20.3 cm and was fitted with a glass vial to capture emerging adult beetles. Emergence was checked daily during the first 2 weeks of the study and weekly thereafter. In December, 1983, 6 additional duff samples were collected from beneath 6 trees attacked the previous summer. Samples were maintained in emergence containers at room temperature until 30 April, 1984. Emergence was checked weekly for the 3 month period.

Observations were made in May, 1983 to identify the overwintering stages of *P. rufipennis* exposed in slices of bark removed from the bole of six black spruce trees at breast

Fig. 1.1. Map of Newfoundland showing areas of productive forest (land capable of producing > 35 m^3 per ha at rotation age), and permanent study site located in mature stands of black spruce at Miguels Lake.


LABRADOR
0 140 km
SCALE
Productive Forest
(land capable of producing
more than 35 cubic metres per ha)
NEWFOUNDLAND
CORNER BROOK
GRAND FALLS
MIGUELS LAKE
STEPHENVILLE
ST. JO
0 100 km
SCALE

height (1.3 m). Also, on 13 December, 1983 one 100 cm^2 bark sample was removed from each of 7 black spruce trees infested by *P. rufipennis*. Three of the 7 trees were also infested by *Dryocoetes affaber* (Mannerheim) and *Crypturgus borealis* Swaine. Therefore, life stages were recorded from the 4 trees infested only by *P. rufipennis*. To compare within-tree brood survival before and after winter, a Fall sampling at Miguels Lake was conducted in 1983 with the aid of Forestry Canada. Bark samples were removed with a 100 cm^2 bark punch (Furniss 1962) from 7 felled trees and from 7 standing severed trees and 3 standing unsevered trees. Seven of the felled trees were sampled at 0.5, 2.0, 3.5 and 5.0 m from the base and 6 trees were sampled at 0.5, 2.0 and 3.5 m from the base. On standing unsevered and severed trees, bark samples were removed at breast height. Because reliable counts of larvae were difficult to obtain from deteriorating bark with multiple infestations, estimates of mortality were obtained for callow adults only. Live and dead adult *P. rufipennis* were separated from these samples and survivorship calculated as % of the total adults collected. Bark sampling was repeated in Spring 1984 for the 17 trees infested in 1983. The Pearson chi-square test of independence (Zar 1984) was used to test the null hypothesis that the frequency of surviving callow adults is independent of overwintering conditions.

Brood Emergence

Emergence studies were conducted in Spring, 1983 and 1984. To obtain reliable emergence estimates, on-tree emergence traps were used to investigate: 1) the peak period and duration of brood emergence; 2) the pattern of emergence along the infested bole; and 3) the sex ratio of emerged beetles. Black spruce with overwintering broods of *P. rufipennis* were identified by checking the entire tree for attack and by removing a slice of bark at breast height.

Each tree also was examined for emergence holes to ensure that adult emergence had not begun. Within-tree emergence was estimated using on-tree traps placed systematically along the bole of infested black spruce. The traps were slightly modified TAM traps (McClelland et al. 1978) consisting of Saran screening stapled and glued between two, 20 x 20 cm pieces of bristleboard, and fitted with collecting vials containing 70% ethanol. The brisdeboard was waterproofed with paraffin. A 20 x 20 cm sponge seal was placed between the bole and the trap. The bark area exposed under each trap was 100 cm^2.

Six trees with overwintered *P. rufipennis* were selected on 19-26 May 1983. Traps were attached with wood screws and roofing nails at heights of 0.5, 2.0, 3.5 and 5.0 m on the east and west sides of four trees and on the north and south sides of two trees. On 29 May 1984, traps were attached on the east and west sides of four trees at heights of 0.5, 2.0, 3.5, 5.0, 6.5 and 8.0 m, and two trees were fitted with traps at 0.5, 2.0, 3.5 and 5.0 m heights on 30 May. In 1984, bark thickness and stem diameter at each sampling height were measured. Traps were monitored twice weekly for the first two weeks and weekly or bi-weekly thereafter. Emerged adults were counted and their sex determined using the two median tubercles on the frons of the male (Bright 1976).

Four freshly-attacked trees were sampled in 1983 for number of attack sites at bole heights of 0.5, 2.0, 3.5 and 5.0 m. Two of the four trees had been girdled in early June to predispose them to beetle attack. At each sample height, 17 bark disks were removed with a 100 cm^2 bark punch and examined for new attacks. Because *P. rufipennis* is polygynous (Simpson 1929), estimates of attack density based on attack sites can only be approximated. To obtain reliable estimates of attack densities, eight bark disks from each of four sample heights were

examined for beetles before parent adults re-emerged to establish a second brood.

Because emergence patterns did not differ significantly between north and south aspects for two trees and between east and west for four trees (t-test, $P \geq 0.05$), the data were pooled by height for analysis. Host characteristics associated with brood emergence data were analyzed by linear regression techniques using the Minitab Statistical Package[1]. Plots of the residual for each regression were inspected and no trend was noted to suggest curvilinearity. Coefficients of determination (r^2) were corrected for degrees of freedom. Examination of the correlation matrix for the parameters bole height, bole diameter and bark thickness, indicated high correlation between diameter and height ($r = -0.854$, $P \leq 0.001$) and between diameter and bark thickness ($r = 0.837$, $P \leq 0.001$). Therefore, to avoid deleterious effects of intercorrelation (Nater and Wasserman 1974), no attempt was made to incorporate the independent variable diameter into the regression model.

A χ^2 test for goodness of fit using Yates Correction Factor (Zar 1984) tested the hypothesis of no difference between the proportion of males and 0.5 (the proportion expected in a 1:1 sex ratio). In all tests, the maximum probability of a type-I error was set at 0.05. Temperature data were obtained from Environment Canada Weather Stations at Gander and Grand Falls, Newfoundland located 70 km to the northeast and 20 km north of the study site, respectively.

Brood emergence was investigated in the laboratory at constant temperature in 1985 to establish patterns of emergence for first and second broods established the previous year. On 25 May, 17 spruce bolts, measuring approximately 30 cm long and 8 cm in diameter, were cut

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[1]Minitab Project, Statistics Dept., Pennsylvania State Univ., University Park, PA.

from 2 felled black spruce trees infested during the spring of 1984, and 5 bolts of similar size were cut from 2 felled trees infested during July of 1984. Bolts were returned to the laboratory, the cut ends waxed to prevent desiccation, and on 31 May placed in individual rearing cages held at room temperature. Each week, *P. rufipennis* and its associated organisms were collected from the rearing cages, sexed and preserved in 70% ethanol.

Flight Behaviour

The seasonal flight period of *P. rufipennis* was investigated using multiple funnel traps (Lindgren 1983). Five traps spaced 30 m apart were erected on 5 June, 1985 in a mature stand of black spruce at Crooked bog, 8 km north of Badger. Each trap was baited with a spruce bolt infested with 10 adult male *P. rufipennis*. All bolts were cut from the same tree and were wrapped with Saran screening to prevent further attack by *P. rufipennis* or its predators and parasites. Traps were sampled weekly and *P. rufipennis* and its associated organisms were collected and placed in 70% ethanol. Flight behaviour was monitored until 24 September.

Host Selection, Attack and Brood Establishment

The first phase of *P. rufipennis* attack was investigated using black spruce trees girdled to predispose them to attack. A total of 17 trees were girdled at a bole height of 0.5 m by removing a 10 cm-wide band of bark with an axe. Ten trees ($\bar{x}$ dbh = 13.9 cm) (dbh = diameter at breast height) were girdled during 24-30 May, at the beginning of the spring flight period in 1983, and 7 trees ($\bar{x}$ dhh = 13.4 cm) were girdled during the first week of July, at the start of parent adult re-emergence. The 10 trees girdled at the start of spring flight were monitored biweekly to determine time of initial attack. Trees girdled at the start of the summer flight period were monitored biweekly to determine time of attack, and at the end of the summer

flight period, 3 attacked trees were sampled with a 100 cm^2 bark punch from the east aspect at 0.5, 2.0, 3.5 and 5.0 m heights. Bark samples were dissected to determine the number of galleries successfully established by *P. rufipennis*.

Twenty black spruce trees were also girdled on 20 June, 1984, 6 days following the first attack by emerging spring brood. Three trees successfully attacked by 4 July were used to study parent adult re-emergence; two bark samples were removed at breast height from the remaining 17 trees on 12 September to determine the number of girdled trees successfully colonized.

The initiation of *P. rufipennis* attack also was observed in the field on 2 adjacent black spruce trees severely damaged by spruce budworm. Attacking beetles were observed for several hours on the evening of 31 May, 1983 as they walked on and bored into bark tissue. At each of 20 newly established attack sites, a sample of bark was cut from the bole with a knife and placed into a glass vial. The freshly attacked bark tissue was returned to the laboratory, dissected, and the number and sex of attacking adults determined.

On 18 May, 1983 10 groups of 3 black spruce trees spaced 25 m apart were used to investigate host selection, attack patterns and brood establishment by *P. rufipennis*. Each group of trees consisted of 1 felled tree, 1 standing severed tree, and 1 standing unsevered (control) tree, 10-15 m apart from each other. None of the trees was delimbed. Each severed tree was secured in an upright position to adjacent trees with rope, after which it was cut at 0.5 m from the base. A wooden board covered with black plastic was placed in the kerf to prevent translocation. Nails were driven through the stem at the kerf to provide additional support.

Trees were checked for beetle attack daily prior to attack and twice weekly thereafter. One week following the appearance of fresh frass on the tree bole, 13 trees were sampled with

a 100 cm^2 bark punch (Furniss 1962) to determine the number of entrance holes, nuptial chambers and galleries established by *P. rufipennis*. Bark samples, consisting of all tissues outside the vascular cambium, were removed from the east and west aspects at breast height from standing severed trees, and at 0.5, 2.0, 3.5 and 5.0 m heights from standing unsevered trees. Samples removed from the west and east aspects of the tree bole were pooled prior to analysis. Felled trees were sampled along the lateral aspects of the bole at 0.5, 2.0, 3.5 and 5.0 m from the base. Bark samples were placed into petri dishes, sealed with tape, labelled, and returned to the laboratory for dissection. Samples not dissected on the collection day were maintained at 8-10° C, and examined within 2 days. Galleries damaged at the edge of bark samples were examined for life stages, and counted but not measured. Adult beetles were sexed, counted and preserved in 70% ethanol. Representative specimens of *P. rufipennis* and its associates were also pinned for subsequent identification. Immature stages were counted, and preserved in 70% alcohol. The height of each tree was recorded, as were diameter and bark thickness at each sample height.

The pattern of gallery construction and relationships between the number of egg niches, eggs and length of gallery arms (female tunnels) were derived from 284 intact galleries pooled from felled, standing severed and standing unsevered trees. To quantify the total number of eggs oviposited by females, any egg niche occupied by a larva or later life-stage was assigned a count of 1 egg.

At the termination of the spring flight period the majority of trees used in the host selection experiment had undergone severe desiccation, making removal of intact bark samples difficult. Furthermore, 2 bark beetle associates, *Dryocoetes affaber* (Mannerheim), and

Crypturgus borealis Swaine, infested many of the trees following successful establisnment by *P. rufipennis*. Therefore, beginning in July, dissection and measurement of individual egg tunnels could not be made with confidence. Rather, the number of galleries per bark sample established by *P. rufipennis* was examined and quantified only from bark samples without multiple infestations.

Three experiments (Exp. I-III) were initiated in 1984 to investigate the seasonal life history of *P. rufipennis*. Ten black spruce trees were felled at Miguels Lake on 30 May, and left in the field to be attacked by newly-emerged *P. rufipennis* (Exp. I). All 10 felled trees were attacked by the third week of June and two 100 cm^2 bark samples were removed from the midbole and base of 7 trees on 11 July and from the mid bole and base of 4 trees on 2, 12, 22, and 29 August, and on 7 and 12 September. The 62 bark samples were dissected and 131 intact female tunnels were measured and the number of egg niches and developing brood counted. At the start of re-emergence on 10 July, 4 black spruce trees were felled and placed adjacent to trees attacked in spring to test whether emerging parent adults were capable of establishing a second brood. Bark samples were first removed from these 4 trees at mid bole and at the base 2 weeks following attack on 2 August, and again on 12, 22, and 29 August, and on 7 and 12 September. Ninety two female tunnels were measured and the number of egg niches and developing brood determined. Also, 2 second brood trees were each fitted with 4 emergence traps to test for parent adult re-emergence. To test for possible third brood establishment by these parents, 4 additional black spruce trees were felled on 20 August and sampled on 12 September as above.

Experiment I was supplemented with a laboratory/field experiment (Exp. II) that utilized

1 m long spruce bolts artificially infested with adult beetles. Beetles were obtained by peeling bark from 3 trees infested in spring, 1984, and removing the parents from their galleries. Five fresh bolts were infested with 50 male and 50 female parent adults and wrapped with Saran screening to protect against further attack by *P. rufipennis* or from parasites and predators. The 5 bolts were placed in the field on 11 July to test for a second *P. rufipennis* brood. All 5 bolts were collected and returned to the laboratory on 23 August. Bark was peeled from the bolts and dissected for examination of developing brood. Female tunnels were measured and the numbers of egg niches and life-stages quantified. Twenty pairs of adults recovered from these bolts were placed on 3, 1 m long fresh black spruce bolts, wrapped with Saran screening and returned to the field to test for a third brood of *P. rufipennis*. These bolts were collected, dissected and assessed for brood production on 13 September.

Experiment III used brood adults retrieved from girdled trees attacked during July of 1983. The majority of these adults overwintered presumably as larvae and therefore represented the progeny of beetles that re-emerged to establish a second brood in summer 1983. Three 1 m long fresh bolts were infested with 40 pairs of *P. rufipennis* on 11 July and left in the field until 23 August, when the bolts were collected and the bark dissected to examine tunnel construction and brood production. Finally, 10 pairs of parent adults recovered from these 3 logs were placed on 2, 1 m long fresh logs and placed in the field on 23 August to test for a second brood. The logs were collected and dissected on 13 September.

Descriptive statistics used to describe colonization patterns on black spruce, including the number of entrance holes, nuptial chambers and galleries, were derived using SAS Procedures notably, Proc Means, Proc Univariate and Proc Freq (SAS 1985). The cumulative number of

beetle attacks over time was described by fitting a smoothed curve using a spline plot (Sigmaplot 1991). Linear relationships between tunnel length and time were derived using regression analysis. The variable tunnel length, measured with error, was regressed against the fixed variable time using Proc Reg (SAS 1985). The linear associations between the random variables egg niche and tunnel length, between egg and tunnel length, and between egg and egg niche, were estimated using Proc Corr (SAS 1985).

Parent Adult Re-emergence

Ten standing black spruce trees with the bole severed at 0.5 m and attacked by *P. rufipennis* in spring were fitted with 100 cm^2 emergence traps to test for parent adult re-emergence. On 1 July 5 emergence traps were placed at breast height on the west aspect of 5 trees and 5 traps were placed on the east aspect of 5 trees. Trees were checked for emergence holes to ensure re-emergence had not already started prior to trap attachment. To facilitate the capture of live beetles each collecting vial contained a small strip of paper on which the emerged beetles could crawl. Beetles were collected weekly, counted, sexed, and placed on caged fresh spruce bolts held at room temperature. After the appearance of copious amounts of frass on the bolts, a second fresh spruce bolt was added to each cage to test for the existence of a possible third brood. To determine which sex of re-emergent beetles initiates attack, 2 cages were set up with males and females, one with only males and one with only females. Near the end of the study season, male-infested bolts were debarked and examined for successful attacks. Bolts infested with females only and with males and females were debarked and examined for attacks and for the presence of developing brood.

Re-emergence was also evaluated in 1984 using on-tree emergence traps placed at breast

height on the east and west aspects of five trees. Three trees had been girdled in spring to initiate attack.

HOST COLONIZATION UNDER SUN AND SHADE

The colonization sequence of *P. rufipennis* in sun and shade was investigated in 1983 and 1984 at 5 locations within the Miguels Lake watershed. Five healthy black spruce trees of similar height and diameter were felled at location 1 on 20 May and at locations 2 and 3 on 26 May, 1983. Each of the 15 trees was cut in half at mid bole, and one-half was placed in a shaded spruce understory while the other half was placed in a clearing exposed to full sunlight. Branches were left intact on all trees and each tree bole was inspected weekly for signs of mass attack. Three bark samples were removed from the side of each tree bole using a 100 cm^2 circular bark punch on 15 August. Tree boles were sampled at positions corresponding to ca. 33, 50 and 67% of their total lengths. The number of egg galleries established and the number of adult beetles in the bark were determined by dissection.

Brood emergence from 4 trees felled and attacked in 1983 was assessed in 1984. One on-tree emergence trap was placed at each of the 3 sample positions on 1 tree in sun and 1 tree in shade at locations 2 and 3 on 30 May, 1984. The 12 emergence traps were removed on 4 July, and emerged adults were collected and counted. Also, 5 trees were felled at locations 4 and 5 on 13 June, 1984 to initiate *P. rufipennis* attack under sun and shade conditions. Bark samples were removed from these trees at midbole from the upper, side and bottom aspects on 18 July at location 4 and on 24 July at location 5. Bark samples were dissected and the number of galleries and adult brood determined. A two-way analysis of variance (Dixon 1988) was used to determine how position along the bole or aspect in combination with light exposure affects

gallery establishment.

In 1984, 40 intact egg galleries established on the lateral aspects of trees felled in sun and shade were dissected to determine mean gallery length. Data were screened for distributional form and analyzed using BMDP statistical procedures (Dixon 1988).

INSECT AND FUNGAL ASSOCIATES OF *P. RUFIPENNIS*

Insects other than *P. rufipennis* that emerged from logs or trees in the field and laboratory, and representative specimens obtained during dissection of bark samples, were collected, and preserved in 70% ethanol or pinned and submitted to the Biosystematics Research Centre, Ottawa, Ont. for identification.

Beetles in three discrete stages of the colonization sequence were examined to identify fungal associates. Beetles were sampled 1) before emergence began in spring, 2) during the spring flight period, and 3) following establishment on black spruce. In addition, phloem and xylem tissues adjacent to newly established galleries were sampled to test for the presence of fungi in infested host tissue.

Five black spruce trees infested by *P. rufipennis* were felled near Crooked Bog on 20 June, 1985. Bolts were cut from the infested trees, labelled, waxed to prevent desiccation, and stored in a cooler at 4° C. Ten beetles from each of 5 trees were obtained on 24 June by dissecting bark and removing brood adults from their overwintering galleries. Pure colonies of fungi were isolated from 27 male and 23 female adults using serial dilutions. Individual adult beetles were placed into a 3 dram vial containing 10 mL of sterile distilled water, and agitated vigorously for 4 min on a Thermolyne mixer to dislodge spores from the beetle. Following agitation the 1 : 10 solution was diluted to give a 1 : 100 dilution. Individual colonies were

isolated from both dilutions by spreading 0.5 mL of solution across agar plates with a sterile glass rod. Two types of media were used to culture potential fungal associates. The first, a 2% malt extract agar laced with tetracycline at 50 ug/mL, was used to select for general fungal microflora including microfungi. The second, a 2% malt extract agar laced with benomyl at 20 ug/mL and tetracycline at 50 ug/mL, favoured basidomycetes, as well as some yeasts. Tetracycline was used in both media to inhibit bacteria. Cultures of fungi were incubated in the dark at room temperature, observed every 2-3 days, and transferred from dilution plates to agar slants following fungal growth and development.

To determine if fungi are associated with *P. rufipennis* during its flight period , 25 male and female adults that emerged from bolts held in rearing cages at room temperature were collected on 19-23 July, and sampled for fungi as described for pre-emergent beetles. Also, 5 newly infested trees near Crooked Bog were sampled on 4 September, 1985, to isolate associated fungi from attacking adults and from phloem and xylem tissue. Ten bark beetle galleries from each of 5 bolts were dissected and 18 male and 32 female adults collected and treated as described above. Furthermore, 3 small chips of phloem and xylem tissue adjacent to 50 female tunnels were removed with a sterile scapel, innoculated onto the 2 media types, cultured at room temperature, and tranferred to agar slants following development of distinct colonies.

Identification of microflora associated with *P. rufipennis* was carried out by Dr. G. Warren, Newfoundland Forest Research Centre, Forestry Canada, and verified by Dr. Y. Dalpé, Biosystematics Research Centre, Ottawa.

RESULTS

COLONIZATION SEQUENCE OF *P. RUFIPENNIS*

Overwintering Site and Stadia

Although several assorted diptera emerged from duff samples, no *P. rufipennis* emerged from duff collected in Spring or Winter, 1983. Examination of bark tissue in Spring 1983 disclosed all brood stages except eggs, the majority consisting of overwintering callow adults. Winter sampling in 1983 revealed overwintering larvae ($\bar{x} \pm SE = 16.8 \pm 9.7/100\ cm^2$, N=4) and callow adults ($17.3 \pm 9.9/100\ cm^2$, N=4) in the bark of *P. rufipennis*-infested black spruce. Comparisons of callow adults in black spruce bark before and after winter disclosed no significant mortality in standing unsevered trees (Fig 1.2). In contrast, adult mortality was significantly higher in standing severed trees following the winter season. Similarly, the callow adult population was significantly reduced at all positions along the bole of felled black spruce following the winter season (Fig. 1.2).

Brood Emergence

Totals of 242 beetles ($5.0/100\ cm^2$) emerged in the traps in 1983 and 255 ($4.0/100\ cm^2$) in 1984. *P. rufipennis* began to emerge on 23 May 1983, and emergence continued for ca. 11 weeks (Fig. 1.3). The majority emerged between 7 June and 1 July; 50% of the adults had emerged by 15 June. In 1984, emergence began on 7 June and continued for seven weeks (Fig.1.3). Peak emergence began on 14 June and 50% of the adults had emerged by 20 June.

Generally, fewer beetles emerged as bole height increased (Table 1.2). The one exception was the 1983 emergence at 5.0 m caused by one anomalous tree from which 83% of the beetles

Fig 1.2 Mortality of *P. rufipennis* adults observed at breast height in standing black spruce trees and at 0.5, 2.0, 3.5 and 5.0 m from the base of felled black spruce trees before and after winter, 1983-84. Probabilities above paired bars indicate differences in mortality before and after winter (χ^2 test).

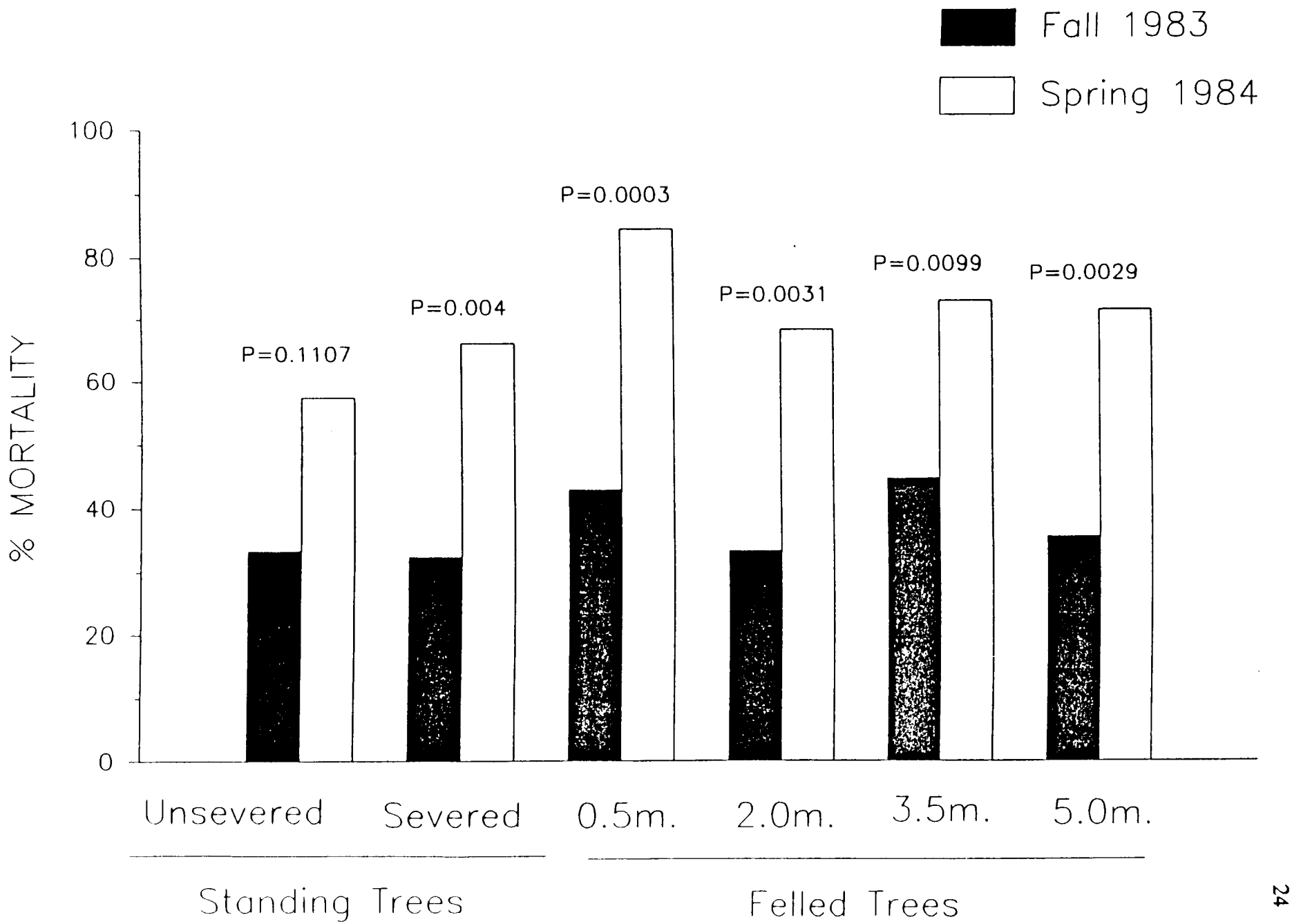
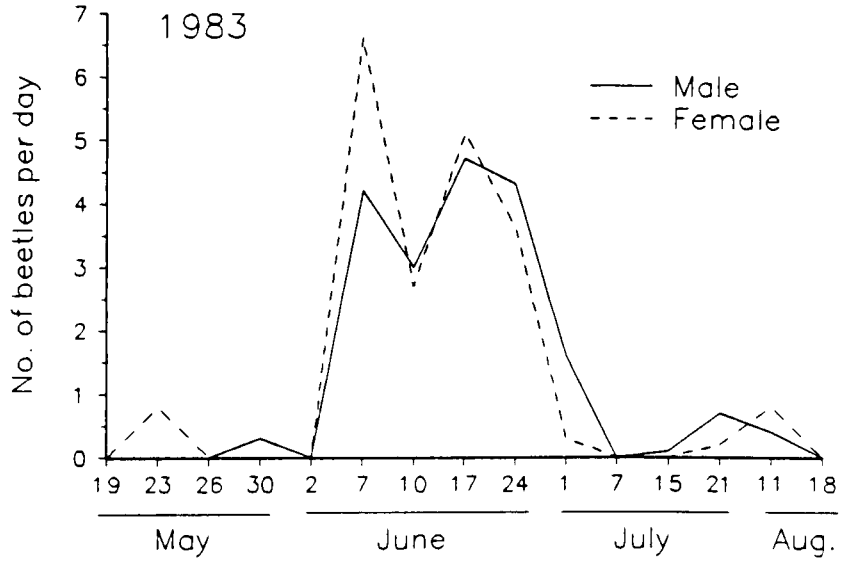

Fall 1983
Spring 1984
% MORTALITY
100
80
60
40
20
0
P=0.1107
P=0.004
P=0.0003
P=0.0031
P=0.0099
P=0.0029
Unsevered
Severed
0.5m.
2.0m.
3.5m.
5.0m.
Standing Trees
Felled Trees

Fig. 1.3. Seasonal emergence of *P. rufipennis* from black spruce in Newfoundland in 1983 (N=6, 48 traps) and 1984 (N=6, 64 traps).


1983
No. of beetles per day
Male
Female
0 1 2 3 4 5 6 7
19 23 26 30 2 7 10 17 24 1 7 15 21 11 18
May
June
July
Aug.

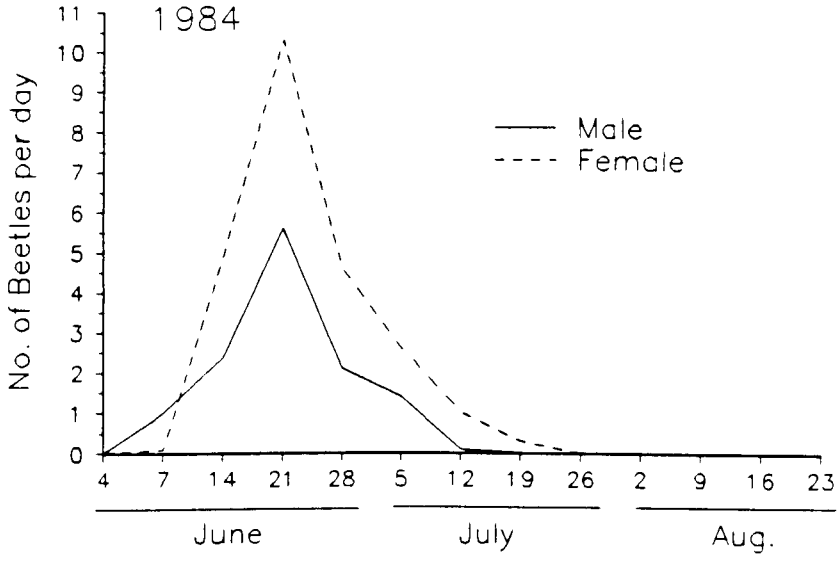

1984
No. of Beetles per day
Male
Female
0 1 2 3 4 5 6 7 8 9 10 11
4 7 14 21 28 5 12 19 26 2 9 16 23
June
July
Aug.

Table 1.2. Mean numbers of emerged *P. rufipennis* from 100 cm^2 bark disc samples at different heights from black spruce (N = 6 trees/yr) in Newfoundland.

Bole height (m)	1983 ($\bar{x} \pm SE$)	1984 ($\bar{x} \pm SE$)
0.5	9.2 ± 2.3	13.5 ± 2.4
2.0	6.3 ± 1.3	10.3 ± 2.6
3.5	5.0 ± 2.3	9.2 ± 3.1
5.0	19.8 ± 10.1	5.2 ± 3.8
6.5	---	5.2 ± 2.5
8.0	---	1.8 ± 0.9

emerged at 5.0 m. Because no significant difference (ANOVA, $P > 0.05$) in the numbers of attack sites or beetle densities was found along the infested bole (Table 1.3), the lower emergence at greater heights probably resulted from reduced oviposition, or lower brood survival.

The ♀ : ♂ sex ratio of *P. rufipennis* varied with season in both years (Table 1.4). A cumulative 1.7 : 1 sex ratio prevailed 15 days following initial emergence in 1983. Similarly, 14 days after the start of emergence in 1984, females predominated in a ratio of 1.5 : 1. However, in 1983 the cumulative ratio fell to 1 : 1.1 after 80 days, but in 1984, it rose to 1.9 : 1 (Table 1.4).

In the laboratory in 1985, 154 male and 293 female *P. rufipennis* emerged from black spruce bolts that were attacked by the beetle in spring 1984. Emergence began on 10 June and peaked near the middle of June (Fig 1.4). The majority of emergence occurred between 14 June and 4 July when 62.3% of males and 63.5% of females emerged. The overall ♀ : ♂ sex ratio was 1.9 : 1, a ratio identical to that found for adults emerging under field conditions in 1984. In contrast to the emergence pattern of the spring brood, very few *P. rufipennis* emerged from black spruce attacked in summer 1984. Only 4 males and 5 females were recovered from bolts cut from trees attacked in July of the previous year.

Flight Behaviour

The seasonal life history of *P. rufipennis* was characterized in 1985 by a flight period beginning on 19 June and terminating on 22 August. Two distinct peaks of flight activity occurred during the season, one in spring and one in summer (Fig 1.5). During the first week of flight, adults responding to male-baited host logs were almost exclusively males.

Table 1.3. Mean numbers of *P. rufipennis* attack sites and adult densities within 100 cm^2 bark disc samples at different heights from black spruce trees in 1983 in Newfoundland. (N = 17 for attack sites and 8 for beetles.)

Bole height (m)	Attack sites/100 cm^2 ($\bar{x} \pm SE$)[a]	Numbers of beetles/100 cm^2 ($\bar{x} \pm SE$)[a]
0.5	5.88 ± 0.83	12.62 ± 4.30
2.0	4.24 ± 0.76	7.63 ± 2.09
3.5	4.06 ± 0.83	10.25 ± 3.02
5.0	5.76 ± 1.15	18.00 ± 3.80

[a] Means within a column are not significantly different, ANOVA, $P \geq 0.05$.

Table 1.4. Cumulative sex ratio of emerged *P. rufipennis* from black spruce in Newfoundland.

Year	Days following first emergence	No. of beetles emerged	♀:♂ sex ratio[a]
1983	15	59	1.7
	18	76	1.5
	25	145	1.3
	32	200	1.1
	45	213	1.0
	59	219	1.0
	80	242	1.1
1984	14	59	1.5
	21	170	1.7*
	28	217	1.8*
	35	245	1.8*
	42	253	1.8*
	49	255	1.9*

[a]Ratio followed by * significantly different from 1:1 (χ^2 test, $P \leq 0.001$).

Fig. 1.4 Emergence of *P. rufipennis* from black spruce under laboratory conditions, 1985.

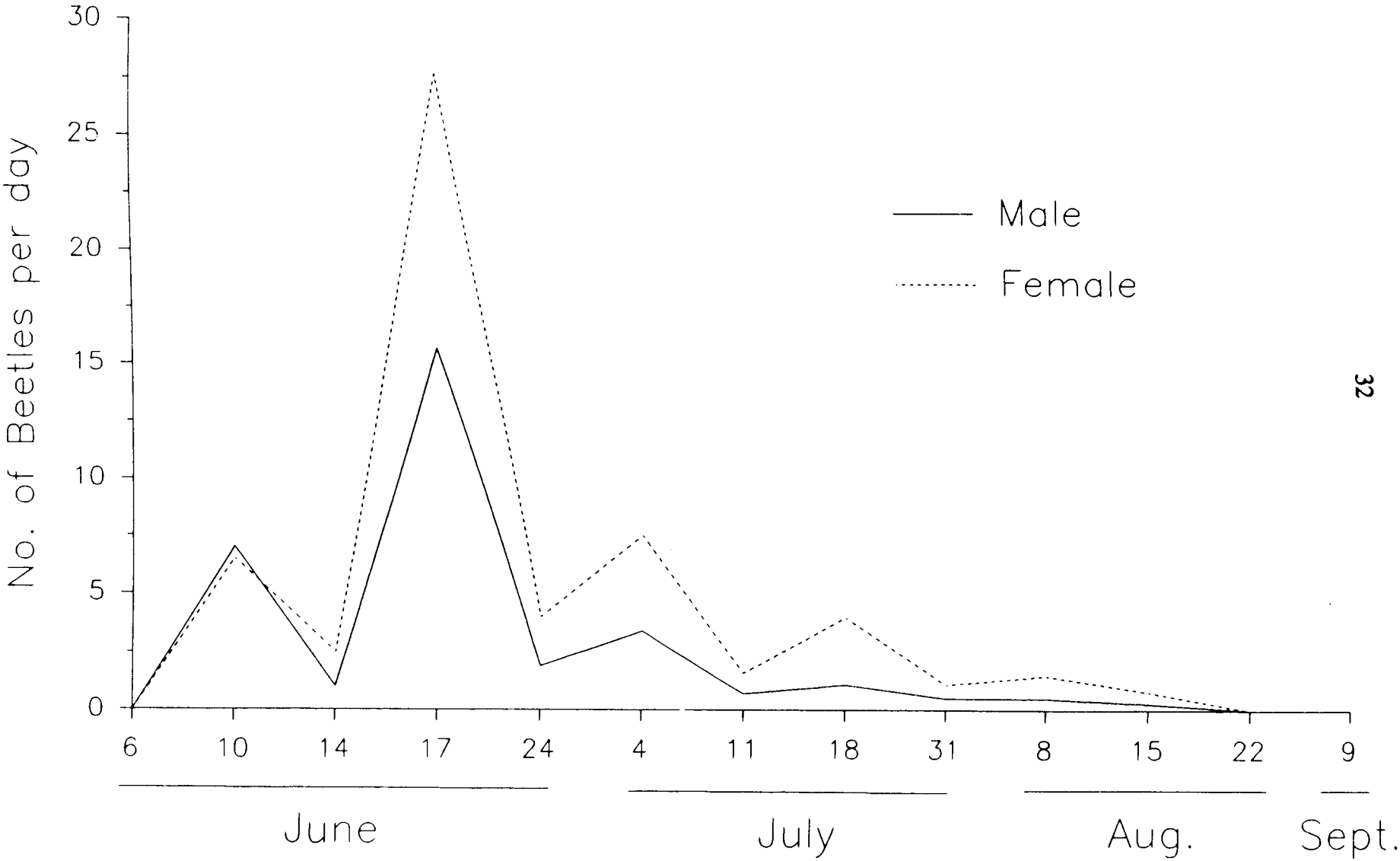
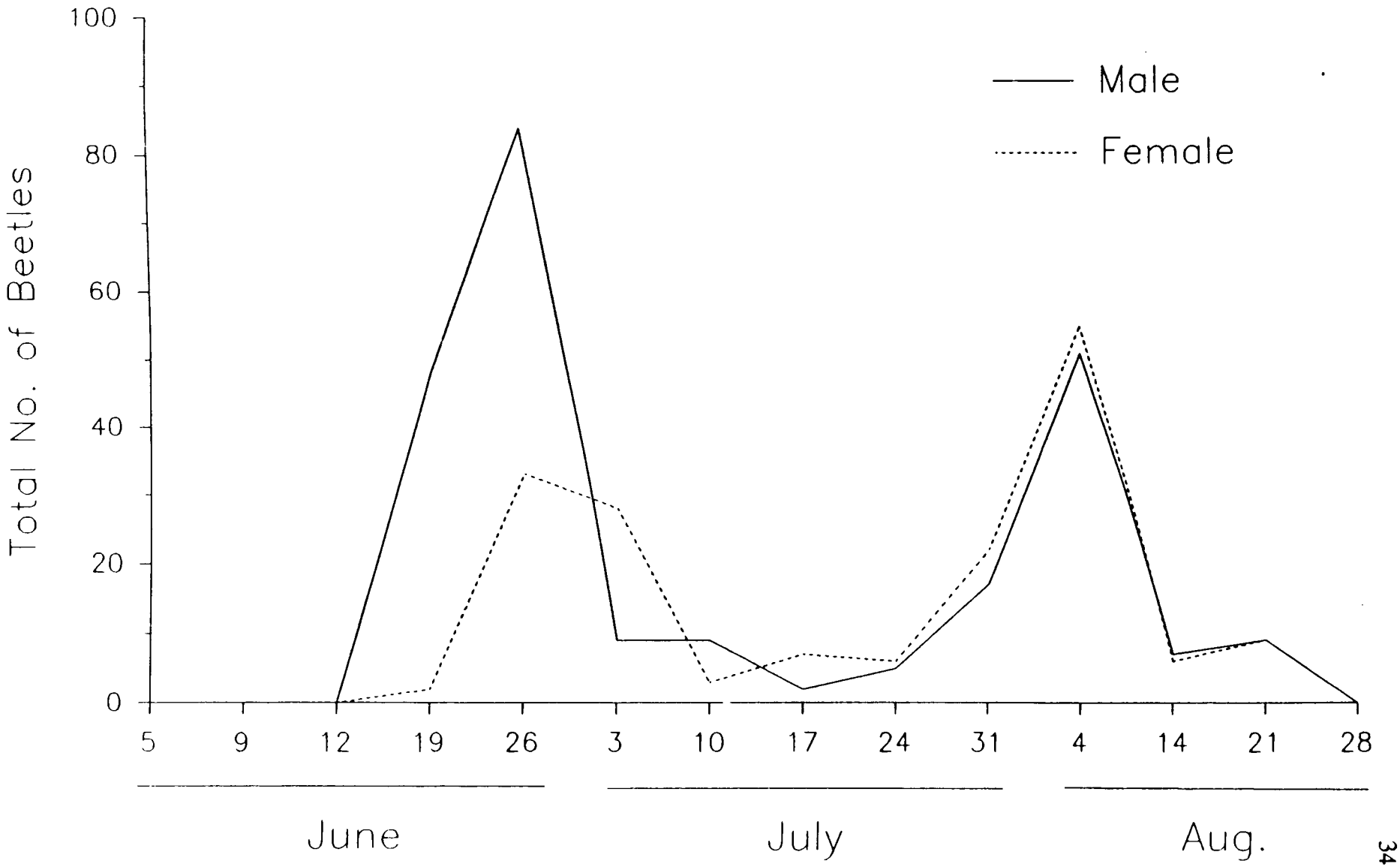

No. of Beetles per day
30
25
20
15
10
5
0
Male
Female
6
10
14
17
24
4
11
18
31
8
15
22
9
June
July
Aug.
Sept.

Fig 1.5 Seasonal flight period of *P. rufipennis* in Newfoundland, 1985. Traps (N = 5) spaced 30 m apart in a mature stand of black spruce at Crooked bog, 8 km north of Badger. Each trap was baited with a spruce bolt infested with 10 adult male *P. rufipennis*.


Male
Female
Total No. of Beetles
100
80
60
40
20
0
5
9
12
19
26
3
10
17
24
31
4
14
21
28
June
July
Aug.

Host Selection, Attack and Brood Establishment

During the spring flight in 1983, 1 of 10 girdled black spruce trees was attacked by *P. rufipennis*. Fresh frass and entrance holes were observed approximately 10 days after the tree was girdled; however no attack was evident above 2 m on the tree bole. Five of 7 trees girdled at the beginning of parent adult re-emergence were attacked in summer, all within 2 weeks after girdling. Bark samples removed on 16 August from 3 attacked trees disclosed 9 galleries at 0.5 m on 1 tree and 4 galleries at each of 0.5 and 2.0 m height on a second tree. No evidence of successful gallery establishment was found on the third tree even though frass was apparent on the external bark. Seven of 20 girdled black spruce trees were successfully colonized by *P. rufipennis* in 1984. Dissection of bark samples on 12 September disclosed developing larvae and callow adults in the phloem tissue.

P. rufipennis initiated attack sites under bark scales and on exposed areas of bark. Nine of 20 attack sites established on 2 standing green trees in spring, 1983, had entrance holes occupied by a lone male. At 7 attack sites the nuptial chamber had been formed; 4 chambers were occupied by 1 male, and 3 chambers were occupied by 1 male and 1 female. Initiation of egg tunnels had commenced at the remaining 4 attack sites; 3 galleries were occupied by 1 male and 2 females and 1 gallery was occupied by 3 females.

P. rufipennis colonized 2 standing unsevered trees, 7 standing severed and 10 felled trees during 1983 (Table 1.5). The mean interval between treatment application and attack was approximately 2 weeks for standing trees and nearly 4 weeks for felled trees. Similarly, the interval between first emergence and first attack was 3 weeks for felled trees, and <2 weeks for standing trees.

Table 1.5. Colonization of standing unsevered, standing severed, and felled black spruce by *P. rufipennis*, Newfoundland, 1983.

	dbh ($\bar{x}\pm$SE)	height ($\bar{x}\pm$SE)	no. of trees attacked		Mean (+SE) number of days[a]	
			spring	summer	treatment-attack	emergence-[b] attack
Felled	10.5±0.5	8.9±0.5	4	3	27.5±4.9	21.8±4.8
Standing severed	10.2±0.7	9.1±0.5	7	3	16.0±1.2	11.4±1.3
Standing unsevered	11.6±0.5	10.3±0.8	2	0	13.0±6.0	9.0±6.0

[a]Mean time intervals determined for trees attacked in spring.
[b]Emergence first observed on 23 May.

No significant difference in the overall mean number of attacks per 100 cm^2 was observed between felled (8.1 $\pm$ 0.92, N=44) and standing severed (9.3 $\pm$ 1.2, N=28) trees. However, significantly fewer attacks (4.7 $\pm$ 0.80, N=28) occurred on standing unsevered trees than on felled or standing severed trees. Moreover, the number of attacks following initial attack in spring, increased considerably faster on felled and standing severed trees than on standing unsevered trees (Fig 1.6).

The number of attacks at each of 4 positions along the bole was consistently lower on standing unsevered trees than on felled trees; however the differences were not statistically significant (*t*-test, $P \geq 0.05$) (Fig 1.7). Furthermore, no linear regression function could be found to describe the relationship between either sample position or bark thickness and the mean number of attacks for felled or for standing unsevered trees. Construction of nuptial chambers and female tunnels (gallery arms) began within 7 days following attack on felled and standing severed trees (Fig 1.8). On standing unsevered trees, no nuptial chambers or parental tunnels were observed 1 week following attack.

Examination of entrance holes and nuptial chambers from trees attacked in spring disclosed that either sex may initiate the attack, although there is a greater tendency for attacks and nuptial chamber construction to be initiated by males than by females (Table 1.6). Only 1 entrance hole was found with 2 females in it and 2 entrance holes were occupied by 1 male and 1 female. Nearly half of the nuptial chambers examined were occupied by lone males; 22 chambers contained 1 female only, and 22 contained 1 male and 1 female.

The majority of early attacks in Spring, 1983 were characterized by 1 and 2-egg galleries (Fig. 1.9). Attacks with one-egg gallery accounted for 67.4, 52.0 and 44.6% of the

Fig. 1.6. Cumulative number of attacks by *P. rufipennis* on felled (N=4), standing severed (N=7), and standing unsevered (N=2) black spruce, 1983. Bark samples with multiple infestations excluded from the analysis.

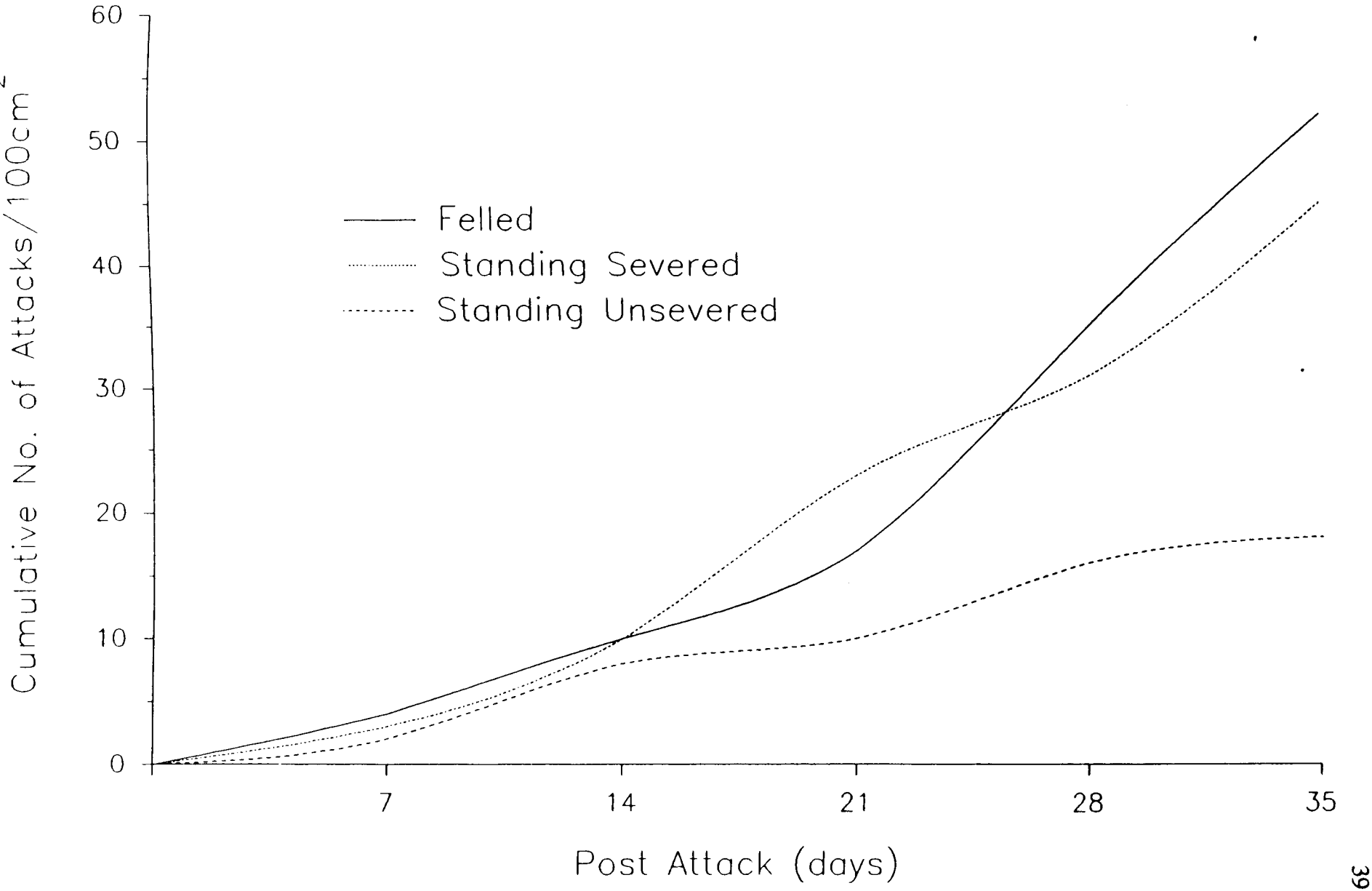

60
50
40
30
20
10
0
Cumulative No. of Attacks/100cm^2
Felled
Standing Severed
Standing Unsevered
7
14
21
28
35
Post Attack (days)

Fig. 1.7. Mean number of attacks per 100 cm^2 by *P. rufipennis* at four positions along the bole of felled (N=44) and standing unsevered (N=28) black spruce, spring, 1983.

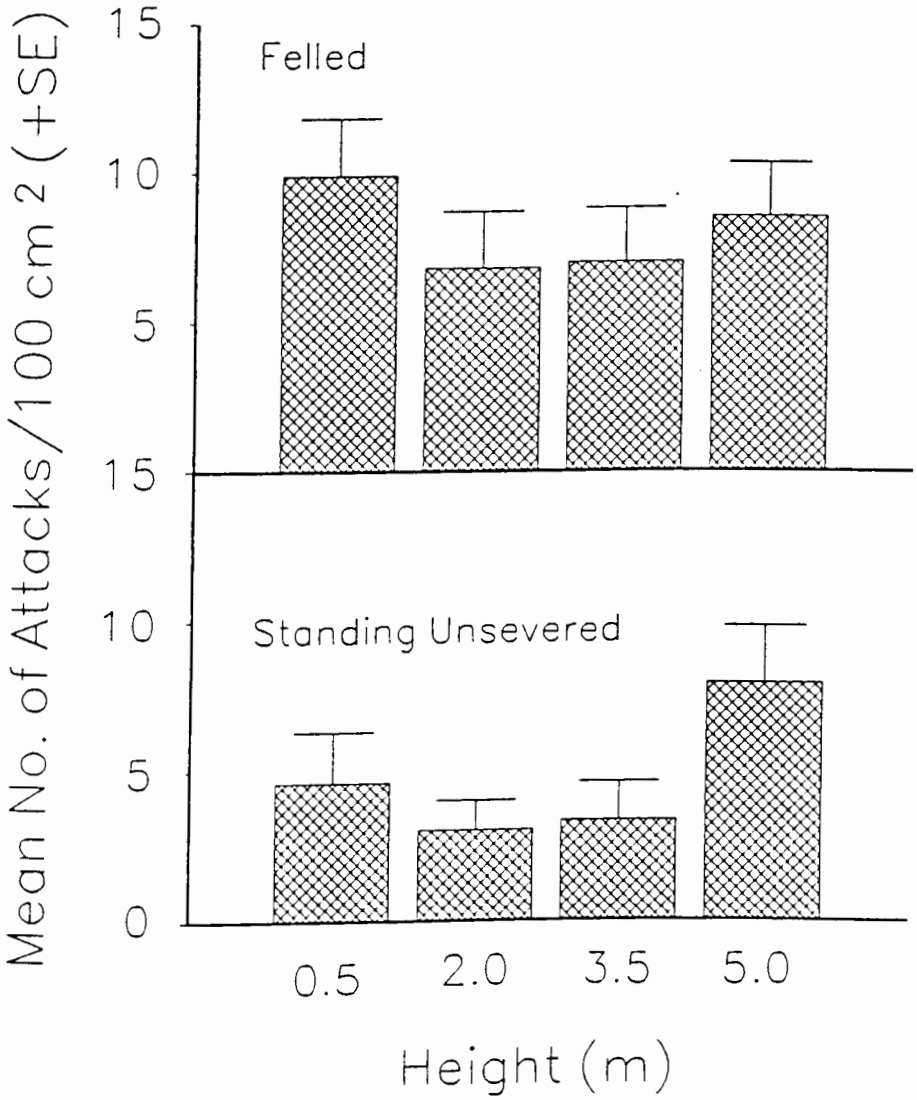

Mean No. of Attacks/100 cm 2 (+SE)
15
10
5
15
10
5
0
Felled
Standing Unsevered
0.5
2.0
3.5
5.0
Height (m)

Fig 1.8 - Proportion of entrance holes, nuptial chambers and egg galleries in felled, standing severed, and standing unsevered trees following attack by *P. rufipennis* in spring, 1983.

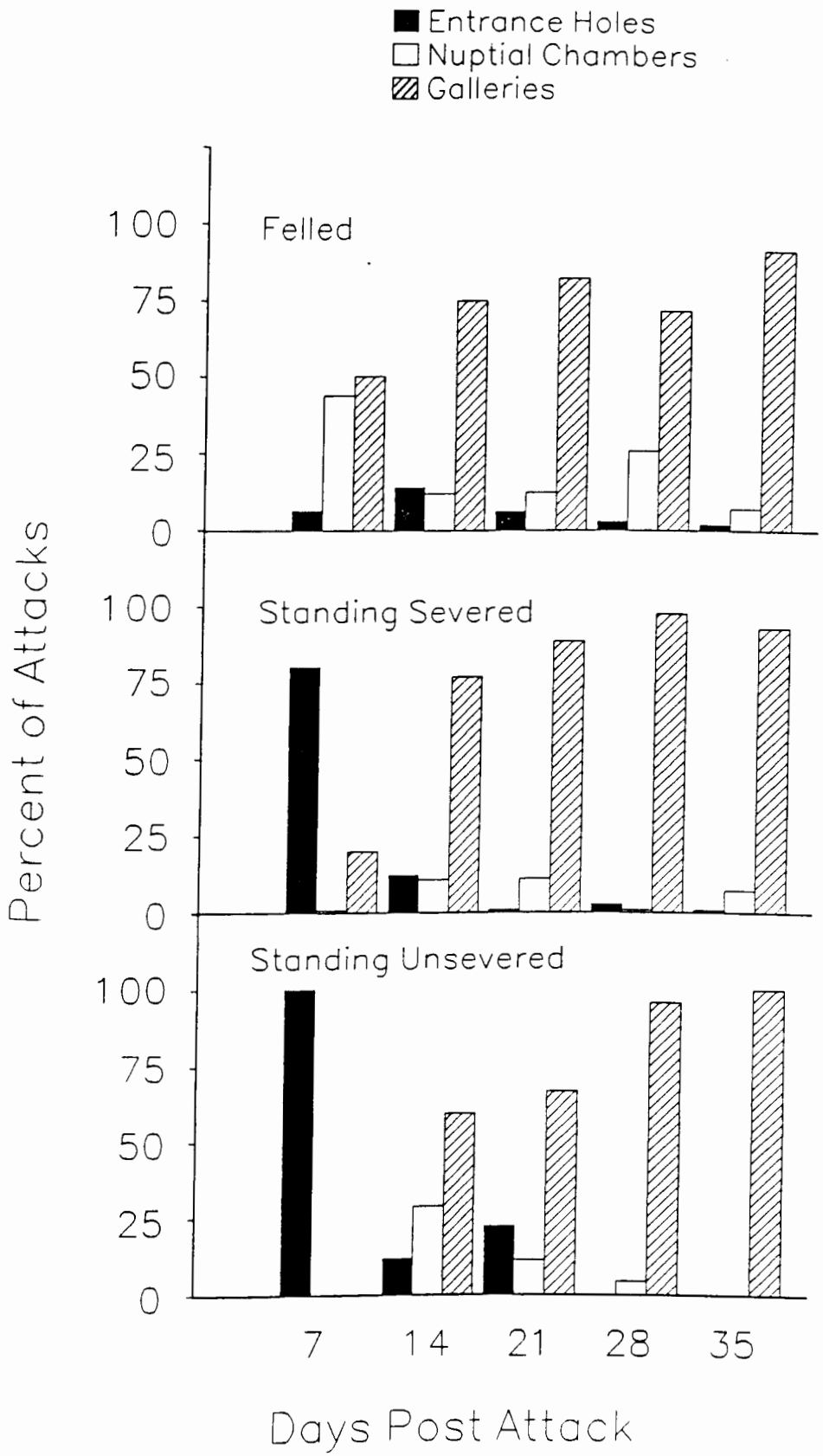
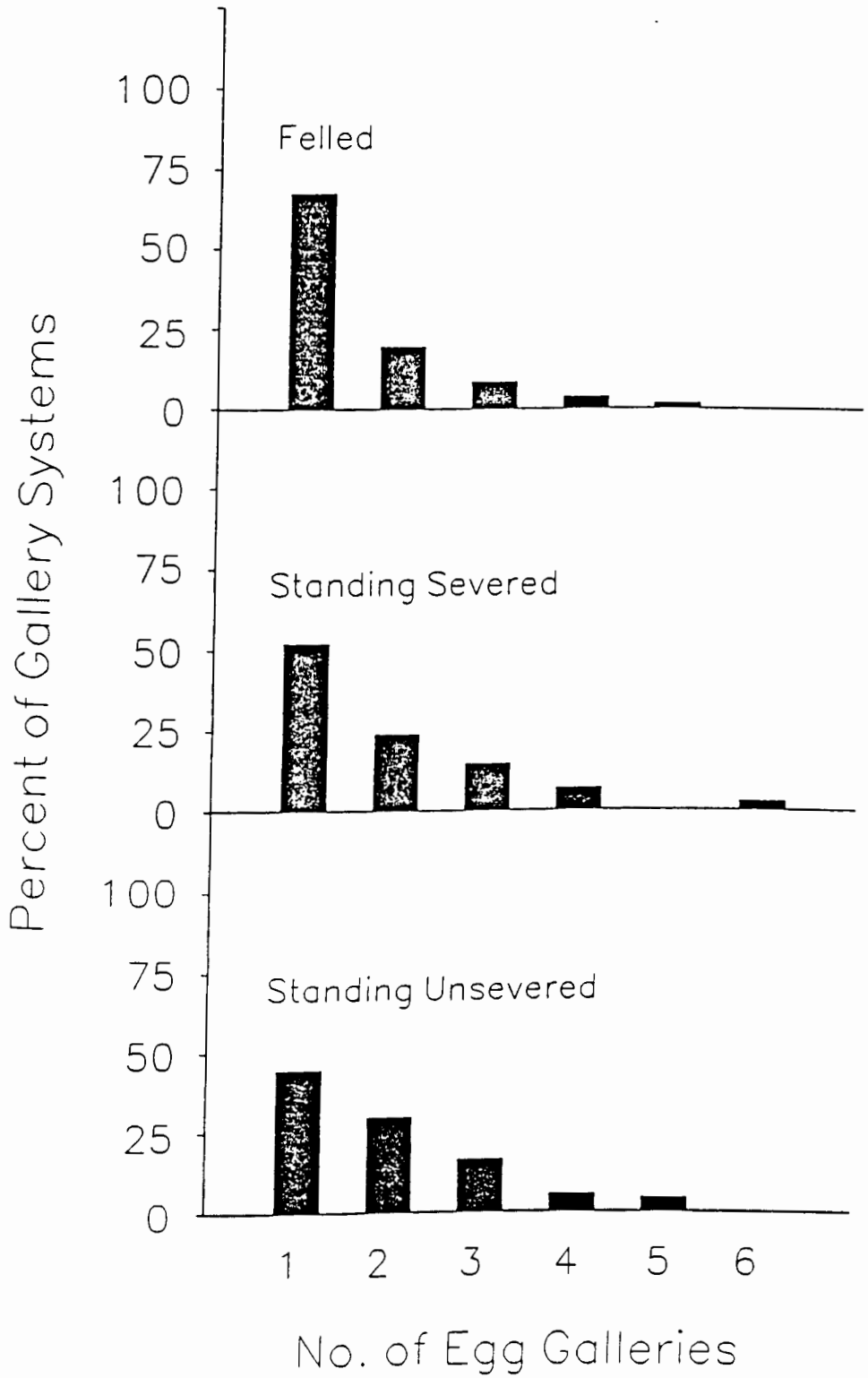

Entrance Holes
Nuptial Chambers
Galleries
Felled
Standing Severed
Standing Unsevered
100
75
50
25
0
Percent of Attacks
7
14
21
28
35
Days Post Attack

Table 1.6. Number of entrance holes and nuptial chambers occupied by male and female *P. rufipennis* attacking black spruce in Newfoundland, 1983.

Sex present[a]	Entrance holes	Nuptial chambers
None	7	2
1 ♂	25	42
1 ♀	14	22
2 ♀	1	3
1 ♂ + 1 ♀	2	22
1 ♂ + 2 ♀	0	6
1 ♂ + 3 ♀	0	3
Total	49	100

[a] Occupancy determined for attacking brood on 13 trees attacked in spring.

Fig 1.9. Proportion of gallery systems with 1 to 6 female egg galleries constructed in black spruce by *P. rufipennis*, spring, 1983. Counts made on intact galleries from felled (N = 135), standing severed (N = 75) and standing unsevered (N = 74) trees.


Percent of Gallery Systems
100
75
50
25
0
Felled
100
75
50
25
0
Standing Severed
100
75
50
25
0
Standing Unsevered
1
2
3
4
5
6
No. of Egg Galleries

galleries on felled, standing severed and standing unsevered trees, respectively. Two attacks with 6 egg galleries were found on bark samples removed from standing severed trees. Fully formed gallery systems were of the radiate type (Chamberlin 1939, 1958), with 2 to 6 egg galleries joined to a large central nuptial chamber. The length of egg galleries increased linearly with time (Fig. 1.10) up to 5 weeks following first attack, when the mean length was 16.8 mm. Although the slope of the regression line was significantly different from zero, only 34.6% of the variation in tunnel length was accounted for by time (Fig. 1.10).

Analysis of brood production on black spruce in spring, 1983, disclosed significant linear associations between the number of egg niches established by female *P. rufipennis* and egg gallery length (Fig. 1.11A), between number of eggs and egg gallery length (Fig. 1.11B), and between the number of eggs and the number of egg niches (Fig. 1.11C). The average number of egg niches per mm of egg gallery in Spring, 1983 was 0.37.

The relationship between the mean number of egg niches per gallery and number of female tunnels per gallery indicated that, with an increase in the number of egg galleries, there are concomitant increases in the numbers of eggs niches and eggs per gallery system (Fig. 1.12). With an increase in the number of egg galleries per gallery system, generally there was an increase in the female to male sex ratio (Fig. 1.12).

In 1984 *P. rufipennis* had established a first brood on felled black spruce in spring, approximately 1 week after the start of emergence. One month later, eggs and larvae comprised 58.7 and 41.3% of the total brood, respectively (Fig. 1.13). Two months following attack, larvae and pupae represented 65.8 and 20.8% of the total brood, respectively. Callow adults were first observed on 22 August, when they accounted for 18.9% of the total brood. At the

Fig 1.10. Mean egg gallery length in relation to time occupied by *P. rufipennis*. Means calculated from 452 female galleries established during the first 5 weeks of spring, 1983.

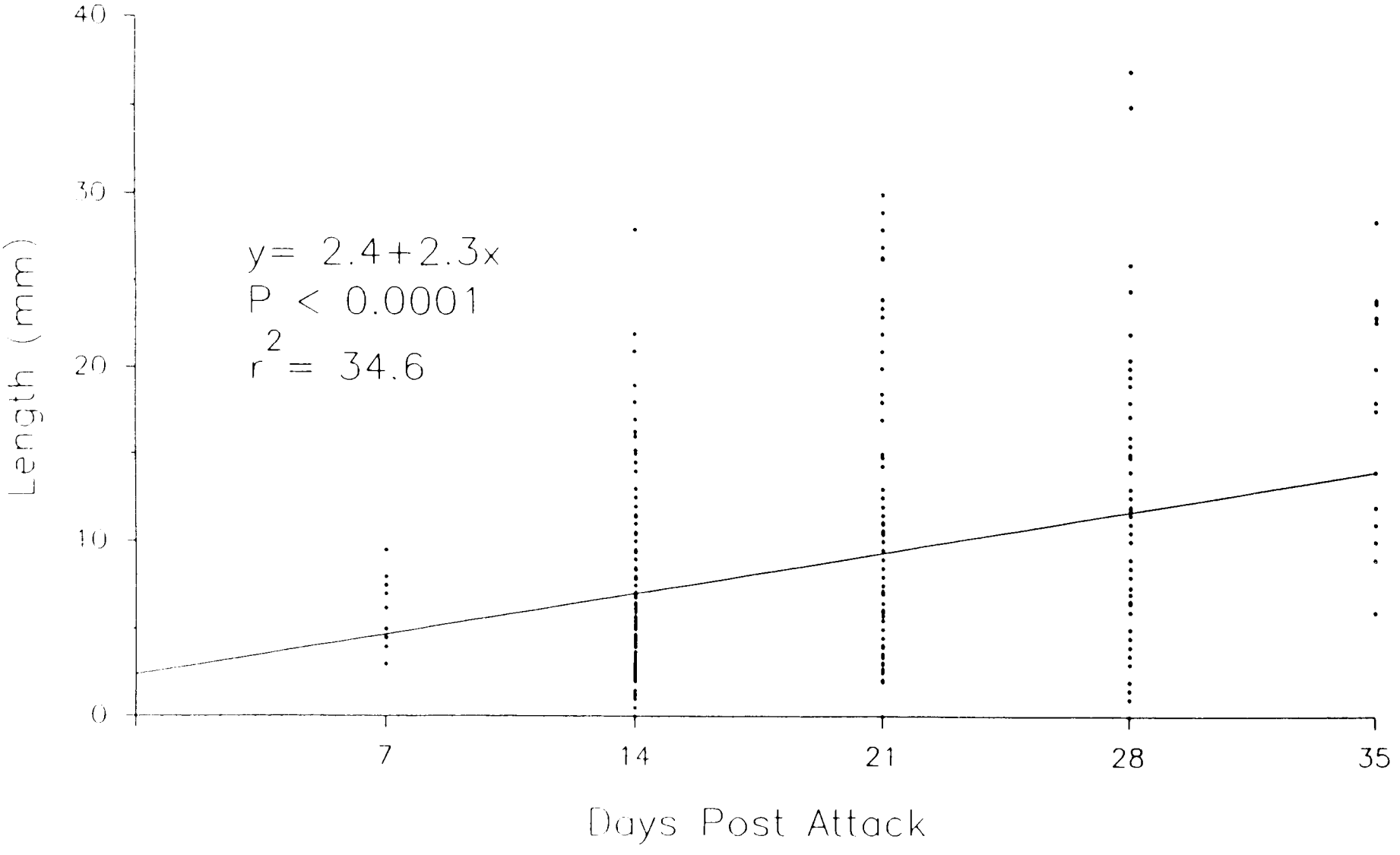
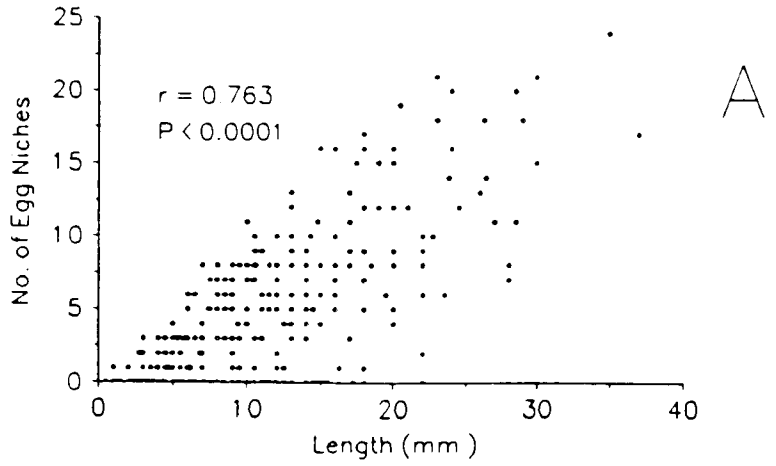
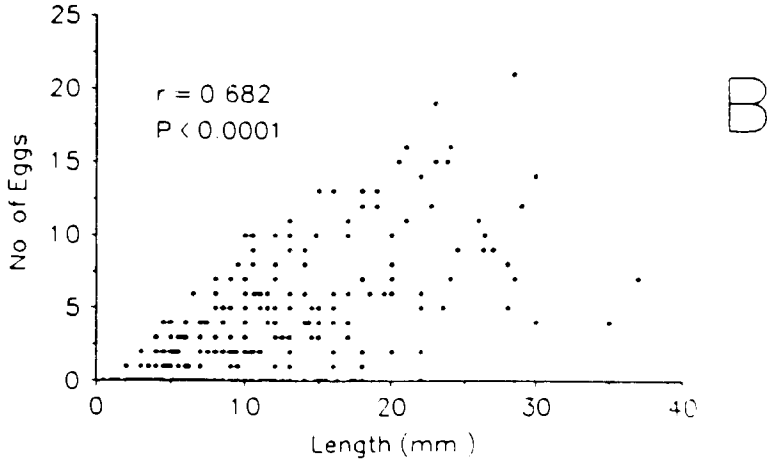

40
30
20
10
0
Length (mm)
y= 2.4+2.3x
P < 0.0001
r 2 = 34.6
7
14
21
28
35
Days Post Attack

Fig 1.11. Relationship between the numbers of A) egg niches and egg gallery length, B) eggs and egg gallery length, and C) eggs and egg niches. Spring brood production by *P. rufipennis*, 1983.


A
r = 0.763
P < 0.0001
No. of Egg Niches
Length (mm)
0
5
10
15
20
25
0
10
20
30
40


B
r = 0.682
P < 0.0001
No. of Eggs
Length (mm)
0
5
10
15
20
25
0
10
20
30
40

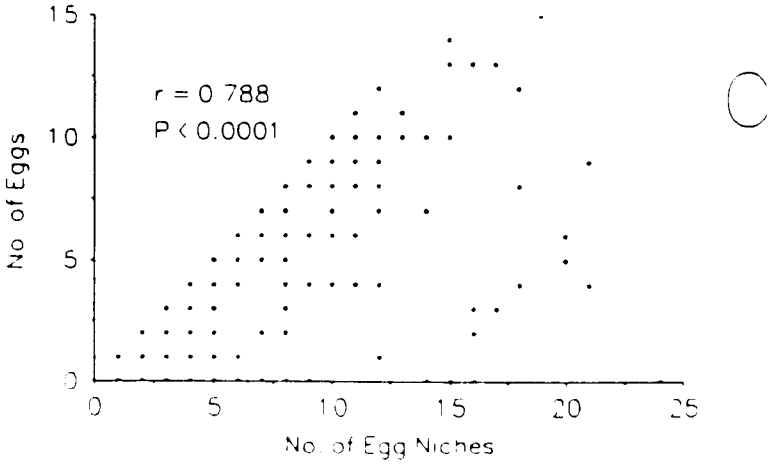

C
r = 0.788
P < 0.0001
No. of Eggs
No. of Egg Niches
0
5
10
15
20
25

Fig. 1.12. Relationship between mean numbers of egg niches and eggs and the number of egg galleries per gallery system. Numbers in parenthesis represent female to male sex ratios for 1, 2, 3, 4, and 5 gallery systems.

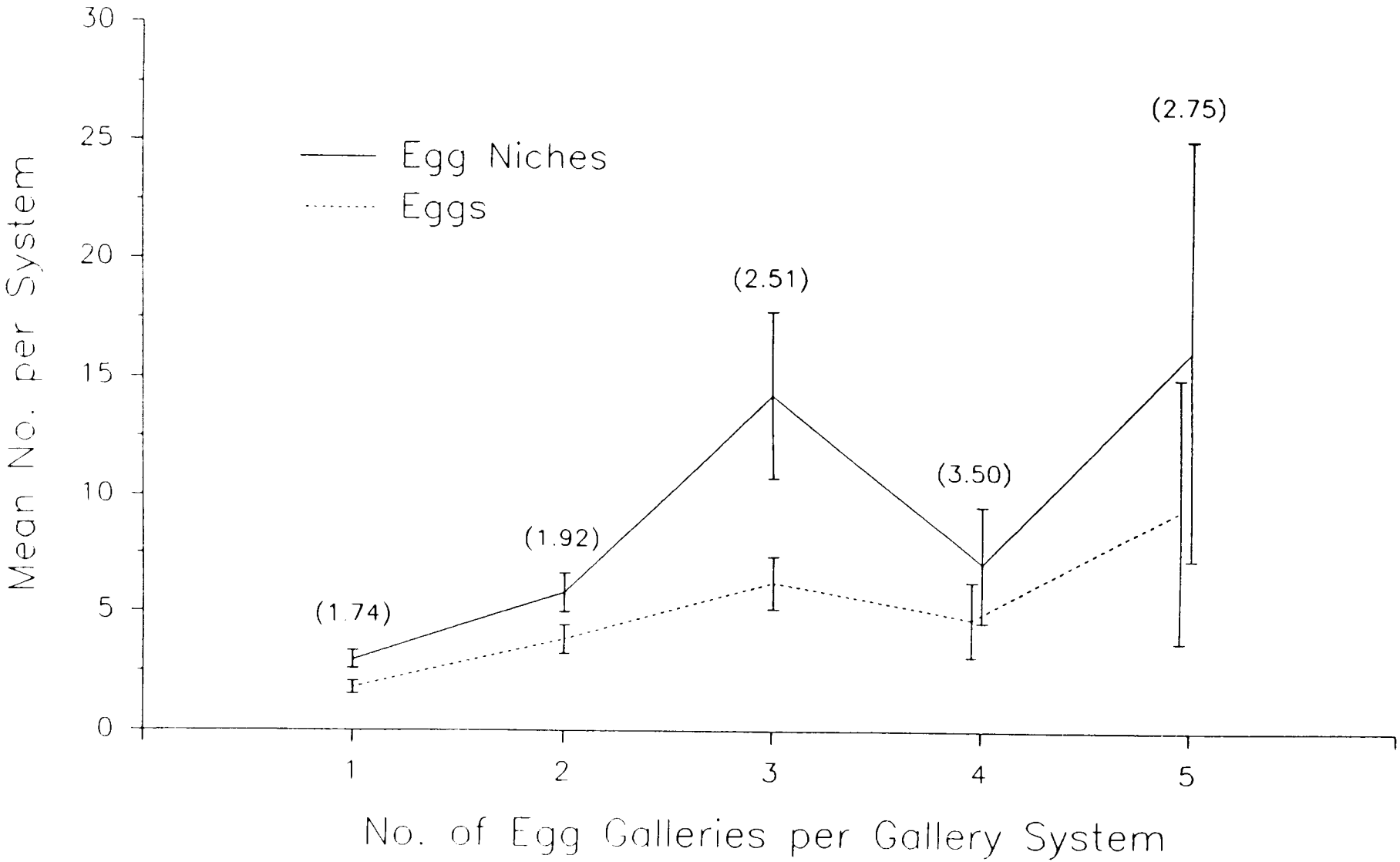
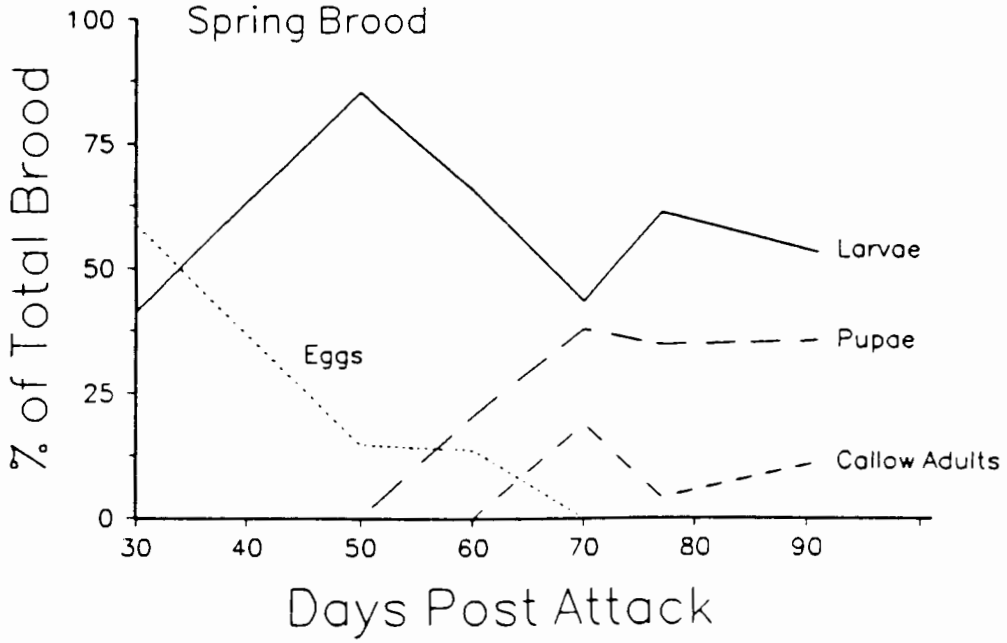
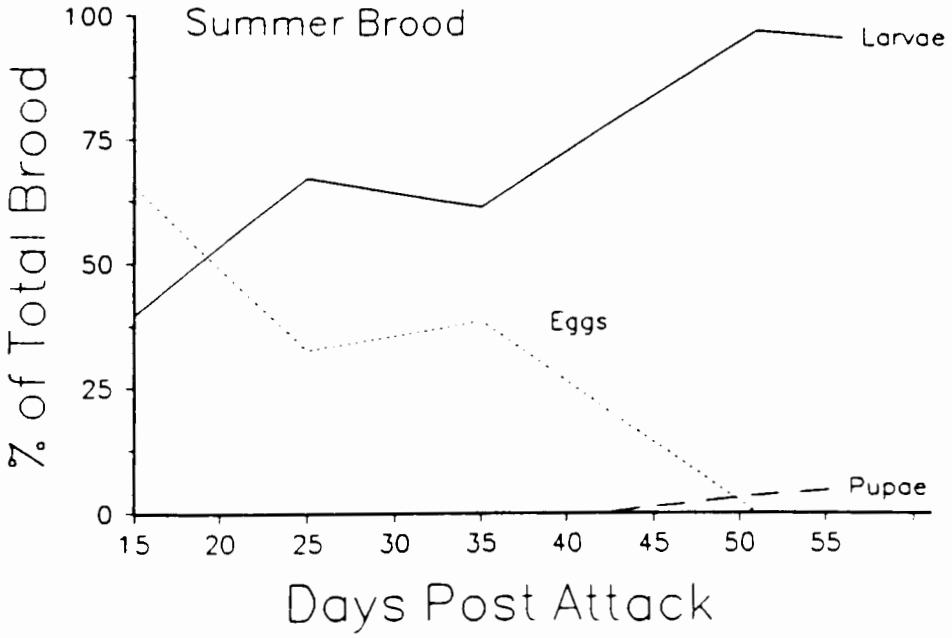

Egg Niches
Eggs
(1.74)
(1.92)
(2.51)
(3.50)
(2.75)
Mean No. per System
0
5
10
15
20
25
30
1
2
3
4
5
No. of Egg Galleries per Gallery System

Fig. 1.13. Seasonal life history of *P. rufipennis* on felled trees attacked in spring and summer, 1984. Proportion of life-stages throughout spring and summer determined from 7 trees attacked on 14 June and 4 trees attacked on 20 July, respectively.


Spring Brood
% of Total Brood
100
75
50
25
0
Eggs
Larvae
Pupae
Callow Adults
30
40
50
60
70
80
90
Days Post Attack


Summer Brood
% of Total Brood
100
75
50
25
0
Eggs
Larvae
Pupae
15
20
25
30
35
40
45
50
55
Days Post Attack

beginning of Fall, the proportions of larvae, pupae and callow adults were 53.3, 35.6 and 11.1%, respectively.

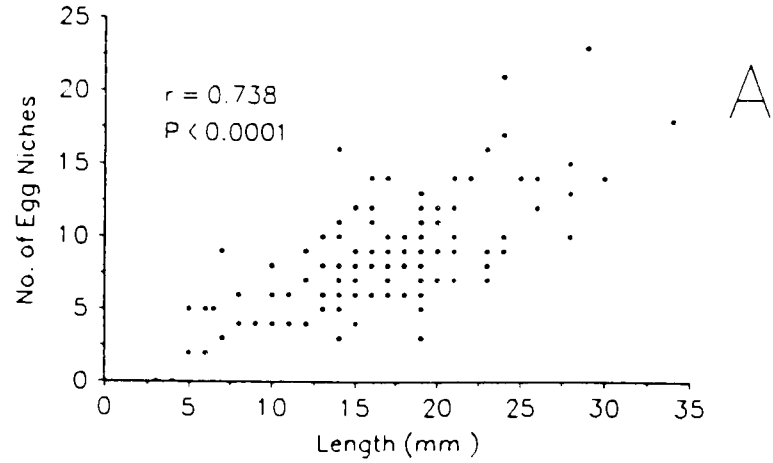
Re-emerged parent adults established a second (summer) brood on felled trees during the third week of July, 1984. Two weeks later, eggs and larvae comprised 65.3 and 39.5% of the total brood, respectively (Fig. 1.13). By 6 September, 55 days following initial attack, pupae accounted for 4.8% of the brood, and no callow adults were present. There was little evidence for a third brood in 1984. Only 1 adult *P. rufipennis* emerged from 2 summer brood trees fitted with emergence traps on 7 August. Moreover, 16 galleries established on trees felled on 20 August contained only eggs and early stage larvae on 29 August and 12 September when dissected.

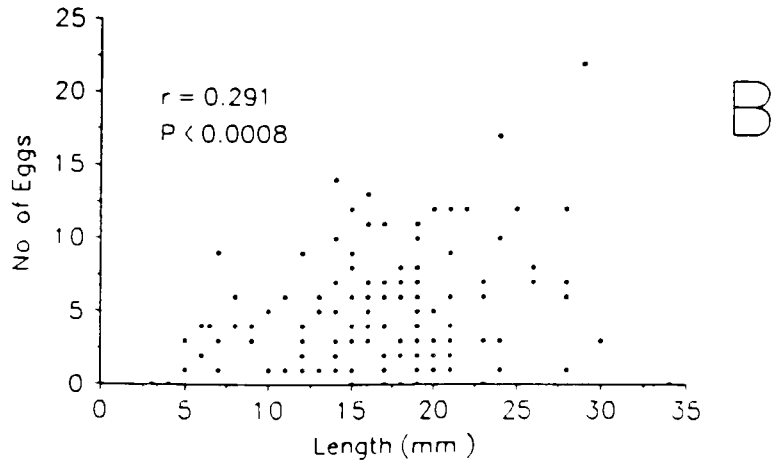
The mean lengths of egg galleries established for first (Spring) and second (Summer) broods by females in 1984 (Table. 1.7, Exp. I) were comparable and nearly identical to the mean lengths of galleries established by females for their first brood in 1983. Furthermore, the mean number of egg niches per mm of gallery length varied little among broods (Table 1.7, Exp. I) in 1984, and was only slightly higher than for 1983. The linear associations between the numbers of egg niches and lengths of egg galleries for the 1984 spring and summer broods (Fig. 1.14A; 1.15A) were nearly identical to that found for the spring brood of 1983 (Fig. 1.11A). In contrast, the linear association between the numbers of eggs and lengths of egg galleries observed in Spring, 1984 (Fig. 1.14B), was weaker than that observed in Summer, 1984 (Fig. 1.15B) and weaker than that observed in Spring, 1983 (Fig. 1.11B). Likewise, a slightly weaker association between eggs and egg niches was evident in Spring than in Summer, 1984 (Fig. 1.14C; 1.15C) and in Spring, 1983 (Fig. 1.11C).

Table 1.7. Mean length of female egg tunnels and number of egg niches produced by *P. rufipennis*, Newfoundland, 1984.

Exp. No.	Brood No.	Mean (+SE) Tunnel length (mm)	Egg niches	Egg niches per mm tunnel
Exp. I.				
	First brood (N=131)	16.1 ± 0.5	8.1 ± 0.3	0.5 ± 0.01
	Second brood (N=92)	16.9 ± 0.8	8.6 ± 0.4	0.5 ± 0.02
	Third brood (N=16)	8.9 ± 1.4	4.6 ± 0.9	0.4 ± 0.06
Exp. II.				
	Second brood (N=30)	18.7 ± 1.4	8.9 ± 1.1	0.4 ± 0.03
	Third brood (N=10)	9.1 ± 1.2	2.6 ± 0.8	0.2 ± 0.06
Exp. III.				
	First brood (N=25)	14.0 ± 1.2	4.5 ± 0.9	0.3 ± 0.07
	Second brood (N=8)	8.7 ± 1.2	1.4 ± 0.6	0.2 ± 0.07

Fig 1.14. Relationship between the numbers of A) egg niches and egg gallery length, B) eggs and egg gallery length, and C) eggs and egg niches. Spring brood production by *P. rufipennis*, 1984.


A
r = 0.738
P < 0.0001
No. of Egg Niches
Length (mm)
0
5
10
15
20
25
30
35


B
r = 0.291
P < 0.0008
No of Eggs
Length (mm)
0
5
10
15
20
25
30
35

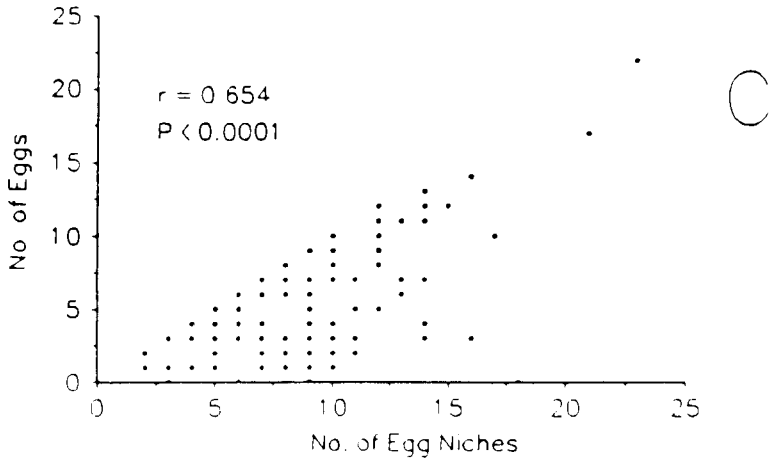
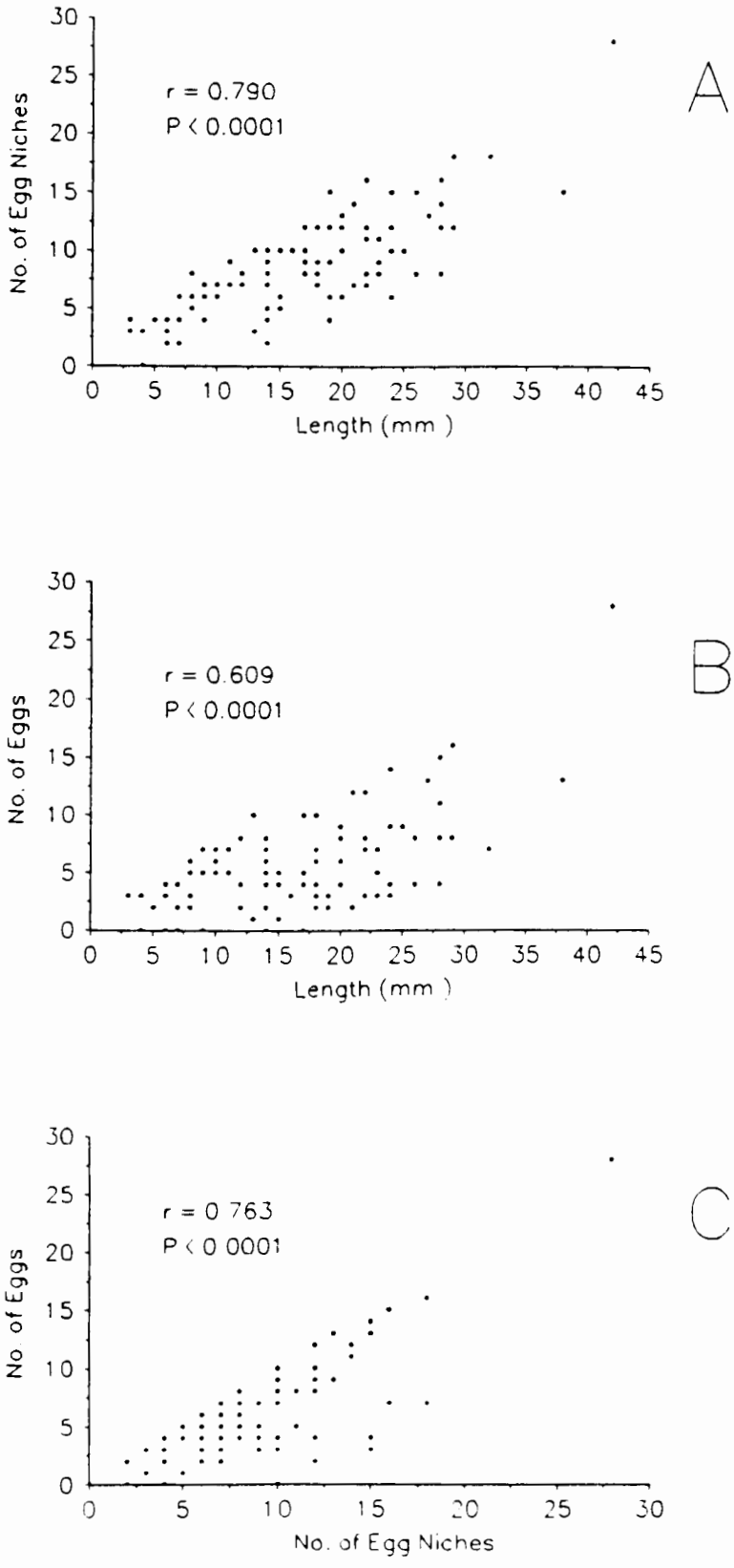

C
r = 0 654
P < 0.0001
No of Eggs
No. of Egg Niches
0
5
10
15
20
25

Fig. 1.15. Relationship between the numbers of A) egg niches and egg gallery length, B) eggs and egg gallery length, and C) eggs and egg niches. Summer brood production by *P. rufipennis*, 1984.


A
r = 0.790
P < 0.0001
No. of Egg Niches
Length (mm)
B
r = 0.609
P < 0.0001
No. of Eggs
Length (mm)
C
r = 0 763
P < 0 0001
No of Eggs
No. of Egg Niches

Dissection of bark samples removed from third brood trees revealed a total of only 16 egg galleries with 74 egg niches containing 48 eggs. No other life-stages were present in trees felled to test for the possibility of a third brood. Also, the mean egg gallery length and the mean number of egg niches produced by attacking females in Fall were reduced by approximately 50%; however the number of egg niches per mm of gallery length was consistent with the number produced by females attacking black spruce in Spring and Summer (Table 1.7, Exp. I).

Brood establishment on bolts artificially infested with parent *P. rufipennis* confirmed that re-emerged adults are capable of producing a second, and possibly a third, brood in Newfoundland. Thirty gallery systems ($\bar{x}$ length of egg galleries = 18.7 $\pm$ 1.4) were established on 5 second brood logs 44 days following infestation in summer, 1984 and 10 gallery systems ($\bar{x}$ length of egg galleries = 9.1 $\pm$ 1.2) were established on 3 third brood logs, 21 days following infestation, in Fall, 1984 (Table 1.7, Exp. II). The mean number of egg niches established in second and third brood logs artificially infested with parent adults (Table 1.7, Exp. II) differed little from the numbers established by natural infestations. Second brood offspring were comprised of eggs, larvae and pupae that accounted for 3.1, 93.8 and 3.1% of the total brood, respectively. Eggs and larvae constituted 58.8 and 41.2% of the third brood, respectively.

Parent adults that presumably overwintered as late instar larvae and were artificially introduced into logs in summer, 1984 produced a first brood comprised of 5.6% eggs and 94.4% larvae, 44 days following infestation. Egg galleries ($\bar{x}$ length = 14.0 $\pm$ 1.2), were similar in length to those established by overwintered brood adults in Spring, 1984 (Table 1.7, Exp. I, III). However, the mean number of egg niches ($\bar{x}$ = 4.5 $\pm$ 0.9) established by parent adults that

overwintered as larvae was nearly one-half that produced by overwintered adults. Production of a second brood by adults that overwintered as larvae was low. Only 5 gallery systems were discovered in bark samples peeled on 13 September, 1984. A total of 8 egg galleries (Table 1.7. Exp. III) contained 3 eggs, 22 days following infestation. No other brood stage was present.

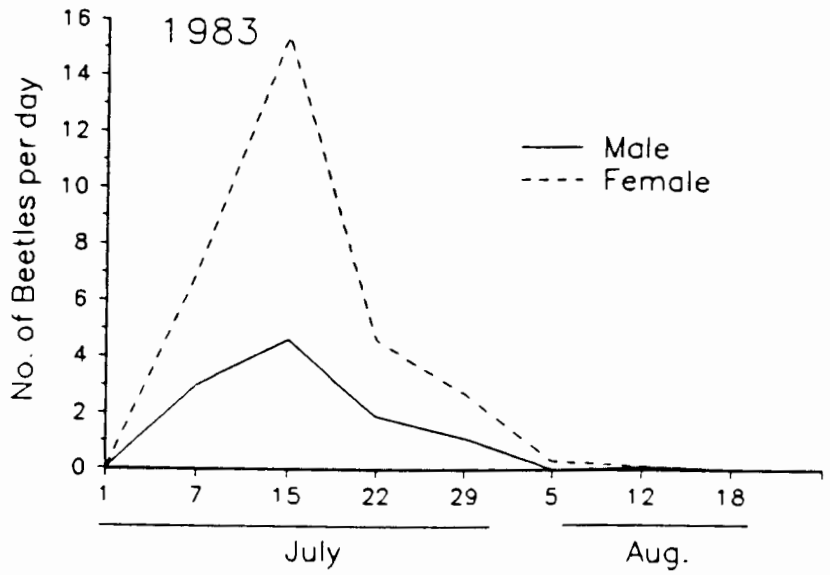
Parent Adult Re-emergence

Re-emergence in 1983 from established gallery systems began approximately 4-5 weeks following attack and peaked near mid July (Fig 1.16). The number of beetles re-emerging then decreased rapidly until 12 August, after which no further re-emergence occurred. Laboratory studies disclosed that parent adults were capable of establishing a second brood, however, there was little evidence for a third brood. Although re-emergence started later in 1984 the general pattern was similar to that in 1983 (Fig 1.16).

HOST COLONIZATION UNDER SUN AND SHADE

In 1983, attacks were first recorded on 14 June on 1 tree exposed to full sunlight and on 2 trees felled in shade. Three weeks later, 9 trees in shade had been successfully attacked but only 2 trees exposed to full sunlight had been attacked. All trees in both sun and shade were infested with *P. rufipennis* by the middle of August. Most trees were colonized all along the bole, from the cut base to as close as 2.5 cm from the tip on some trees. Significantly higher numbers of gallery systems were established on trees felled in shade than in full sunlight (Table 1.8). No significant differences due to position along the bole were apparent and the interaction of position and light exposure was also not significant. Furthermore, the number of adults remaining in the bark of trees exposed to shade was nearly double that found in trees exposed to full sunlight.

Fig 1.16. Re-emergence of *P. rufipennis* from black spruce, in 1983 and 1984.


1983
No. of Beetles per day
16
14
12
10
8
6
4
2
0
Male
Female
1
7
15
22
29
5
12
18
July
Aug.

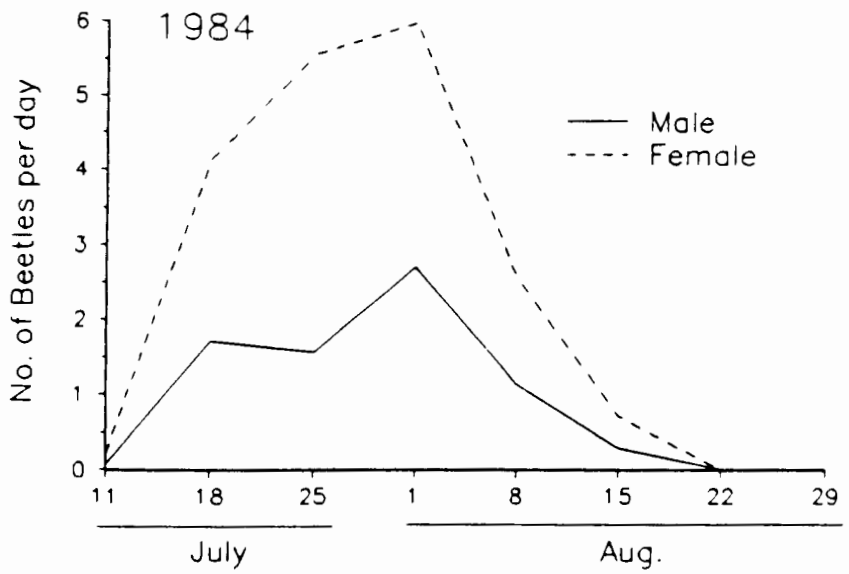

1984
No. of Beetles per day
6
5
4
3
2
1
0
Male
Female
11
18
25
1
8
15
22
29
July
Aug.

Table 1.8. Colonization of felled black spruce exposed to full sunlight (N=14) or dense shade (N=15) by *P. rufipennis*, Newfoundland, 1983.

Exposure	Position	Bark thickness (mm.)	Gallery Systems No.	Gallery Systems Mean ± SE[a]	Adult brood ♂	Adult brood ♀	Adult brood Total	Dead adults No.	Dead adults %
Sun	Base	4.5 ± 0.4	30	2.1 ± 0.6	13	19	32	15	48.4
	Midbole	3.7 ± 0.4	34	2.4 ± 0.5	10	18	28	13	46.4
	Top	3.3 ± 0.3	34	2.4 ± 0.5	14	32	46	16	34.8
Shade	Base	4.8 ± 0.4	67	4.5 ± 0.7	13	65	78	16	20.8
	Midbole	4.0 ± 0.4	67	4.5 ± 0.8	24	58	82	23	28.0
	Top	3.0 ± 0.3	46	4.2 ± 0.7	10	57	67	23	33.9

[a]Significant difference in numbers of galleries between sun and shade exposure (ANOVA, $P = 0.0003$), but not between positions ($P = 0.9687$), or for interaction between position and exposure ($P = 0.9139$).

In 1984, light exposure and bole aspect interacted to influence beetle establishment on felled black spruce (Table 1.9). Few attacks were found on the upper aspect of trees exposed to full light. In contrast, all aspects of trees felled in shade and the side and bottom of trees felled in light were successfully attacked by *P. rufipennis*. With the exception of the upper bole of trees exposed to light, where few galleries were established, the level of adult mortality was lower in trees under shade than those exposed to sunlight. No significant difference was observed between the mean length of egg galleries (mm) established in the lateral aspects of trees exposed to full sunlight ($\bar{x} = 13.3 \pm 0.9$) and the mean length of egg galleries established in trees subjected to dense shade ($\bar{x} = 15.1 \pm 1.0$).

INSECT AND FUNGAL ASSOCIATES OF *P. RUFIPENNIS*

Soon after attack by the four-eyed spruce beetle trees often were invaded by *D. affaber* and *C. borealis*. In 1983, 461 *D. affaber* adults (9.6/100 cm^2) emerged from 6 black spruce trees, with 70.3% emerging at or below 2 m from the base of the tree. In 1984, 322 adults (5.0/100 cm^2) emerged from 6 black spruce trees, with the majority emerging below 2 m. *D. affaber* began to emerge on 23 May 1983, and emergence peaked during the first 2 weeks of June. A second smaller peak in emergence was evident during the middle of August when the study terminated (Fig. 1.17). The majority of *D. affaber* adults emerged between 7 June and 1 July; 57.9% of the adults had emerged by 1 July. In 1984, emergence began during the first week of June (Fig. 1.17), and as in 1983, 2 peaks were observed during the season. The first peak in emergence was observed during the middle of June and the second in the middle of August. In 1984, 79.5% of the adults had emerged by 1 July.

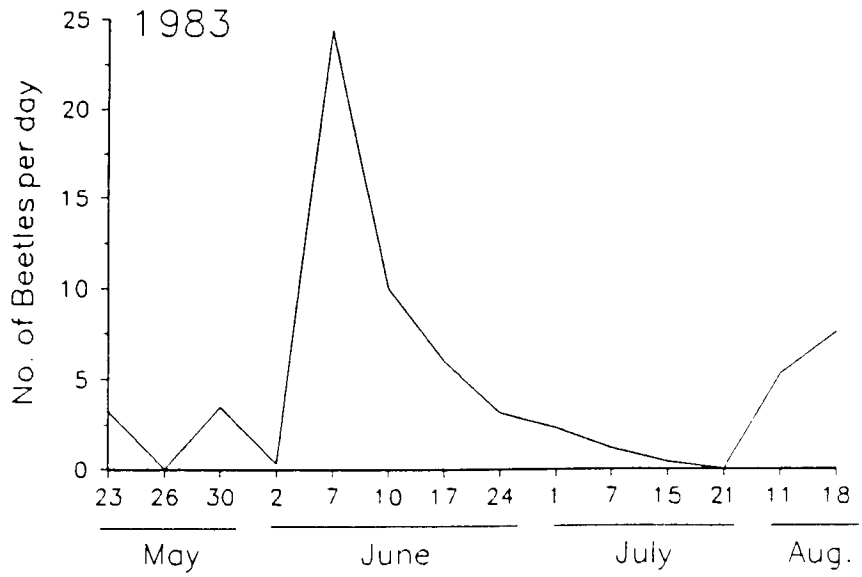
Emergence of *D. affaber* in the laboratory at room temperature (Fig. 1.18) was similar

Table 1.9. Colonization of felled black spruce exposed to full sunlight (N=10) or dense shade (N=10) by *P. rufipennis*, Newfoundland, 1984.

Exposure	Aspect	Bark thickness (mm.)	Gallery system		Adult brood			Dead adults	
			No.	Mean ± SE[a]	♂	♀	Total	No.	%
Sun	Upper	3.6 ± 0.1	4	0.4 ± 0.2	0	1	1	0	-
	Side	3.4 ± 0.2	51	5.1 ± 0.9	18	41	59	8	13.6
	Bottom	3.6 ± 0.1	77	7.7 ± 0.6	16	64	80	6	7.5
Shade	Upper	3.7 ± 0.1	66	6.6 ± 0.5	28	117	145	6	4.1
	Side	3.6 ± 0.1	54	5.4 ± 0.6	32	112	144	5	3.5
	Bottom	3.7 ± 0.1	46	4.6 ± 0.9	30	92	122	6	5.0

[a]Significant difference in numbers of galleries between sun and shade exposure (ANOVA, P = 0.0364), between aspects (P = 0.0005), and for interaction between aspect and exposure (P = 0.0001).

Fig 1.17. Seasonal emergence of *D. affaber* from black spruce in Newfoundland in 1983 and 1984.


1983
No. of Beetles per day
25
20
15
10
5
0
23 26 30 2 7 10 17 24 1 7 15 21 11 18
May
June
July
Aug.

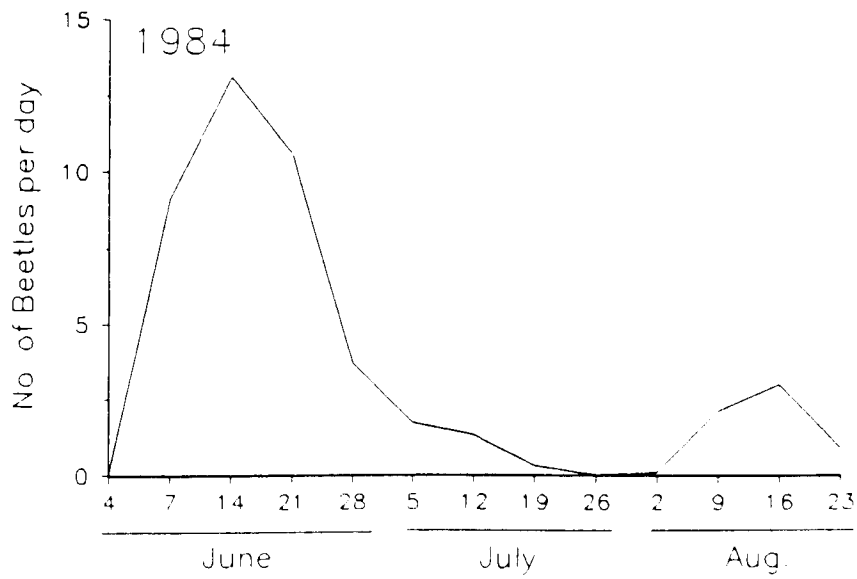
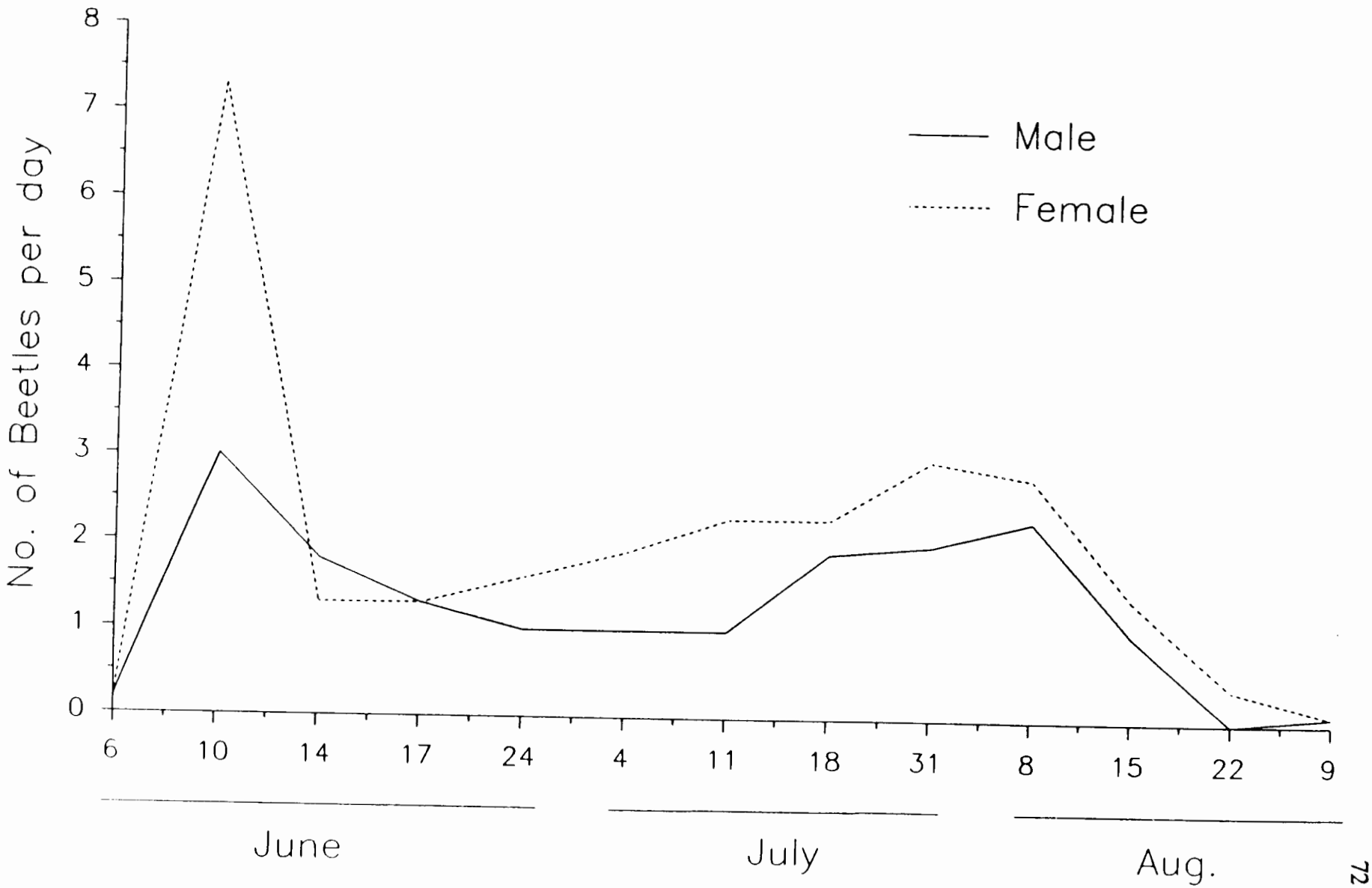

1984
No of Beetles per day
15
10
5
0
4 7 14 21 28 5 12 19 26 2 9 16 23
June
July
Aug.

Fig 1.18. Emergence of *D. affaber* from black spruce in the laboratory, 1985.


No. of Beetles per day
0
1
2
3
4
5
6
7
8
Male
Female
6
10
14
17
24
4
11
18
31
8
15
22
9
June
July
Aug.

to the pattern of emergence observed in the field in 1983 and 1984. Two peaks in emergence were evident; however under laboratory conditions the second peak occurred earlier and was not as pronounced as that observed under field conditions.

In 1985, the flight period of *D. affaber* began on 12 June and was characterized by a sharp peak in flight activity near the middle of June; 77.0% of the total catch occurred from 12-26 June (Fig. 1.19). During the first week of flight the catch was comprised entirely of males. Females were first trapped on 19 June but the number of females captured in multiple funnel traps was low throughout the season; females comprised only 14.7% of the total catch.

In 1983, 828 *C. borealis* adults (17.3/100 cm^2) emerged from 6 black spruce trees, with 83.1% emerging at or below 3.5 m from the base of the tree. In 1984, 1179 adults (18.4/100 cm^2) emerged from 6 black spruce trees, with the majority emerging at or below 3.5 m. *C. borealis* began to emerge on 30 May 1983 with a peak in emergence from 17 June to 15 July (Fig. 1.20). A second smaller peak in emergence was evident on 18 August when the study terminated. In 1984, emergence was first observed on 21 June (Fig. 1.20) and as in 1983, 2 peaks were observed during the season. The first peak in emergence was observed from 5-19 July and the second from 9-16 August. Only 1 *C. borealis* adult emerged from black spruce in the laboratory in 1985 and none was captured in multiple funnel traps.

Besides *P. rufipennis*, *D. affaber* and *C. borealis*, 343 other insects emerged from black spruce bolts held at room temperature in 1985. *Medetera* sp. (Diptera: Dolichopodiidae) and *Lasconotus intricatus* Kraus. (Coleoptera: Colydiidae), accounted for 70.9 and 12.8%, respectively of these associated insects. Additional Coleoptera included 25 *Dryocoetes autographus* (Ratzeburg), 15 *Trypodendron lineatum* (Olivier) (Scolytidae), and 1 *Thanasimus*

Fig 1.19. Seasonal flight pattern of *D. affaber,* Badger, Newfoundland, 1985.

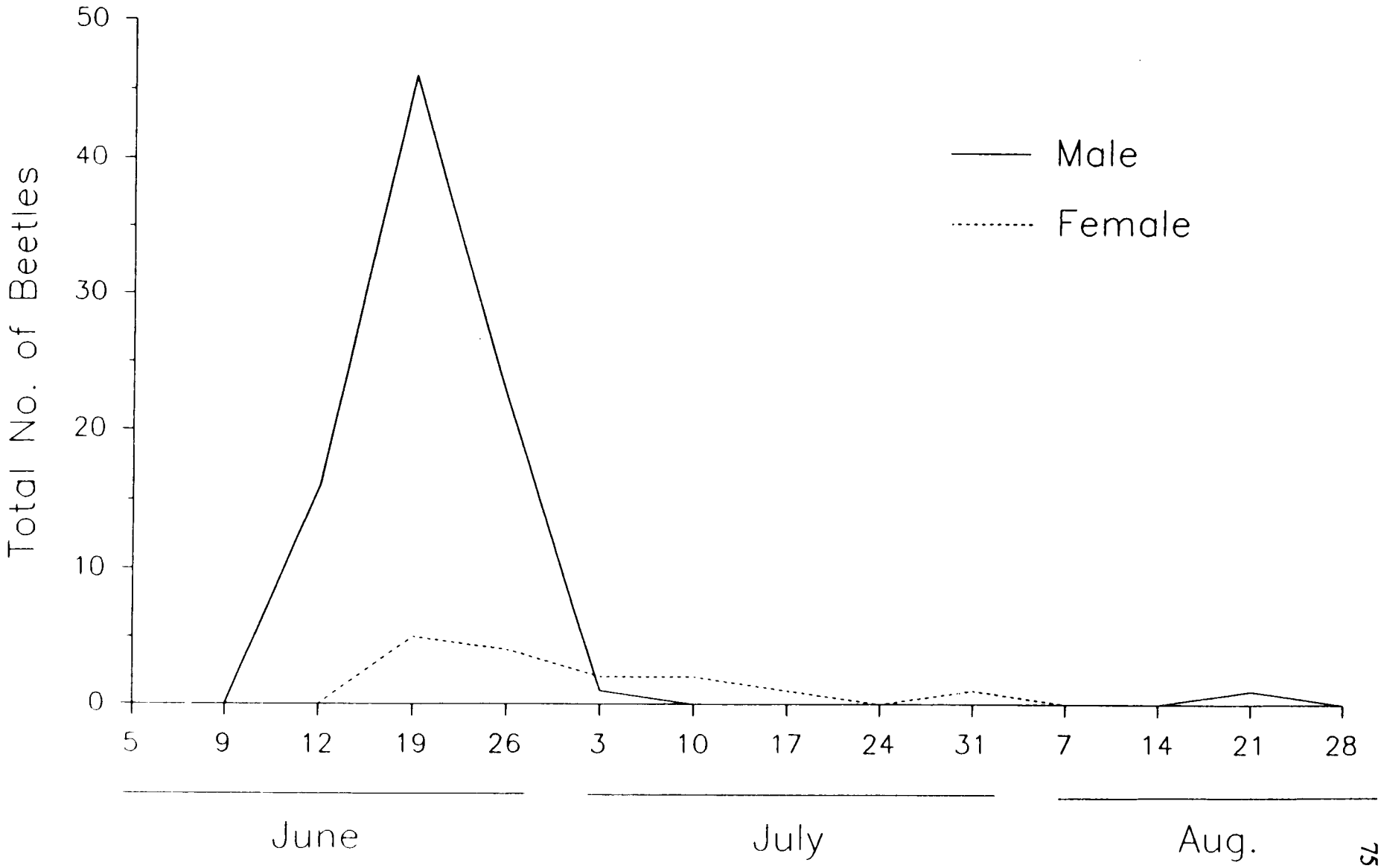
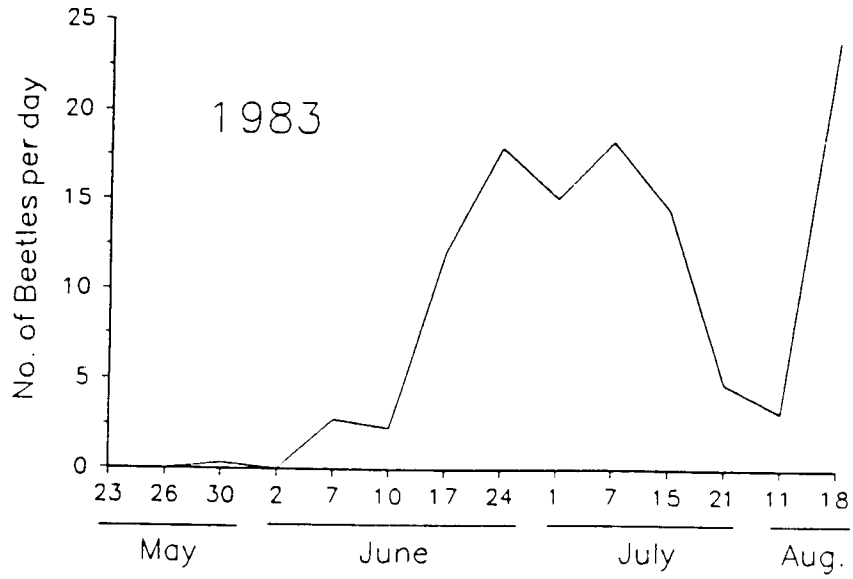
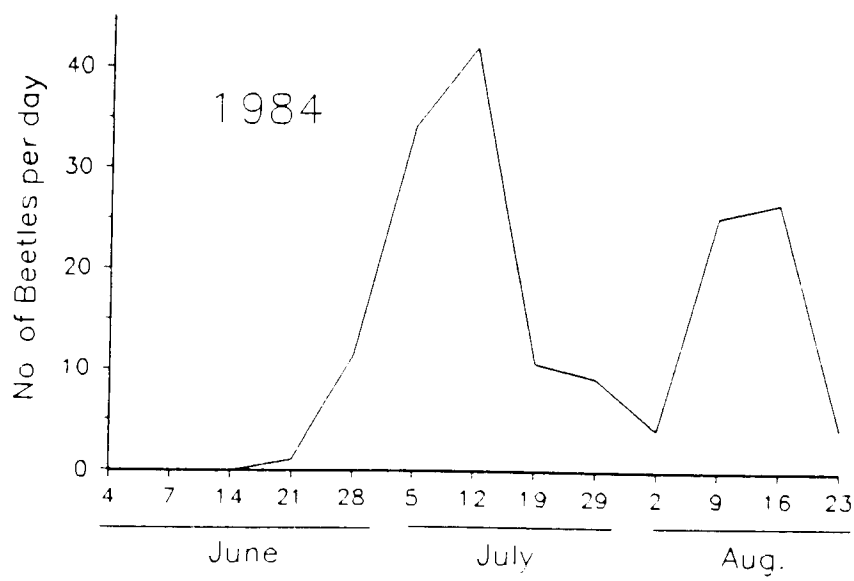

Total No. of Beetles
50
40
30
20
10
0
Male
Female
5
9
12
19
26
3
10
17
24
31
7
14
21
28
June
July
Aug.

Fig. 1.20. Seasonal emergence of *C. borealis* from black spruce in Newfoundland in 1983 and 1984.


1983
No. of Beetles per day
25
20
15
10
5
0
23 26 30 2 7 10 17 24 1 7 15 21 11 18
May
June
July
Aug.


1984
No of Beetles per day
40
30
20
10
0
4 7 14 21 28 5 12 19 29 2 9 16 23
June
July
Aug.

undatulus (Say) (Cleridae). Specimens in the Hymenoptera included 3 specimens of *Ecphylus* sp., 2 *Roptrocerus xylophagorum* (Ratzeburg), 1 *Eubazus* sp. and 1 *Cosmophorus rufovariegatus* Vier. Two staphylinids, and several spiders were recovered from the emergence cages but were not identified.

One species of fungus, *Ceratocystis piceaperda* (Rumb.) C. Moreau, was associated with *P. rufipennis* during all phases of the colonization sequence (Table 1.10). The overall incidence of the fungus on adult beetles was 26%. The incidence of the fungus was significantly higher on emerged female beetles than on emerged male beetles. No significant difference (χ^2 test, $P > 0.05$) was found between the incidence of *C. piceaperda* on overwintered males and females or on males and females that had recently established on black spruce. Bacteria and yeast cultured, but not identified were also isolated from *P. rufipennis* throughout its colonization sequence. Also, numerous miscellaneous fungi imperfecti and basidomycetes were isolated, but these were not associated consistently with the beetle.

Table 1.10. Proportion of *P. rufipennis* adults infested with the fungus, *Ceratocystis piceaperda*, Newfoundland, 1985.

Sex	Overwintered adults		Emerged[a] adults		Attacking adults		Total adults	
	n	%	n	%	n	%	n	%
Male	27	44	25	8	18	17	70	24
Female	23	26	25	40	32	19	80	29
Total	50	36	50	24	50	18	150	26

[a]Significant difference between the number of males and females infested by *C. piceaperda* (χ^2 test, P = 0.0081).

DISCUSSION

Unlike some other bark beetles (Chamberlin 1958; Thomas 1961) *P. rufipennis* spent the winter within phloem tissue rather than in the duff. Low winter temperatures can cause substantial mortality in bark beetles, e.g. the spruce beetle, *Dendroctonus rufipennis* (Kirby) (Massey and Wygant 1954; Terrell 1954; Frye et al. 1974). Similar overwintering mortality probably caused the reduction in survival of *P. rufipennis* brood adults in felled and standing severed trees during the winter in Newfoundland. The greater survival in standing unsevered trees than in cut trees may have been caused by desiccation of bark tissue in the latter hosts. Overwintering as an adult offers an advantage in northern climes, because reproduction can commence immediately after temperatures warm up in spring and the opportunity for 2 broods per season is enhanced. Although the number of beetles that overwintered below 0.5 m on the bole of black spruce was not investigated, hibernation near the root collar might have high survival value for *P. rufipennis*. Below the snowline, winter temperatures may not be lethal to overwintering broods and snow cover may protect larvae and callow adults from woodpecker predation.

Host colonization by *P. rufipennis* followed the typical host selection sequence of scolytids (Wood 1982; Borden 1982), including emergence from the overwintering site, dispersal, host selection and establishment on felled and standing trees. In both 1983 and 1984 83% of the beetles emerged in the field and in the laboratory during a discrete period in June. *P. rufipennis* apparently synchronizes its emergence with the onset of suitable environmental conditions, facilitating mass attack that can monopolize breeding material which would otherwise be colonized by competing insects (Bartels and Lanier 1974). Delay of emergence until late May

or early June will avoid sporadic, late-spring frosts that occur in Newfoundland. The onset of emergence may have been delayed in 1984 due to prolonged cold periods in early June. The lowest maximum ambient temperature at which emergence occurred was 5.4°C, a threshold much lower than for other bark beetles in similar climates (Bakke 1968a).

P. rufipennis overwintered in Newfoundland as callow adults and larvae, agreeing with observations in other locations (Simpson 1929; Hilton 1968). Overwintering larvae probably resulted from late-emerging adults colonizing trees in July, or from re-emerged parents that established second and third broods. Extended emergence after 15 July in 1983 probably resulted from progeny that overwintered as larvae in galleries established in July or August 1982. The initiation and peak periods of emergence (Figs. 1.3A, 1.3B) agree with flight period data from Maine (Hosking and Knight 1975). The longer duration of emergence in Newfoundland than in Maine probably reflects the lack of sustained warm spring weather in Newfoundland. While *P. rufipennis* in Newfoundland emerged and flew mostly in June (Figs. 1.3, 1.5), peak activity of *P. rufipennis* in Alaska occurred in July (Beckwith 1972), resembling the trend reported by Annila (1977) for the European species *P. poligraphus* and *P. punctifrons* Thoms.

The weak linear relationship of emerged beetles to height in 1984 ($r^2 = 0.28$) implies that relatively little of the variation in emergent beetles is accounted for by height. The r^2 value rose to 0.45 when bark thickness was incorporated in 1984 into the regression model. Bark thickness has been implicated as a major factor in determining brood productivity for several scolytids (Bakke 1968a; Amman 1969, 1972; Haack *et al.* 1984a,b). Price (1966) related survival of *P. rufipennis* colonizing different host species to bark thickness, and to competing organisms, which reduced the feeding area available to *P. rufipennis* larvae. In my study, bark thickness ranged

from 6.5 mm in the lower bole to 1.0 mm in the upper bole, where competition for food would intensify, larvae would be subjected to high (possibly lethal) subcortical temperatures, and parasitoids with short ovipositors would be most effective (Beaver 1967; Richerson and Borden 1972).

The preponderance of females in the early stages of emergence probably ensures outbreeding (Borden 1982). The low captures of females in male-baited traps during early flight in 1985 suggests that female brood emerging early in the season may be weakly responsive to male attractants, further promoting outbreeding. Delays in response between the sexes and within broods is common for several species of bark beetles (Gara 1963; Bedard 1966; Atkins 1969).

The approximately 1 : 1 sex ratio of emerged bark beetle broods in 1983 followed Fisher's (1930) principle of a 1 : 1 sex ratio, but the 1.9 : 1 female : male ratio in 1984 did not. Female-biased sex ratios occur in other harem polygynous species (Reid 1958; Cameron and Borden 1967; Hosking and Knight 1976). In several *Ips* spp., aberrant female sex ratios may result from gynogenesis (parthenogenesis stimulated by mating) or from a maternally transmitted cytoplasmic factor that is more effective against males than females (Lanier and Oliver 1966; Bakke 1968b). Thelyotoky in *Pityophthorus puberulus* (LeConte) results in broods composed entirely of parthenogenetic females (Deyrup and Kirkendall 1983). Intra-specific competition during larval development could shift the sex ratio in favour of females (Cole 1973), because of differential larval mortality in polygynous organisms (Williams 1966). In natural populations of mountain pine beetles, *Dendroctonus ponderosae* Hopk., overwintering larvae and adults exposed to low temperatures showed differential sexual mortality (Safranyik 1976). The departure of the 1984 brood sex ratio from 1:1 is consistent with a hypothesis of differential

mortality caused by cold temperatures. This phenomenon would vary among trees with different bark characteristics and thicknesses. Indeed, the skewed sex ratio in 1984 was caused by two trees which accounted for the biased ratio in the entire population. These findings suggest that host characteristics can interact with weather to determine differential levels of stress-induced mortality between the sexes of overwintering *P. rufipennis* larvae and adults.

It is generally accepted that both emergence and initiation of flight in scolytids are clearly influenced by air temperature (Bakke 1968a; Annila 1977; Saarenmaa 1989). Observations on the flight activity of *P. rufipennis* indicated that after adults leave the host, flight activity continues throughout the summer when warm weather conditions prevail in Newfoundland. Peaks in flight activity coresponded strongly to patterns of spring emergence and summer re-emergence when first and second broods are established.

The short interval between girdling of trees and arrival by *P. rufipennis* implies that adults may respond to host odours to locate a suitable breeding substrate. Several species of scolytids exploit host volatiles (Chapman 1962), most notably ethanol (Moeck 1981) to locate suitable breeding material. However, such primary attraction could be confounded by pheromones released by early attacking beetles. Furthermore, the time interval between cutting and first attack on felled trees was fairly long suggesting that visual orientation may also be important in host selection. This hypothesis is consistent with observations that *P. rufipennis* is not capable of orienting to weakened hosts through olfaction alone (Gara and Holsten 1975).

The doubled attack density on felled over standing severed trees, and the finding that only 2 standing unsevered trees were attacked, supports the hypothesis that *P. rufipennis* is a secondary bark beetle on black spruce and requires some means of host predisposition for

establishment and optimal reproduction. Moreover, the rate of increase on standing unsevered trees was slower than on felled and standing severed trees, possibly due to a greater level of tree resistance.

In Maine, Hosking and Knight (1975) compared window trap catches from three heights on the bole, and reported highest numbers attacking at 7.5 m. In Newfoundland, *P. rufipennis* almost always attacked in the lower bole first, and only after mass attack were trees attacked higher on the bole. The lack of a significant relationship between attack density and sample height or bark thickness is surprising. For many species, significant relationships exist between densities of attack or beetle brood and parameters such as tree height and bark thickness (Shepherd 1965; Amman 1969, 1972; Coulson *et al.* 1976; Haack *et al.* 1984; Amman and Pasek 1986). Possibly, by dispersing evenly over the bole, *P. rufipennis* can fully utilize the host resource, and can avoid excessive competition from con- and hetero-specifics, and can lessen the chance of parasitism by not concentrating in areas of bark where levels of parasitoid-attracting kairomones might be high.

There has been disagreement over which sex of *P. rufipennis* initiates attack (Hopkins 1899; Blackman and Stage 1918; Simpson 1929; Hilton 1968; Rudinsky *et al.* 1978). My observations that the male usually initiates the attack and excavate the nuptial chamber is in agreement with the trend for most harem polygynous taxa. Aggregation pheromones are almost invariably produced by the initiating sex, a phenomenon that was confirmed for *P. rufipennis* (Chapter 3). The habit of male *P. rufipennis* remaining with the females after copulation and guarding the entrance hole is common in polygynous bark beetles. This behavior was interpreted by Kirkendall (1983) as 'resource defense'; males who guard reproducing females after mating

probably derive a net benefit over those who leave the resource early and risk loss of sperm through ejaculate competition or loss of brood to predators.

The increase in female to male sex ratio as the number of female galleries per gallery system increases (Fig 1.12), confirms that the number of egg galleries is a reliable indicator of the number of females per male, and therefore can be considered a measure of male reproductive success. However, variation in harem size may also be the result of differences in resource quality (Kirkendall 1983). My results also indicate that as males acquire more females, each female generally produces more eggs, a second measure of reproductive success (Fig. 1.12). Blackman and Stage (1918) found the opposite result for *P. rufipennis* on larch, suggesting that black spruce is a better host.

Although egg gallery length increased linearly during the first 5 weeks of spring, 1983, the majority of the variation in gallery length remains unexplained. Possibly there is an uneven decline in the amount or quality of phloem tissue over time; individual gallery systems may also be prone to different levels of intraspecific competition. Significant correlations between the number of eggs and length of female galleries in both spring and summer broods support the hypothesis that such factors may limit *P. rufipennis* success in black spruce. Although a significant association existed between number of eggs and number of egg niches for both spring and summer broods, the high degree of scatter suggests that counts of egg niches may not be a reliable measure of female fecundity since some females appear to excavate egg niches but fail to oviposit.

My findings support those of Simpson (1929) that *P. rufipennis* is univoltine, but may have up to 3 broods per year. In Newfoundland, *P. rufipennis* established at least 2 broods per

year. Pupae of the first brood developed into callow adults so late in the season, that they could not emerge until the following spring. The second (summer) brood, overwintered primarily as larvae (Fig. 1.13), although a few individuals could have reached adulthood before winter. Parents artifically removed from second brood trees were cabable of establishing new galleries with very few eggs and larvae in Fall, 1984. Therefore, a third brood is considered likely only under the most favourable conditions. Simpson (1929) reported that in areas where *P. rufipennis* produces a third brood, the third brood progeny hibernate as larvae for 2 winters. The question as to why beetles re-emerge is intriguing. A nutrient deficiency may occur after a period of feeding in the fungus-infested tissue, and required nutrients may only be available from a new host. Similarly, re-emergence may avoid deteriorating bark conditions that could contribute to disease because of the increased likelihood of pathogenic organisms such as fungi, nematodes and mites. Finally, parent adults may re-emerge to avoid overcrowing (Anderbrant 1985). In Newfoundland, the total time from egg to callow adult was estimated to be approximately 60 days, as compared with 40 days in New Brunswick (Swaine 1929), probably because of cooler summer temperatures in Newfoundland.

My results agree with those of Price (1966), who reported that the upper aspects of red spruce logs were not attacked by *P. rufipennis*, and most attacks occurred on the lower aspects protected from direct sunlight. Subcortical temperature and moisture affect the development and survival of most bark beetles (Gaumer and Gara 1967; Schmid 1981), and gallery construction may proceed only as long as moisture and temperature conditions are suitable (Reid 1962). The preference by *P. rufipennis* for trees in shade, or the shaded portions of trees in sun, reflects a strong influence of bark temperature and moisture. Because black spruce bark is relatively thin,

especially on small diameter trees, the rate of dessication in sun was much faster than in shade. In laboratory experiments, brood success of *P. rufipennis* on white spruce was also reduced as bark moisture levels decreased (Beanlands 1967).

The sequence of emergence and arrival of *D. affaber* and *C. borealis*, to trees attacked by *P. rufipennis*, followed a characteristic temporal pattern. In the field and laboratory, emergence of *D. affaber* coincided with that of *P. rufipennis*, but on only a few trees did *D. affaber* attack before *P. rufipennis*. It is probable that the less aggressive *D. affaber* exploits hosts that have been weakened by *P. rufipennis*. However the 2 species apparently compete for resources because galleries of both species often occur adjacent to each other and may sometimes intersect. Peak emergence of *C. borealis* occurred approximately 3 weeks later than for *P. rufipennis* and *D. affaber*, reflecting the need to utilize the entrance holes and galleries of other insects to gain entry into bark after which they excavate their own galleries by mining perpendicularly to the main gallery (Chamberlin 1939; Bright 1976; Wood 1982). Although the frequence of *C. borealis* adults and larval mines in gallery systems established by *P. rufipennis* and *D. affaber* suggested exploitative competition, their small size precluded comparative assessment of brood establishment and development.

The cylindrical bark beetle, *L. intricatus* was a frequently found representative of the numerous associates of *P. rufipennis* (Hilton 1968). The full impact of cylindrical bark beetles on scolytid populations has not been elucidated but they may prey on immature beetles. *Medetera* spp. are also known predators of bark beetle eggs and larvae (Schmid 1971). Because *Medetera* sp. comprised 70.9% of the total associates that emerged from black spruce bolts it may have a significant impact on the four-eyed spruce bark beetle, as hypothesized by Blackman

and Stage (1918). Unidentified clerid larvae were frequently encountered during dissection of bark samples in 1983, reflecting their importance as predators of bark beetles (Chamberlin 1939; Amman 1972; Berisford 1980). The incidence of 4 species of hymenopterous parasitoids in black spruce infested with *P. rufipennis* is noteworthy. Some or all of *Ecphylus* sp., *R. xylophagorum, Eubazus* sp., and *C. dendroctoni* may be effective in reducing populations of the beetle.

The association of *C. piceaperda* with *P. rufipennis* during all phases of the colonization sequence supports the hypothesis of a symbiosis between them. Similar associations are common between other species of bark beetles and fungi (Whitney 1971; Barras and Perry 1975; Levieux *et al* 1989; Gibbs and Inman 1991). *C. piceaperda* was first isloated and described from *D. rufipennis* (Kirby) infesting white spruce, *Picea glauca* (Moench) Voss, in Nova Scotia (Rumbold 1936). It is possible that *C. piceaperda* is pathogenic to black spruce, and by creating conditions conducive to beetle establishment and brood development, may account for the importance of *P. rufipennis* as a significant mortality agent of black spruce in Newfoundland.

CHAPTER 2

It is essential to understand beetle-host interactions in order to manage forests stands effectively and to minimize the impact of bark beetle pests (Payne 1983). A knowledge of beetle-host interactions could help explain the cause of beetle outbreaks and allow forest managers to predict the trend and consequence of infestations. Although the reasons for initial population build-up, subsequent epidemics and collapse are not fully understood, a number of hypotheses have been proposed to explain the causes and trends of bark beetle infestations. Outbreaks have been linked to changes in weather patterns (Safranyik 1978; Thomson and Sahota 1984), a paucity of natural enemies (Hopkins 1892, 1899), and abundance of breeding material and habitat suitability (Rudinsky 1962; Lorio *et al.* 1982; Worrell 1983). Much emphasis has been placed on the hypothesis that stress on the host is a prerequisite for beetle outbreaks.

Most species of bark beetles readily attack physiologically stressed conifers (Caird 1935; Rudinsky 1962; Berryman 1972). Stark (1965) suggested that water deficit was the most important factor leading to outbreaks and several workers have shown correlations between drought and beetle epidemics (Blackman 1924; Craighead 1925; King 1972; Ferrell 1978; Michaels *et al.* 1985). Other stress conditions hypothesized to contribute to beetle epidemics include lighting and fire (Furniss 1965; Anderson and Anderson 1968; Hodges and Pickard 1971; Schowalter *et al.* 1981), windthrow (Chamberlin 1939; 1958), pollution (Stark *et al.* 1968; Cobb *et al.* 1968a; 1968b), and disease (Cobb *et al.* 1974; Ferrell 1974; Goheen and Cobb 1980). More recent research disclosed that declining growth rates (Mahoney 1978) or low

growth efficiency (Waring and Pitman 1980) render conifers susceptible to scolytids.

There is strong evidence that defoliation may act alone or in concert with other factors as a predisposing agent to insect attack (Patterson 1929; Dewey et al. 1974). Wickman (1963, 1978) and Berryman (1973) reported that Douglas-fir tussoock moth, *Orgyia pseudotsugata* (McDunnough), outbreaks were a major cause of fir engraver, *Scolytus ventralis* LeConte, epidemics in grand fir, *Abies grandis* (Douglas) Lindley, and of outbreaks of Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins in Douglas-fir, *Pseudotsugate menziesii* (Beissn.) Franco. The dominant factor determining the number of bark beetles that attack trees weakened by tussock moth was shown by Wright et al. (1984) to be food quantity in the form of heavily defoliated trees. Following defoliation of ponderosa pine, *Pinus ponderosa* Laws., by the pine butterfly, *Neophasia menopia* (Felder), 16.7% of the trees died of subsequent attacks by the western pine beetle, *Dendroctonus brevicomis* LeConte (Evenden 1940).

Despite the proclivity of the four-eyed spruce bark beetle for attacking weakened conifers (Simpson 1929), the level of cumulative budworm damage associated with the beetle has not been determined and the relationship between damage and subsequent *P. rufipennis* attack is unknown. Without detailed knowledge of how the beetle contributes to black spruce mortality, projections of black spruce volume loss probably are underestimated. Furthermore, improved management of black spruce, including the development of risk- and/or hazard-rating systems requires information on the interaction of *P. rufipennis* with its host. Herein, I describe the incidence and infestation characteristics of *P. rufipennis* in central Newfoundland following spruce budworm attack, and report the results of research aimed at understanding the interaction between the beetle and its black spruce host.

MATERIALS AND METHODS

Beetle Incidence and Infestation Trend

Sixteen permanent black spruce plots established by the Forest Insect and Disease Survey (FIDS) of Forestry Canada were used to investigate the association between *P. rufipennis* and trees damaged by spruce budworm. Twelve plots were established in 1982 in mature stands 80-120 years old and 4 plots were established in 1983 in semimature stands 40-50 years old. In stands of mature black spruce, plots were stratified according to mortality class with 4 plots established in each of light, moderate and severe budworm damage. In semimature stands, 4 plots were established in areas of light budworm damage. Stratification of plots was made on the basis of aerial and ground surveys. Plot numbers, mortality classes and locations are presented in Table 2.1.

Information on the association of damaged black spruce and the four-eyed spruce bark beetle was collected over a 3-year period beginning in 1983, 2 years following budworm collapse. The incidence of *P. rufipennis* attack was determined by its presence or absence along the tree bole. Current attacks were recognized by the presence of fresh frass at the entrance hole and by removing phloem tissue at breast height to expose adults and developing brood. Adults and egg gallery shape were used to identify bark beetle species encountered. Previous attacks were identified by the absence of fresh frass and the presence of clean emergence holes on the tree stem as well as the deteriorated condition of the phloem tissue. Each year in August, the stands were assessed for bark beetle attack and in September, Forest Insect and Disease Survey Rangers (Forestry Canada, St. John's, Newfoundland) measured each tree for cumulative crown damage

Table 2.1. Numbers, mortality classes and locations of permanent plots used to study the interaction betwen *P. rufipennis* and black spruce damage.

Plot numbers	Damage[a] category	Plot[b] location
1, 2	Severe	Barney Brook, Springdale
3, 4	Light	Powderhorn Lake, Badger
5, 6	Moderate	2 km. north of Catamaran Park, Badger
7, 8	Light	Miguels Lake
9, 10	Severe	Miguels Brook
11, 12	Moderate	Miguels Lake
13-16	Light	Rattling Brook Road

[a]Plots 1-12 established in 1982 by FIDS in mature stands; plots 13-16 established in 1983 in semimature stands.
[b]Plot size = 1000 m^2

using a 10% interval rating (Sutton 1981). Additional tree parameters measured for each tree included crown class, tree height, and diameter at breast height.

The hypothesis that beetle attack is independent of year and stand condition was examined using Everitt's method (1977) to fit a log-linear model to the cell frequencies of a three-dimensional contingency table. However, no adequate model could be found to describe the interactions among the three categorical variables. Therefore, the data were reduced to two-dimensional tables with respect to levels of stand damage class and year. A test of linear trend (Cochran 1954) with beetle attack as a binary variable and year and damage classes as ordered categories was employed to determine whether beetle attack is independent of year and damage class.

Within each damage category tests of linear trend were employed to determine whether proportions of attack increase or decrease as a function of tree diameter class, height class, crown class and defoliation class. The tree characteristics of diameter, height and crown classes were assessed in 1982. Crown condition was assessed yearly.

Finally, a binary logistic regression model (Cox 1970; Walker and Duncan 1967; Press and Wilson 1978) was developed to estimate the probability of beetle attack (P_A) on black spruce. The basic form of the model may be expressed as

$$E(y|x_1,\ldots,x_n) = \{1 + \exp[-(\beta^\circ + \beta_1 x_1 + \ldots + \beta_n x_n)]\}^{-1}$$

with probability estimates restricted to $0 \leq E(y) \leq 1$. When the dependent variable is binary, the mean response is a probability, and so $E(y|x_1,\ldots,x_n) = P$. $\beta_\circ$ and β_1 are model parameters

to be estimated by the coefficients b_0 and b_1.

It was assumed that over the range of damage categories, trees with similar characteristics are not necessarily equally likely to be attacked. Therefore, attack data from the 3 damage categories were analyzed separately to provide models for each of the 3 damage classes. To optimize the predictive value of tree characteristic variables, and to minimize confounding effects of *P. rufipennis* dynamics, the modeling effort for each damage class was limited to the onset of the beetle outbreak. The independent variables evaluated as predictors of attack consisted of 2 continuous variables, diameter at breast height (dbh) and height (ht), and 2 ordered discrete variables, crown class(cc) and crown damage (cd). None of the continuous variables was normally distributed. Tree diameter and height were both skewed with the medians outside the 95% confidence interval for the means. The dependent variable, attack, was treated as the observed response taking values of 1 (attack) or 0 (no attack).

Each of the 4 independent variables was screened as a possible important predictor of attack, using the BMDPLR procedure (Dixon 1988). The procedure computes maximum likelihood estimates (Bishop *et al.* 1975) of parameters of the logistic model. Selection proceeded in a stepwise manner by first fitting a constant term, followed with independent variables in order of importance. At each step in the stepping process, a variable was added or removed from the model based on the maximum log likelihood ratio, G. Variables were judged to be important enough to enter the model if the p-value for G was <0.1000. Similarly, to determine whether a variable should be deleted a minimum p-value of 0.1500 was chosen. The improvement χ^2 was used to test the hypothesis that the term entered or removed at each step significantly changed the prediction. After the optimal set of predictor variables had been

selected a final model that appeared to be suitable for predicting the probability of attack was specified. Criteria for evaluating the adequacy of the model were two summary goodness-of-fit χ^2 statistics, the Hosmer-Lemeshow test (Hosmer and Lemeshow 1989) and the Brown Score test (Brown 1982). Classification of accuracy was determined from plots of the percent of trees correctly classified over a range of cutpoints. Finally, histograms of the predicted probabilities of attacked and unattacked trees were examined for amount of overlap to assess the suitability of predictor variables.

Baited Tree Experiments

In 1984 and 1985, experiments were conducted at Rattling Brook to investigate host susceptibility to bark beetle attack. The hypothesis that increased budworm damage on black spruce promotes host stress and facilitates bark beetle attack was tested experimentally by baiting trees with logs infested by male *P. rufipennis*. Growth recovery as indicated by refoliation in the absence of beetle was also assessed on untreated trees and on trees protected with a chemical insecticide. Treatments included: (1) trees treated with insecticide to protect the bole, (2) trees baited with male-infested logs to induce beetle attack, and (3) untreated control trees. Prior to beetle emergence in 1984 and 1985, 399 live trees located in 5, 0.01 ha plots were protected with a 2.0% emulsifiable concentrate of Lindane (1,2,3,4,5,6-Hexachloro-cyclohexane, gamma isomer). Spray was applied with backpack sprayers equipped with a cone-spray nozzle and extension wand. Spray was applied to the point of "runoff" over the complete bole of trees <7 m high. Trees ranging in height from 7-10 m received approximately 75% coverage of the bole.

P. rufipennis bait logs were created by placing 8 newly emerged adult males in 30 cm long

fresh spruce bolts, and then covering the bolt with saran screen to prevent further attack. The bolts were attached at breast height with string on standing spruce trees with varying degrees of crown damage. In each of 1984 and 1985, 60 unattacked trees located in 4, 0.005 ha plots were baited with male-infested bolts.

In both years all trees were tagged and assessed for budworm damage in June, and re-assessed in July and September following spring and summer beetle flights. Trees were visually categorized according to percent crown damage using the categories < 30%, 30-69%, and > 70% damage. To increase the sensitivity of the rating for the more highly stressed trees, the >70% category was further classed as 70-79%, 80-89%, 90-99%, and 100% (no green foliage).

Attacks were considered successful if brood established in the phloem tissue and unsuccessful if entrance holes had copious resin and no evidence of gallery establishment. Unsuccessfully attacked trees were interpreted as a measure of tree resistance. Observed frequencies of untreated and lindane-treated trees were each analyzed in 6 x 6 square tables using McNemar's test of symmetry (Dixon 1988). The test measured a change in tree condition by testing the equality of frequencies in all pairs of cells that are symmetrical around the diagonal. Frequencies along the diagonal are ignored.

RESULTS

Beetle Incidence and Infestation Trend

Significant relationships between *P. rufipennis* attack and cumulative budworm damage in mature stands of black spruce were evident in both time and space (Fig. 2.1). The highest incidence of beetle attack occurred in severely damaged stands in 1983, with 32.6% of the trees successfully attacked. In 1984 and 1985 the proportion of newly attacked trees in severely damaged stands decreased to 16.6 and 6.0%, respectively. In stands of moderate budworm damage, the proportion of trees attacked by *P. rufipennis* decreased from 13.5% in 1983 to 6.7% in 1984 to 5.1% in 1985. The proportion of trees attacked by the beetle in lightly damaged stands varied little over time, with 2.1, 2.9 and 2.2% of the trees attacked in 1983, 1984 and 1985, respectively.

Analysis of the frequencies of beetle attacks disclosed highly significant linear decreases in the proportion of attacks across time in areas of moderate and severe budworm damage (Table 2.2). No significant linear trend in the proportion of attacked trees over time was found in areas of light budworm damage. Within each of 3 years a significant linear trend in the proportion of attacked trees across damage classes was also evident (Table 2.3).

Tests of the null hypothesis that beetle attack is independent of tree diameter, height, crown class and crown damage disclosed a number of significant associations among tree variables and beetle attack. Significant but weak relationships between beetle attack and each of tree diameter, height and crown class were evident in stands of moderate damage (Tables 2.4-2.9). Although the overall χ^2 goodness of fit test of the association between attack and crown class in moderately damaged stands, was not significant (Table 2.9), the χ^2 value due to

Fig. 2.1. Percent of black spruce trees attacked by *P. rufipennis* in plots of light, moderate and severe spruce budworm damage in central Newfoundland, 1983-85.

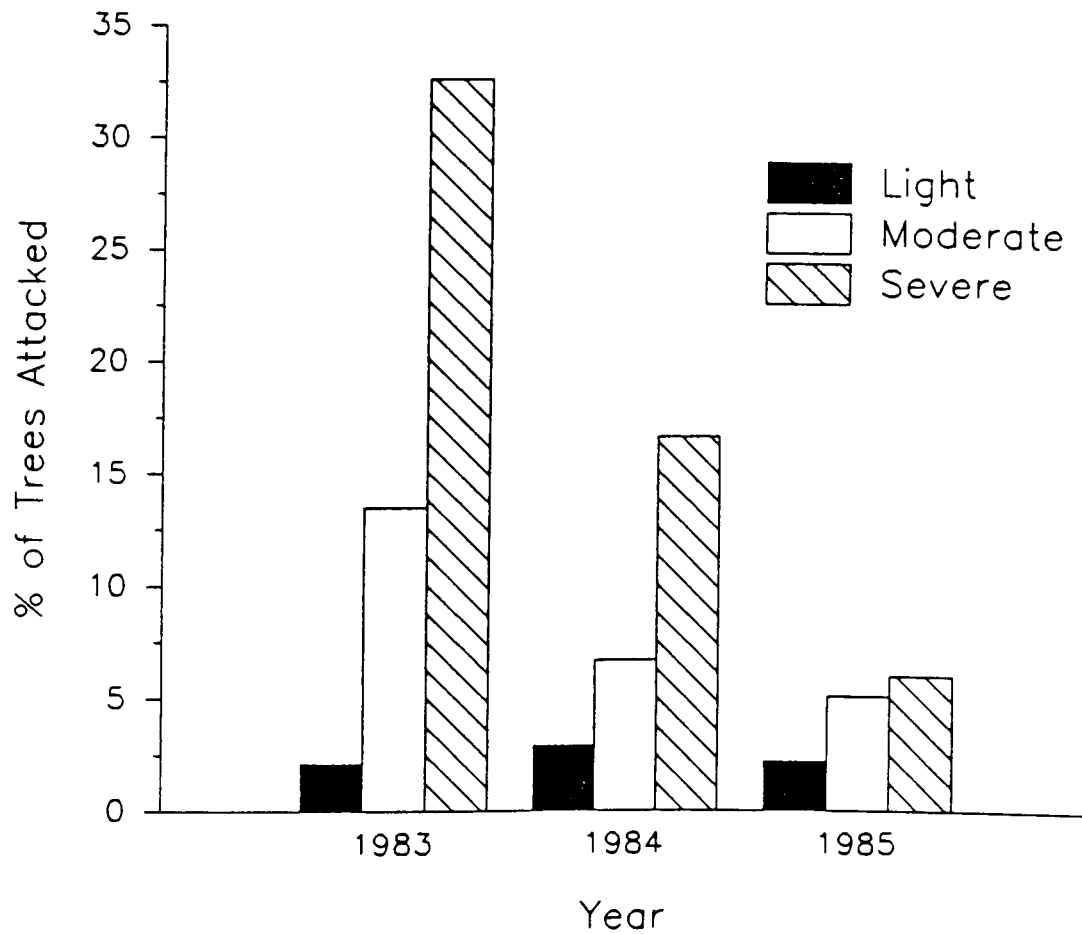

35
30
25
20
15
10
5
0
% of Trees Attacked
Light
Moderate
Severe
1983
1984
1985
Year

Table 2.2. Components of Person chi-square due to linear trend for tree attacks classified according to year.

Source	Light damage			Moderate damage			Severe damage		
	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.
Due to linear regression of beetle attack on year	1	0.019	>0.05	1	28.929	<0.0001	1	44.197	<0.0001
Departure from regression (by substraction)	1	1.131	>0.05	1	3.378	>0.05	1	0.564	>0.05
Total chi-square	2	1.150	>0.05	2	32.307	<0.0001	2	44.761	<0.0001

Table 2.3. Components of Person chi-square due to linear trend for tree attacks classified according to damage.

Source	1983			1984			1985		
	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.
Due to linear regression of beetle attack on damage	1	161.294	<0.0001	1	39.729	<0.0001	1	8.029	<0.005
Departure from regression (by substraction)	1	5.088	<0.05	1	4.438	<0.05	1	0.733	>0.05
Total chi-square	2	166.382	<0.0001	2	44.167	<0.0001	2	8.762	<0.025

Table 2.4. Attack by diameter class of trees infested with *P. rufipennis*, in stands of light, moderate and severe budworm damage.

Damage class	Year	Attack by diameter class					
		<8.1	8.1-11.0	11.1-14.0	14.1-17.0	17.1-20.0	>20.0
Light	Before 1983	0	10	10	10	3	4
	1983	0	4	4	3	0	2
	1984	0	6	5	5	1	1
	1985	0	3	5	5	0	0
	Totals	0	23	24	23	4	7
	%	0	12.6	11.2	15.4	4.9	20.1
Moderate	Before 1983	2	47	13	8	2	4
	1983	3	59	25	5	3	0
	1984	0	26	6	5	4	1
	1985	1	15	7	5	1	0
	Totals	6	147	51	23	10	5
	%	18.2	40.0	27.6	23.9	16.1	19.2
Severe	Before 1983	13	331	254	100	37	8
	1983	0	14	32	8	7	0
	1984	0	15	9	5	1	0
	1985	0	6	1	1	1	0
	Totals	13	393	296	114	46	8
	%	92.8	87.1	84.6	83.2	88.5	100.0

Table 2.5. Components of Person chi-square due to linear trend for tree attacks classified according to tree diameter.

Source	Light damage			Moderate damage			Severe damage		
	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.
Due to linear regression of beetle attack on diameter	1	0.019	>0.05	1	13.793	<0.001	1	0.238	>0.05
Departure from regression (by substraction)	4	8.452	>0.05	4	11.307	<0.025	4	3.829	>0.05
Total chi-square	5	8.471	>0.05	5	25.100	<0.0001	5	4.067	>0.05

Table 2.6. Attack by height class of trees infested with *P. rufipennis*, in stands of light, moderate and severe budworm damage.

Damage class	Year	Attack by height class (m)					
		<5.1	5.1-7.0	7.1-9.0	9.1-11.0	11.1-13.0	>13.0
Light	Before 1983	0	1	16	12	6	2
	1983	0	0	3	7	3	0
	1984	0	1	8	6	3	0
	1985	0	1	6	5	1	0
	Totals	0	3	33	30	13	2
	%	0	5.3	14.3	11.6	11.5	66.7
Moderate	Before 1983	3	5	26	36	4	2
	1983	0	5	36	42	12	0
	1984	0	4	17	14	6	1
	1985	0	1	12	13	3	0
	Totals	3	15	91	105	25	3
	%	17.6	11.6	36.1	39.2	23.8	37.5
Severe	Before 1983	10	97	332	227	84	3
	1983	0	9	36	31	12	0
	1984	0	5	13	10	2	0
	1985	0	2	5	0	2	0
	Totals	10	113	376	268	100	3
	%	76.9	86.2	84.6	87.0	88.5	100.0

Table 2.7. Components of Person chi-square due to linear trend for tree attacks classified according to tree height.

Source	Light damage			Moderate damage			Severe damage		
	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.
Due to linear regression of beetle attack on height	1	0.771	>0.05	1	8.194	<0.005	1	1.490	>0.05
Departure from regression (by substraction)	4	11.692	<0.025	4	29.965	<0.0001	4	1.374	>0.05
Total chi-square	5	12.463	<0.05	5	38.159	<0.0001	5	2.864	>0.05

Table 2.8. Attack by crown class of trees infested with *P. rufipennis*, in stands of light, moderate and severe budworm damage.

Damage class	Year	Attack by crown class				
		Dominant	Codominant	Intermediate	Suppressed	Other
Light	Before 1983	8	11	6	0	12
	1983	4	5	2	1	1
	1984	5	9	1	2	1
	1985	3	5	5	0	0
	Totals	20	30	14	3	14
	%	9.0	13.6	9.1	5.7	100.0
Moderate	Before 1983	29	12	8	3	24
	1983	45	28	17	2	3
	1984	18	15	7	2	0
	1985	14	8	6	1	0
	Totals	106	63	38	8	27
	%	32.9	28.0	22.5	27.6	79.4
Severe	Before 1983	168	226	264	22	63
	1983	21	39	24	1	3
	1984	5	9	15	0	1
	1985	2	1	5	1	0
	Totals	196	275	308	24	67
	%	86.7	83.1	88.0	82.8	88.1

Table 2.9. Components of Person chi-square due to linear trend for tree attacks classified according to tree crown class.

Source	Light damage			Moderate damage			Severe damage		
	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.	d.f.	χ^2	Prob.
Due to linear regression of beetle attack on crown class	1	0.268	>0.05	1	4.948	<0.05	1	0.186	>0.05
Departure from regression (by substraction)	2	4.206	>0.05	2	1.085	>0.05	2	3.589	>0.05
Total chi-square	3	4.474	>0.05	3	6.033	>0.05	3	3.775	>0.05

regression, was significant. Except for the significant association between tree height and beetle attack in stands of light damage (Table 2.7), overall χ^2 tests of association between attack and each of the variables diameter, height and crown class were non-significant in light and severe damage categories. For each of 3 years and across all damage categories, beetle attack increased with higher levels of crown damage (Figs. 2.2-2.4). However, only in stands of severe budworm damage in 1983 could the relationship between the two variables be adequately explained by a linear model (Table 2.10). In other damage classes and years the large and significant departures from regression indicate that even though a significant linear component exists, the data are not adequately explained by a linear model.

Both theoretical and empirical considerations suggest that when the dependent variable is binary, the response function is logistic - S-shaped with asymptotes at 0 and 1 (Neter and Wasserman 1974; Berryman 1986). Results of fitting a logistic regression model indicated that crown damage was the only independent variable significantly associated with *P. rufipennis* attack in stands of light budworm damage (Table 2.11). However, assessment of the fitted model indicated poor fit, suggesting that in stands with light damage, the probability of beetle attack cannot be reliably predicted using the tree characteristic, crown damage. Logistic regression identified 3 variables, crown damage, height, and diameter, as key tree characteristics significantly associated with beetle attack in each of moderate and severe damage categories (Table 2.11). For both categories, crown damage entered the model first; it had the largest χ^2 value and smallest p-value at step 0. The candidate term, crown class, did not enter either model because it's χ^2 value did not exceed the default χ^2-to-enter limit of 0.1000. Crown class was therefore dropped and final models were fitted to describe the joint effects of crown damage, height and diameter on beetle attack. Models for moderate and severe categories may be

Fig 2.2. Observed frequencies of attacked and unattacked black spruce by defoliation class in stands of light budworm damage, 1983-85.

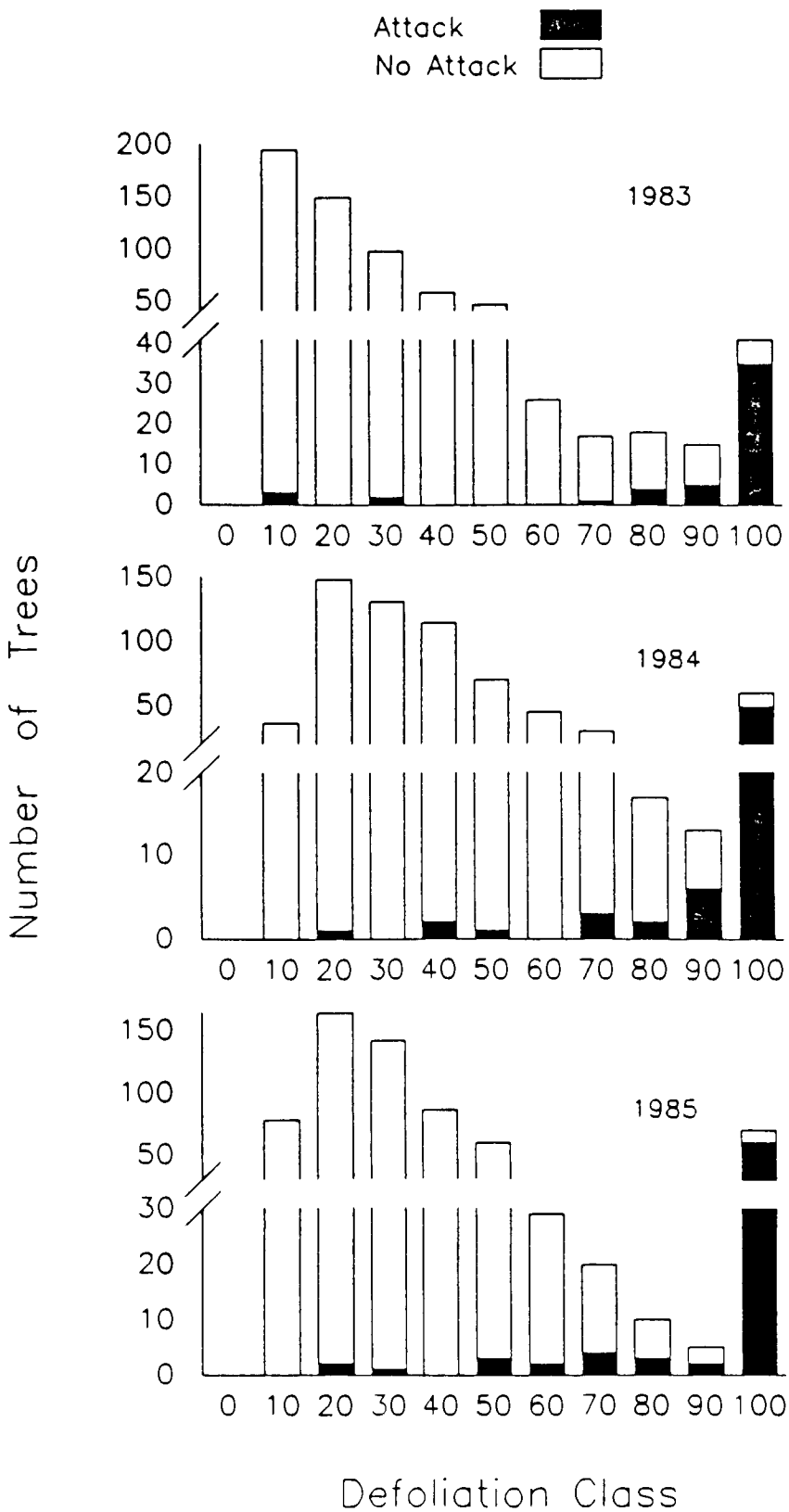

Attack
No Attack
1983
1984
1985
Number of Trees
Defoliation Class
0 10 20 30 40 50 60 70 80 90 100

Fig. 2.3 Observed frequencies of attacked and unattacked black spruce by defoliation class in stands of moderate budworm damage, 1983-85.

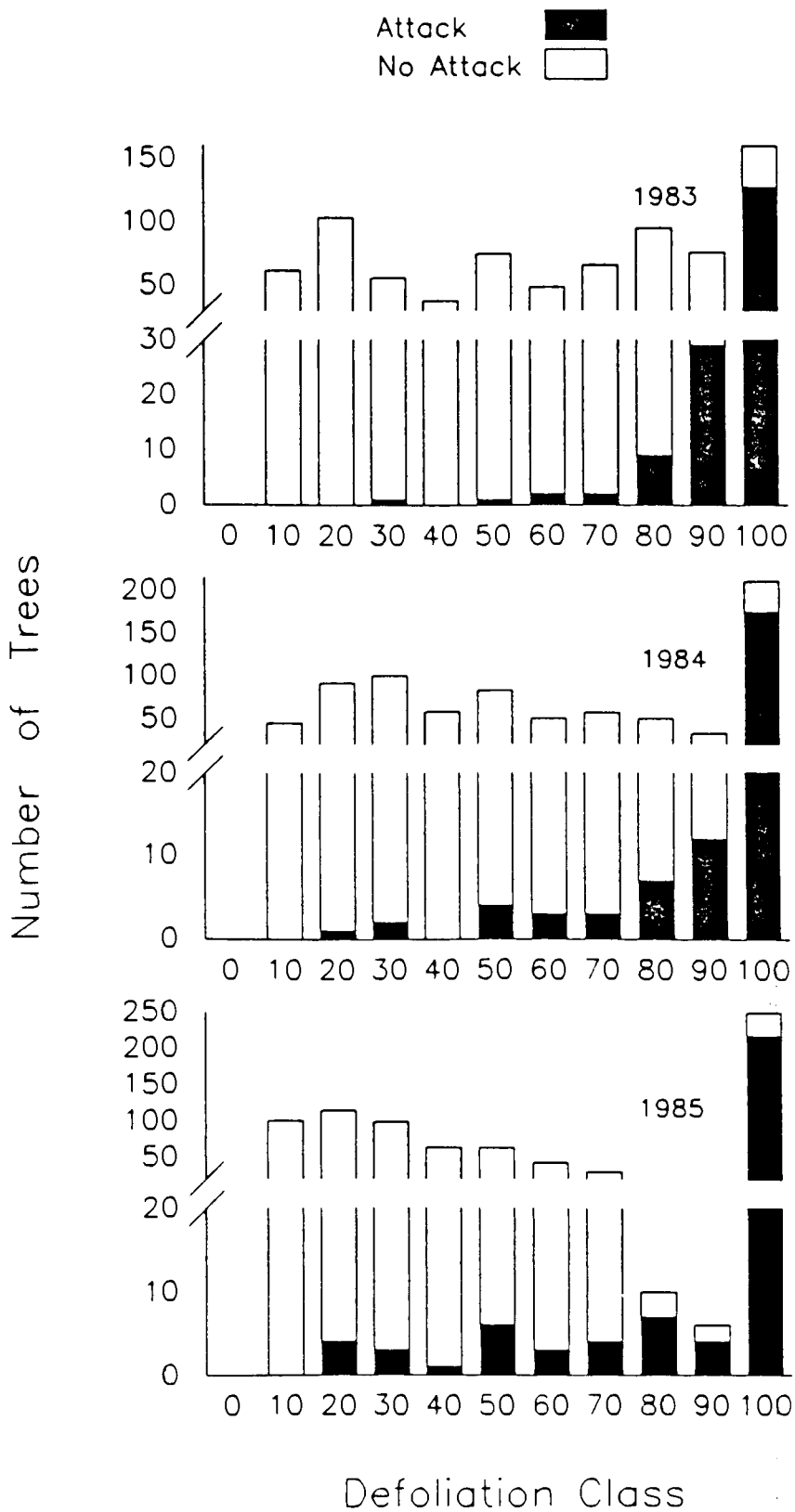

Attack
No Attack
1983
1984
1985
Number of Trees
Defoliation Class
0 10 20 30 40 50 60 70 80 90 100

Fig. 2.4 Observed frequencies of attacked and unattacked black spruce by defoliation class in stands of severe budworm damage, 1983-85.

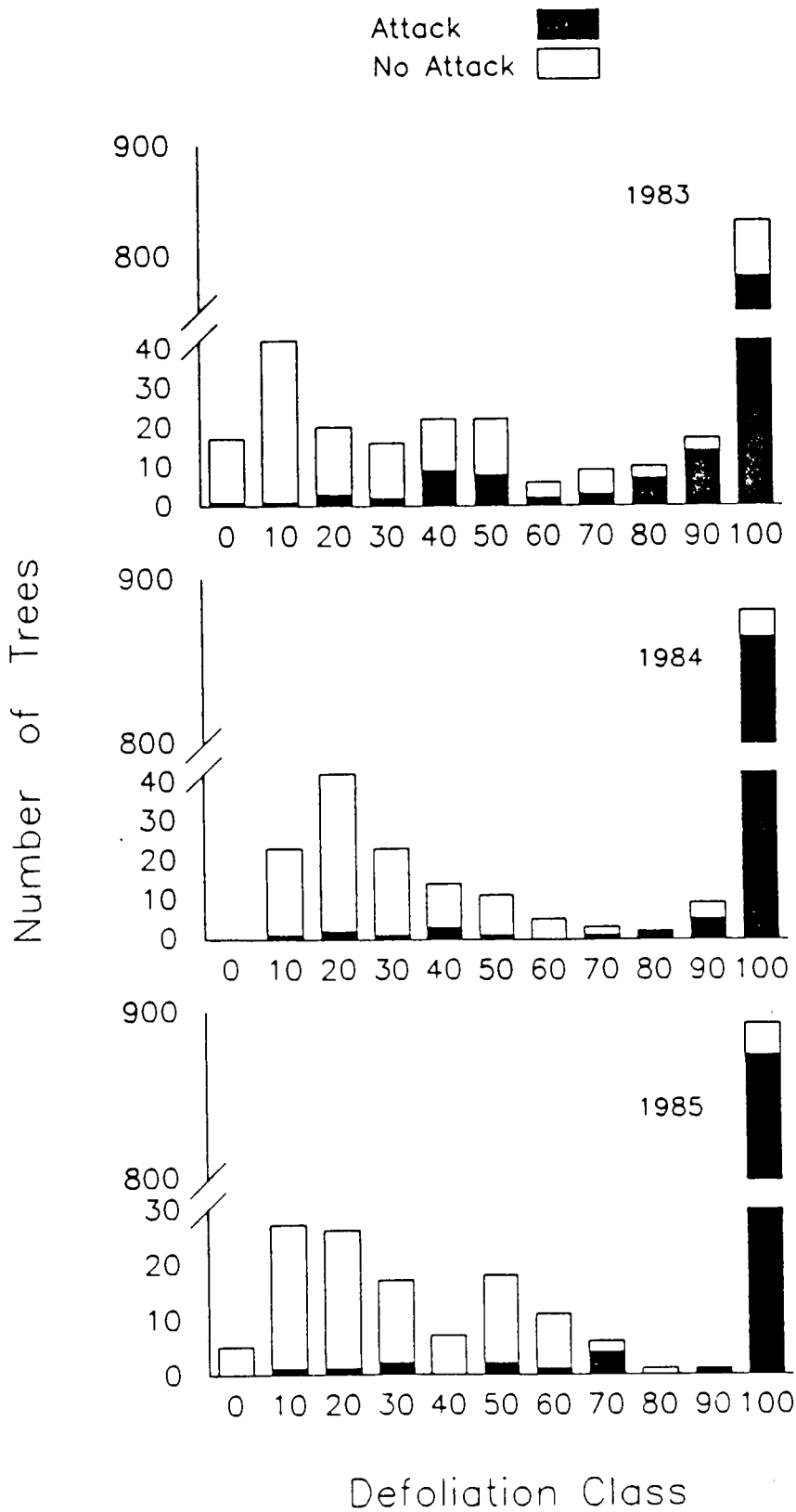

Attack
No Attack
1983
1984
1985
900
800
40
30
20
10
0
0 10 20 30 40 50 60 70 80 90 100
Number of Trees
Defoliation Class

Table 2.10. Components of Person chi-square due to linear trend for tree attacks classified according to defoliation class.

Source	Light Damage d.f.	χ^2	Prob.	Moderate damage d.f.	χ^2	Prob.	Severe damage d.f.	χ^2	Prob.
1983									
Due to linear regression of beetle attack on defoliation	1	237.856	<0.0001	1	270.845	<0.0001	1	512.817	<0.0001
Departure from regression (by substraction)	8	176.613	<0.0001	8	172.726	<0.0001	9	12.192	>0.05
Total chi-square	9	414.469	<0.0001	9	443.571	<0.0001	10	525.009	<0.0001
1984									
Due to linear regression of beetle attack on defoliation	1	276.400	<0.0001	1	359.457	<0.0001	1	749.413	<0.0001
Departure from regression (by substraction)	8	151.495	<0.0001	8	132.879	<0.0001	8	36.157	<0.0001
Total chi-square	9	427.895	<0.0001	9	492.336	<0.0001	9	785.570	<0.0001
1985									
Due to linear regression of beetle attack on defoliation	1	339.264	<0.0001	1	471.074	<0.0001	1	725.688	<0.0001
Departure from regression (by substraction)	8	105.790	<0.0001	8	71.032	<0.0001	9	44.990	<0.0001
Total chi-square	9	445.540	<0.0001	9	542.106	<0.0001	10	770.678	<0.0001

Table 2.11. Estimated coefficients, standard errors, and probability values, for fitted logistic regression models describing beetle attack in stands of light, moderate and severe budworm damage.

Damage category	Variable	Model coeff	Standard error	Coeff/ S.E.	Prob (≤)
Light					
	Intercept	-5.5656	0.6390	-8.710	0.0001
	Crown damage	0.0349	0.0093	3.775	0.0002
	Log-likelihood = -52.911				
	Hosmer-Lemeshow χ^2 = 12.960, df = 6, P = 0.044				
	C.C. Brown Goodness-of-fit χ^2 = 9.343, df = 2, P = 0.0009				
Moderate					
	Intercept	-9.7520	1.3690	-7.122	0.0001
	Crown damage	0.0786	0.0195	7.182	0.0001
	Height	0.4143	0.1226	3.379	0.0004
	Diameter	-0.2183	0.0686	-3.182	0.0007
	Log-likelihood = -182.093				
	Hosmer-Lemeshow χ^2 = 5.199, df = 8, P = 0.736				
	C.C. Brown goodness-of-fit χ^2 = 2.395, df = 2, P = 0.302				
Severe					
	Intercept	-2.6038	0.7329	-3.553	0.0003
	Crown damage	0.0076	0.0036	-2.114	0.0435
	Height	0.2659	0.1051	2.530	0.0088
	Diameter	-0.1265	0.0637	-1.985	0.0428
	Log-likelihood = -279.710				
	Hosmer-Lemeshow χ^2 = 5.066, df = 8, P = 0.750				
	C.C. Brown goodness-of-fit χ^2 = 0, df = 0, P = 1.000				

expressed as follows:

$$p = 1/[1 + \exp(b_o + b_1X_1 + b_2X_2 + b_3X_3)]$$

where: p = the estimated probability of attack (P)

exp = the base of the natural logarithm

X_1 = crown damage as determined in the previous year

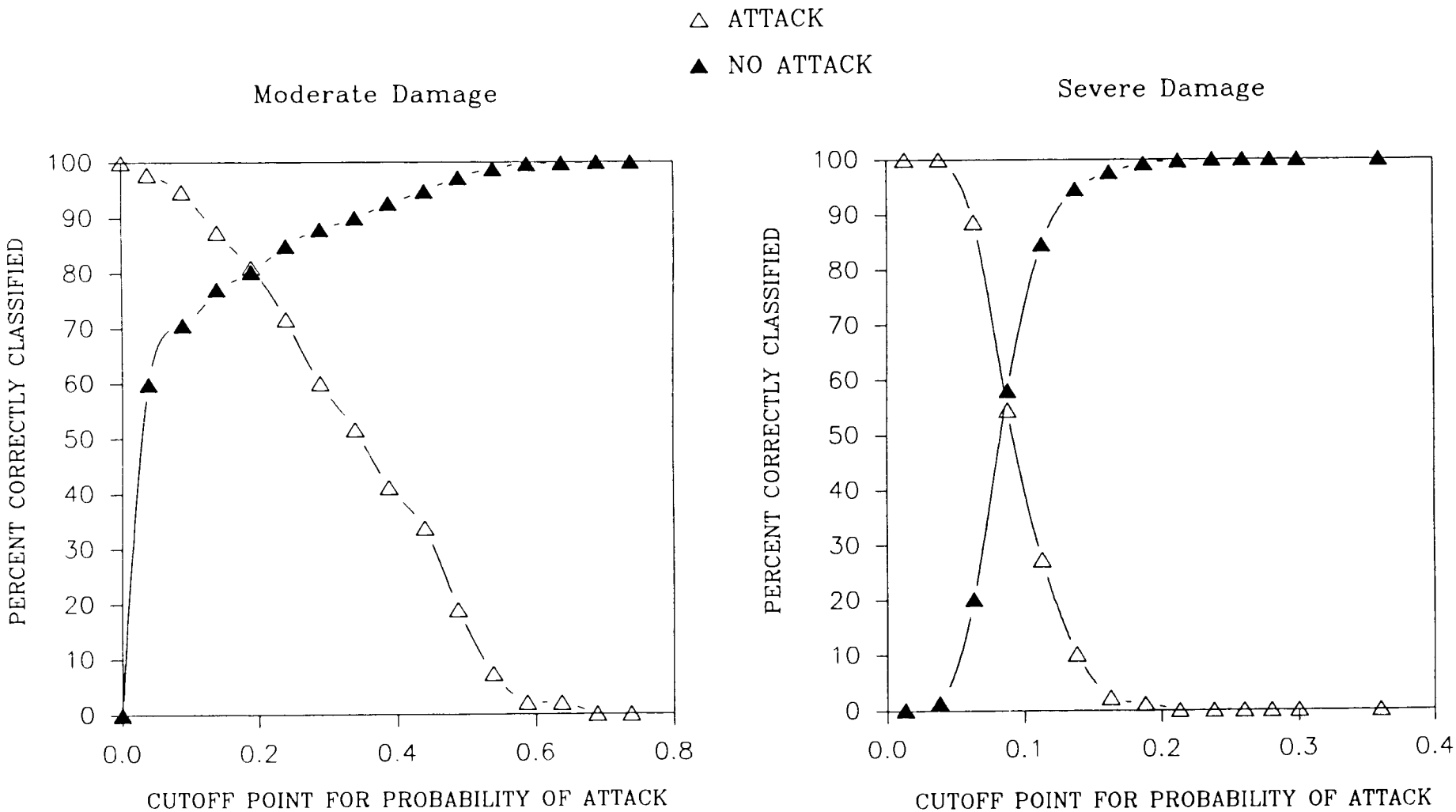
X_2 = tree height

X_3 = tree diameter at breast height

b_i = the ith estimated regression coefficient (i = 0,1,2,3)

In contrast to the fitted logistic model describing beetle attack in lightly damaged stands, the fitted models for attack in stands of moderate and severe damage were judged acceptable (Table 2.11). In stands with moderate damage, the value of the Hosmer-Lemeshow goodness-of-fit statistic is 5.199 and the corresponding *p*-value is 0.736 indicating that the model fits very well. Similarly, for severe stands, the value of the Hosmer-Lemeshow goodness-of-fit statistic is 5.066 with a corresponding *p*-value of 0.750. Furthermore, assessment of fit using the Brown Score test disclosed significant low χ^2 values indicating that the logistic model appropriately describes beetle attack in moderate and severe budworm-damaged stands.The overall rate of correct classification for beetle attack in stands of moderate damage was approximately 82% using a cutpoint of 0.2 (Fig. 2.5). In stands with severe budworm damage, the overall rate of correct classification was approximately 55% using a cutpoint of 0.08. The lower sensitivity in stands of severe damage indicates that additional or improved predictors are warranted. The histograms of predicted probabilities for the attacked and unattacked trees in stands of moderate damage

Fig. 2.5. Percent of black spruce trees correctly classified as attacked or not attacked for cutoff points between 0.0 and 0.8 in plots with moderate budworm damage and between 0.0 and 0.4 in plots with severe budworm damage.


△ ATTACK
▲ NO ATTACK
Moderate Damage
Severe Damage
PERCENT CORRECTLY CLASSIFIED
100
90
80
70
60
50
40
30
20
10
0
0.0
0.2
0.4
0.6
0.8
CUTOFF POINT FOR PROBABILITY OF ATTACK
PERCENT CORRECTLY CLASSIFIED
0.0
0.1
0.2
0.3
0.4
CUTOFF POINT FOR PROBABILITY OF ATTACK

had modest overlap, suggesting that tree variables serve as reasonable predictors of attack. However, the histograms of predicted probabilities for attacked and unattacked trees in stands of severe damage showed substantial overlap, confirming that the tree variables choosen may not be optimal for predicting beetle attack in these stands.

In total, 2131 trees were examined in semimature stands. At the time of plot establishment in 1983, 10.5% of the trees had been attacked by *P. rufipennis*. The incidence of attacks decreased to 3.8% in 1984 and to 1.1% in 1985. The relationship between defoliation class and beetle attack in semimature stands (Fig. 2.6) followed closely the trend of attack in mature stands. The numbers of attacks increased significantly (Table 2.12), with increased crown damage. Furthermore, in both 1984 and 1985 the departure from linear regression is represented by large χ^2 values, indicating that a logistic function may also be appropriate for these data.

Baited Tree Experiments

The results of baited-tree experiments (Table 2.13) confirm *a priori* expectations of greater attack success on trees in the higher damage classes. The overall proportion of successful colonization was 20.8%; however, 55.0% of the baited trees were visited by *P. rufipennis* but were not successfully colonized. The majority of the apparently resistant trees were in damage classes below 80%. Only 24.2% of the baited trees went unattacked over the 2 year period. As was found in permanent sample plots, the relationship between budworm damage and beetle attack on baited trees had a significant linear component (Table 2.14). For baited tree attacks the departure from regression was non-significant.

No lindane-treated trees were attacked by bark beetles and only 2 % of the untreated trees were successfully attacked. McNemar's test of symmetry of the square tables of untreated and protected trees for 1984-85 indicated significant shifts across the diagonals (Table 2.15).

Fig. 2.6. Observed frequencies of attacked and unattacked black spruce by defoliation class in semimature stands, 1984-85.

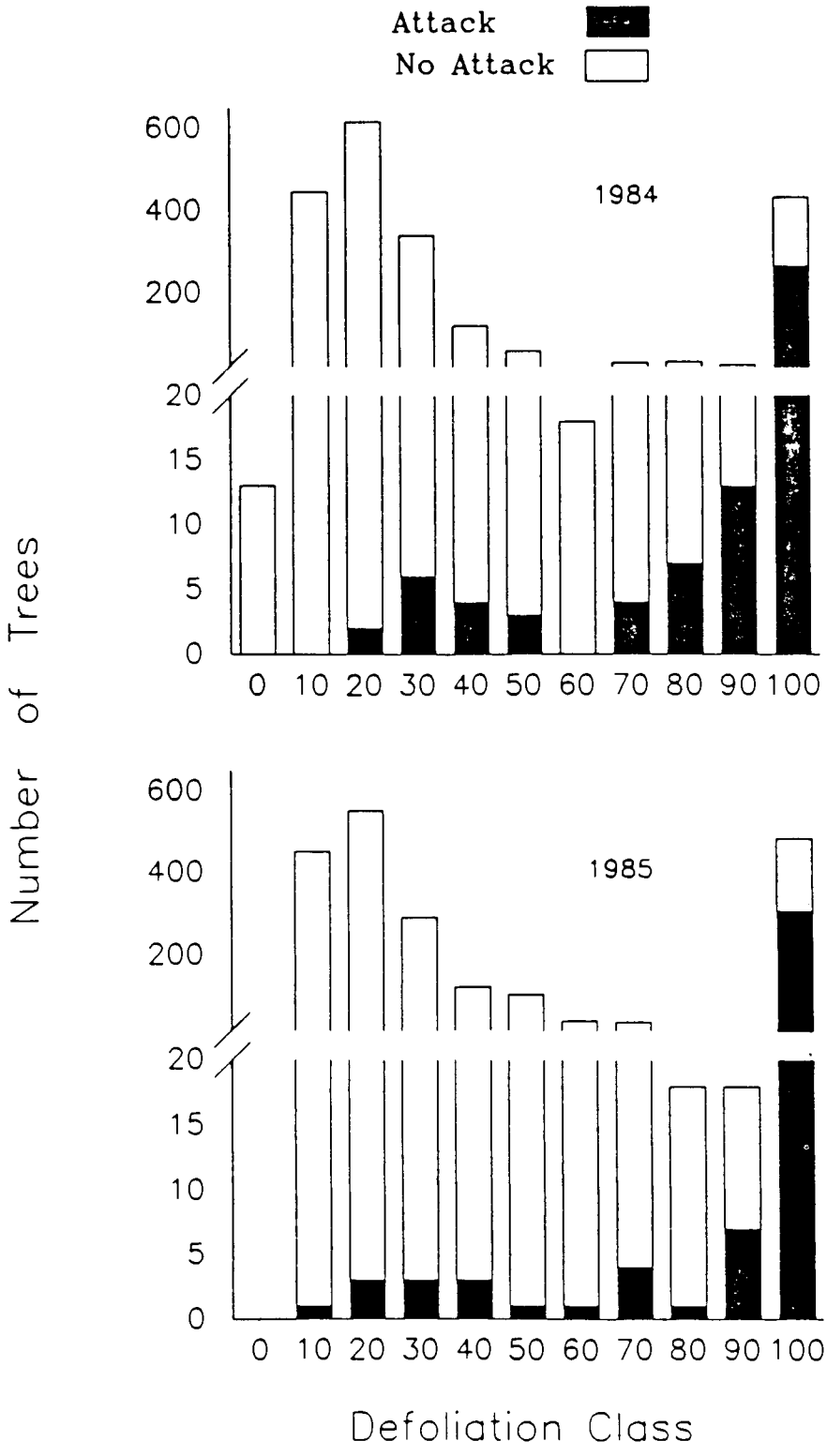

Attack
No Attack
1984
1985
600
400
200
20
15
10
5
0
0 10 20 30 40 50 60 70 80 90 100
Number of Trees
Defoliation Class

Table 2.12. Components of Person chi-square due to linear trend for tree attacks classified according to crown damage.

Source	1984 d.f.	1984 χ^2	1984 Prob.	1985 d.f.	1985 χ^2	1985 Prob.
Due to linear regression of beetle attack on damage	1	960.594	<0.0001	1	964.741	<0.0001
Departure from regression (by substraction)	9	93.695	<0.0001	8	154.526	<0.0001
Total chi-square	10	1054.284	<0.0001	9	1116.267	<0.0001

Table 2.13. Observed frequencies of successfully attacked, unsuccessfully attacked and unattacked black spruce trees baited with *P. rufipennis* infested logs, 1984-85, N = 120.

Attack status	Attack by damage class					
	<30	30-69	70-79	80-89	90-99	Totals
Number trees baited	27	47	12	12	22	120
Successful attack						
N	0	3	3	7	12	25
%	0	6.4	25.0	58.4	54.5	20.8
Unsuccessful attack						
N	15	34	7	4	6	66
%	55.6	72.3	58.3	33.3	27.3	55.0
Unattacked						
N	12	10	2	1	4	29
%	44.4	21.3	16.7	8.3	18.2	24.2

Table 2.14. Components of Person chi-square due to linear trend for attack on baited trees classified according to damage.

Source[a]	d.f.	χ^2	Prob.
Due to linear regression of beetle attack on damage	1	35.568	<0.0001
Departure from regression (by substraction)	3	3.005	>0.05
Total chi-square	4	38.573	<0.0001

[a]Linear regression performed on successfully attacked trees vs. total of unattacked and unsuccessfully attacked trees for 1984-85.

Table 2.15. Observed frequencies of untreated and lindane-treated trees according to damage class, 1984-85.

Treatment	1984 damage class	Attack in 1985 by damage class[a]						
		<30	30-69	70-79	80-89	90-99	100	Totals
Untreated	<30	13	0	0	0	0	0	13
	30-69	8	47	1	1	0	1	58
	70-79	0	10	0	1	0	0	11
	80-89	0	11	8	0	2	1	22
	90-99	0	1	3	7	5	4	20
	100	0	0	0	0	0	28	28
	Totals	21	69	12	9	7	34	152
Lindane-treated	<30	49	2	0	0	0	0	51
	30-69	30	130	4	0	0	3	167
	70-79	0	28	8	5	0	10	51
	80-89	0	10	9	7	11	1	38
	90-99	0	5	3	7	12	12	39
	100	0	0	0	0	0	53	53
	Totals	79	175	24	19	23	79	399

[a]McNemar's test of symmetry indicates lack of symmetry, $\chi_{MC}^2 = 41.919$,df = 10, P = 0.0001 for untreated trees and $\chi_{MC}^2 = 88.532$,df = 11, P = 0.0001 for lindane-treated trees.

The proportion of untreated trees that recovered was 31.6% compared to only 7.2% that continued to decline. Similarly, 23.1% of the protected trees showed signs of recovery while 12.0% continued to decline.

DISCUSSION

At the peak of the black spruce decline in Newfoundland, the incidence of *P. rufipennis* was higher than at any time in recent history. Following the collapse of spruce budworm the cumulative dead volume of black spruce was estimated at 3,194,000 m^3 and the volume of severely damaged spruce estimated at 915,000 m^3 (Raske and Sutton 1986). Topkill occurred on nearly 100% of surviving spruce, bringing the total stand volume affected by budworm to 10,322,000 m^3 over 95,700 ha. The number of trees successfully attacked by the beetle was low from 1977 to 1980, increased rapidly following budworm collapse in 1981, peaked in 1983 and declined to low levels by 1985. The trend of beetle infestation in Newfoundland in time and space (Fig 2.1) conforms to other bark beetle epidemics in Oregon, Washington (Wickman 1958, 1978; Wright et al. 1984), and Idaho (Berryman 1973), where secondary bark beetles tracked defoliator activity.

A large body of knowledge has developed to explain the interaction and interrelationships between bark beetles and their hosts (Rudinsky 1962; Coulson 1979; Raffa and Berryman 1983; Lorio 1986; Christiansen et al. 1987). Current theory suggests that environmental and genetic factors interact to determine individual tree and stand susceptibility (Cates and Alexander 1982). Among the factors that have been invoked to provide a rational basis for understanding scolytid-conifer interactions are physical factors, including stand and tree characteristics (Amman 1978, 1985; Sartwell and Stevens 1975; Worrell 1983), and chemical factors, including resin quality of preformed and induced resin systems (Raffa and Berryman 1982, 1987; Christiansen and Horntvedt 1983; Miller and Berryman 1985).

Analysis of two-dimensional tables indicated a significant association between attacked trees and time (Table 2.2) in moderate and severe damage, and a significant dependency of

beetle attack on stand damage level for each of 3 years (Table 2.3). At the peak of the beetle outbreak, 2.1, 13.5 and 32.7% of the black spruce trees sampled in permanent plots were successfully attacked in light, moderate and severe damage areas, respectively. It is probable that the low incidence of 2.0% in lightly damaged stands approaches endemic levels for the four-eyed spruce bark beetle, while the higher incidence in stands with moderate and severe damage is the result of tree predisposition to attack. A pattern of infestation similar to the pattern found in Newfoundland was reported by Wright et al. (1984) who noted that, following an outbreak of the Douglas-fir tussock moth, numbers of *S. ventralis* and *D. pseudotsugae* peaked 1-2 years after defoliation ended and then rapidly declined.

Analysis of Tables 2.4-2.9 disclosed a significant but weak relationship between *P. rufipennis* and tree diameter, height and crown class indicating that these factors probably play a minor role in outbreaks of *P. rufipennis*. In contrast, the crown condition of individual trees (Figs. 2.2-2.4) played a dominant role in determining the success of the beetle. Successful colonization of a tree by *P. rufipennis* is probably a function of these interacting variables, as well as additional variables including the number of beetles available and the weather. However, the higher number of attacks on weakened trees point to the abundance of susceptible host type as the primary variable contributing to *P. rufipennis* outbreaks. These findings support the hypothesis that the distribution and abundance of susceptible hosts is a dominant factor in the success of bark beetles (Rudinsky 1962; Coulson 1979).

An important aspect that is very difficult to ascertain in studies of the relationship between defoliation and subsequent bark beetle attack is just how much defoliation is required before beetle attacks occur. Berryman (1982) proposed a conceptual model which predicted that beetle populations move from an endemic domain to an epidemic domain given the presence of

some stress factor. The pattern of beetle attack in budworm damaged stands in Newfoundland supports Berryman's model and implies that the increase in numbers of *P. rufipennis* is largely a symptom of black spruce injury and mortality. For each of moderate and severe damage areas, the conceptual model proposed by Berryman can be extended to a more appropriate logistic model suitable for predicting the probability of attack. Examination of Table 2.11, reveals p-values < 1.0, indicating that the logistic regression approach is suitable for prediction. Aldrich and Nelson (1984) have noted that the interpretation of the coefficients in a logistic model is more difficult than in regression because of the nonlinear relationship between the predictor variables and the binary dependent variable. The sign of the estimated coefficient determines the direction of the effect, but the magnitude of the effect varies with the magnitude of all the predictor variables in the model. Therefore, to determine any change in probability as a result of a change in one predictor variable, it is necessary to set the values of the remaining independent variables. The preference by *P. rufipennis* for damaged black spruce was confirmed in baited-tree experiments (Table 2.13). On trees baited with male *P. rufipennis*, a strong relationship was evident between tree damage and beetle attack. There was a concomitant increase in the percent of successful attacks with increased damage as was found in permanent plot studies. The inverse relationship was found for unsuccessful attacks. The rapid increase in successful attacks on trees with 70% or more damage suggests that the 70% damage level may be an important threshold for *P. rufipennis*. The majority of trees with $\leq 70\%$ crown damage were resistant to bark beetle attack, and could therefore potentially recover from budworm damage.

The potential for conifers to recover following insect damage has been given increased attention in recent years. Rapid recovery following insect damage has been reported for balsam

fir (Piene 1989), white spruce, *Picea glauca* (Moench) Voss (Reeks and Barter 1951) and white fir, *Abies concolor* (Gord. and Glend.) Lindl. (Wickman 1963). In contrast, Scots pine, *Pinus sylvestris* L., recovers its foliar biomass slowly after defoliation (Ericsson *et al.* 1985; Austara *et al.* 1986). There is evidence that black spruce also recovers rapidly following budworm attack. Raske (1984) reported an immediate increase in average annual terminal shoot growth in black spruce following the collapse of spruce budworm in central Newfoundland. Furthermore, assuming that refoliation is a reliable indicator of increased foliar biomass, shoot production and volume increment, the lack of symmetry in Table 2.15 indicates that in the absence of *P. rufipennis*, black spruce is capable of rapid recovery. Although 64.9% of the trees showed no observable change in refoliation, 23.1% exhibited an increase in foliar biomass. Only 12.0% continued to decline. Recovery is apparent in all classes of live trees, including trees with as little as 10% live crown. Furthermore, 20.7% of the trees with $\geq$70% crown damage showed evidence of recovery. One somewhat surprising result was the low numbers of attacks observed on untreated trees. It is possible that with recovery in progress and populations declining, baited trees in adjacent plots outcompeted untreated trees and attracted the majority of newly emerged beetles.

As timber resources decline, and the need for better forest management grows, increasing importance has been ascribed to forecasting the probability of beetle outbreaks accurately and predicting the biological and economic consequences of infestations. One tactic used to forecast and predict losses is the development and implementation of stand hazard rating systems (Salman and Bongbery 1942; Safranyik *et al.* 1974; Schmid and Frye 1976; Alfaro 1977; Amman *et al.* 1977; Mahoney 1978; Hedden *et al.* 1981; Paine and Stephen 1985). Most systems developed to date attempt to assess the susceptibility of a particular stand by using site, stand,

and tree characteristics along with indirect measures of beetle populations. Similarly, the probabilistic models developed for predicting *P. rufipennis* attack produce valuable insight about the conditions under which beetle attack on black spruce occurs, and could form the basis for a hazard rating system. For that reason, damage must be assessed carefully to determine the level of risk associated with budworm feeding. As a beginning my models may provide a screening tool to identify stands that have high or low probabilities of attack. Equations based on tree characteristics could prove to be useful to managers, because potential high hazard areas can be readily identified and management priorities such as salvage operations can be best implemented. Although the performance of each model can only be rated as fair (Fig. 2.5), the resultant probabilities provide evidence that decision-making can be enhanced using logistic regression models. The high percentage of unexplained variance is not surprising given that only a few predictors were considered. Berryman (1981) maintained that some estimate of vigor is essential in assessing the risk of outbreaks. One important predictor may be average radial growth just prior to attack, because it is known to be an indictor of current tree vigor (Hard et al. 1983). Finally, the candidate independent variables selected for the models were choosen based on individual tree characteristics that are easily measured in the field. The models might be significantly improved if estimated probabilities were related to stand and site characteristics.

A central question that has not been adequately answered in the literature is how defoliation causes increased susceptibility of trees to bark beetles. Depending on the severity of defoliation and on the tree species, a multitude of physiological changes may act to predispose a tree to beetle attack. Waring and Pitman (1980) suggested that trees that are most efficient photosynthetically show the best growth potential and are most resistant to mountain pine beetle.

Coulson (1979) reports that susceptibility is a function of the physiological condition of the individual trees comprising a stand. In addition to causing a reduction in carbohydrate production, defoliation invariably leads to a series of metabolic disturbances that interfere with rates and balances among internal physiological processes. Furthermore, the physiological impact of a localized attack in one part of a tree is usually transmitted to distant organs and tissues and eventually affects the whole tree (Kozlowsi 1969). The end result is often a decrease in tree resistance.

Several hypotheses may be invoked to explain the mechanism by which defoliation increases the susceptibility of trees to insect attack. The relationship between nutritional changes and tree vigor has been investigated by Webb and Karchesy (1976) who found that carbohydrate content of Douglas-fir, *P. menziesii,* was reduced proportionally to the intensity of defoliation by the Douglas-fir tussock moth. A reduction in starch can be expected to decrease energy reserves and reduce evapotranspiration (Webb 1981), thereby lowering tree resistance. Reduced transpiration and an increase in water content have been confirmed in trees defoliated by gypsy moth (Stephens et al. 1972). Furthermore, cessation of transpiration as a result of defoliation is reported by Evenden (1940) to cause oversaturation of bark and sapwood tissues. It is probable that, with high levels of crown damage, moisture stress predisposes black spruce to *P. rufipennis*, especially when individual trees have 70% or more of their foliage killed. It should be noted that above-ground foliar damage is often accompanied by underground events that also contribute to tree predisposition. For example, Redmond (1959) recorded rootlet mortality in balsam fir defoliated by budworm. Mortality of rootlets was over 30% in trees with 70% of new shoots destroyed. During my study no information on rootlet mortality was collected from permanent plots but during surveys for Armillaria root rot at Miguels Brook, Raske (1984)

exposed 6 major roots on each of 8 trees and disclosed that all damaged trees had a reduced number of rootlets compared to undamaged trees. Therefore, I hypothesize that defoliation-induced stress results in root mortality in black spruce which further promotes bark beetle attack.

A major effect of defoliation in determining tree susceptibility is believed to be related to resin production. The ability of resin-producing trees to inhibit beetle attack by copious resin production is well established for some species (Person 1931; Smith 1961, 1964, 1966; Heikkenen and Hrutfiord 1965; Rudinsky 1966; Berryman 1969, 1972; Hanover 1975; Bordasch and Berryman 1977; Hodges et al. 1979). In studies with grand fir, *A. grandis*, Wright et al. (1979) reported that the concentration of monoterpenes in bark lesions was significantly reduced in direct proportion to cumulative defoliation. Furthermore, trees that produced the least amounts of monoterpenes were the ones successfully attacked by *S. ventralis*. Presumably, a reduction in monoterpene levels can lower the resistance of conifers to bark beetle attack.

Recent work on the nature of defensive systems in conifers also has revealed that the primary constitutive resin system is supplemented by a secondary wound response or hypersensitive reaction (Raffa and Berryman 1982; Matson and Hain 1985). This reaction is characterized in most conifers by a localized autolysis of parenchyma cells and secondary resinosis at the entrance holes of beetles and their associated organisms (Shrimpton 1973; Wong and Berryman 1977). For both mechanisms of defense, synthesis of terpenes is dependent on carbohydrates and is an energy-demanding process (Chung and Barnes 1977). The relative importance of these 2 mechanisms is unknown for black spruce, but following attack on standing and felled trees, resin flow and necrotic tissue were present near entrance holes and along beetle galleries, confirming that both defensive mechanisms are employed against *P. rufipennis*.

Therefore, one possible mechanism to explain the increase in susceptibility of black spruce following defoliation may be the inability of weakened trees to respond with either the quality or quantity of compounds required for defense. Lowered resistance would favor colonization of black spruce by the beetle and its associated fungus, *C. piceaperda*. The colonization pattern agrees with that proposed for secondary bark beetles by Raffa and Berryman (1982), who maintained that the cost of locating rare weakened trees, many of which have poor quality phloem, is countered by the higher potential for successful brood survival because of low tree resistance.

In addition to lowering levels or affecting quality of defensive compounds, crown damage also might disrupt the relative amounts of terpenes present in black spruce throughout the season. Major changes in both total and relative amounts of some terpenes occur in buds and young leaves following bud burst (von Rudloff - pers. comms.). For example, black spruce bud oil contains 3% to 10% bornyl acetate, but the relative amount rises to 45% to 50% in the new leaves by early July, and the percentage of β-pinene drops from 5% to 1% during this period. Disruption of terpene composition must also be considered as a possible mechanism influencing *Polygraphus*-black spruce interactions.

The contribution by *P. rufipennis* to total spruce mortality is difficult to determine, but several inferences are possible from Figs. 2.2-2.4. Many trees attacked by the beetle were severely damaged or already dead, indicating that some trees in the higher damage classes unattacked by bark beetle would have died from cumulative budworm damage alone. However, the incidence of attack across all defoliation classes indicates that *P. rufipennis* is aggressive enough to inflict losses on trees with little crown damage. Furthermore, there is evidence to show that in the absence of *P. rufipennis* many damaged black spruces are capable

of recovery (Table 2.15). During low intensity of secondary insect attack the usefulness of dead wood in Newfoundland is estimated to last 4 to 5 years. With secondary bark beetle activity, the time frame is significantly reduced (Hudak and Basham 1981). A major factor affecting utilization of damaged timber is a 50% reduction in moisture content 3 years after death. Loss of moisture lowers wood quality by decreasing hardness and reducing paper brightness. Consequently, with fast rates of deterioration in trees attacked by *P. rufipennis* the time available for salvage is shortened. The increased costs of salvage coupled with the increased hazard to loggers must significantly increase the costs of harvesting.

The ecological role of *P. rufipennis* in the black spruce ecosystem is largely unknown. Scolytids clearly influence successional patterns in forests (Amman 1977; Wellner 1978), either by speeding up or slowing down the rate at which succession proceeds. Insect herbivore populations increase rapidly on stressed hosts, and are known to regulate long-term cycling patterns by accelerating changes in competitive relationships between plant species (Connell and Slatyer 1977; Schowalter 1981). Although long-term ecological research is needed to elucidate the total influence of *P. rufipennis* on forest succession, observations in pure black spruce stands in central Newfoundland indicate that the beetle may promote the establishment of kalmia heath, one of 6 major heath types recognized for Newfoundland (Meades 1983; Damman 1975). Where beetle-killed trees had created gaps in the forest canopy, allowing in more light, an understory dominated by northern sheep laurel, *Kalmia angustifolia* frequently occurred. Once established, this native shrub grows vigorously and long-term occupancy may transform productive black spruce sites into ericaceous heath, precluding forest regeneration (Meades 1983; Mallik 1990).

Beetle-killed trees also increased the number of snags, blowdown and woody litter in black spruce stands, thereby contributing to already heavy fuel loads, which in turn may have

increased the probability of fire. Fire has been an important disturbance factor in the forests of central Newfoundland for millennia. The typical fire regime for black spruce forests is one of frequent fires and varying intensities. It is generally agreed that fire frequency and intensity play an important role on the success or failure of black spruce regeneration. Following the end of the budworm-beetle outbreak in the early 1980s, a considerable mass of downed material accumulated on the forest floor in budworm-damaged stands in central Newfoundland. Shortly thereafter, in 1986, these areas suffered their worst fire season since 1961. Accordingly, it is postulated that spruce budworm, *P. rufipennis* and fire act in concert to determine the successional pattern of black spruce in Newfoundland.

Although the hypotheses put forward to explain the black spruce-*P. rufipennis* interaction require further testing, several conclusions emerge. The evolutionary fitness of *P. rufipennis* appears to be largely dependent upon the beetles' ability to locate and exploit suitably weakened trees. Consequently, the spatial structure and condition of black spruce stands probably determine the beetle's foraging strategies and attack patterns. A testable hypothesis that might be considered is that the beetle utilizes nonrandom search behavior to exploit patches of rare susceptible hosts. Knowledge of how the insect locates its host would improve prediction equations and potentially allow for more effective management of beetle populations.

Finally, the *P. rufipennis*-black spruce interaction in the boreal forest ecosystem provides a new model for evaluation of reciprocal selection pressures between bark beetles and their hosts. Knowledge from this system should extend the theory of bark beetle epidemiology and provide additional valuable insight into the principles underlying beetle-conifer relationships.

CHAPTER 3

Despite knowledge that many scolytids utilize semiochemicals in host selection and colonization (Shorey 1973; Borden 1974, 1982; Birch 1978; Payne 1979), no experiments have tested the hypothesis that *P. rufipennis* produces an aggregation pheromone. Evidence as to whether or not an aggregation pheromone is produced by the beetle is critical to an understanding of its host selection sequence. Furthermore, isolation and identification of a secondary attractant could potentially provide a means to survey and possibly suppress beetle populations. Hence, experiments were initiated to characterize semiochemical-based communication by *P. rufipennis* as a basis for future pest management applications.

Parasites and predators of bark beetles have developed complex interspecific communication links with their prey in the course of their long evolutionary history. The ability of natural enemies to exploit bark beetle aggregation pheromones as host-finding kairomones was first demonstrated by Bedard (1965) who reported interspecific communication between the pteromalid, *Tomicobia tibialis* Ashmead, and male *Ips paraconfusus* Lanier. Since then, field and laboratory studies have shown that at least 25 entomophagous species utilize the pheromones of their bark beetle hosts as host-finding kairomones (Borden 1982). In the present study, the cylindrical bark beetle, *Lasconotus intricatus* Kraus., was strongly associated with the four-eyed spruce bark beetle. Therefore, I also tested the hypothesis that *L. intricatus* utilizes the pheromone of *P. rufipennis* as a host-finding kairomone.

MATERIALS AND METHODS

Insect Rearing

Beetles from natural populations in Newfoundland and British Columbia, were used in field attraction studies and in laboratory experiments. Overwintered *P. rufipennis* adults were obtained in the spring from infested black spruce near Powderhorn Lake and Miguels Lake in central Newfoundland and near Thorburn Lake in eastern Newfoundland. In British Columbia, adults were obtained in the fall from infested black spruce at Nazko and Cottonwood Creek near Quesnel and from infested white spruce, *Picea glauca* (Moench) Voss, at Penticton and Bowron Lake. Uninfested black spruce trees were cut and 40 cm logs from these trees were used as a fresh phloem source for feeding newly-emerged beetles. Infested logs were sealed at the ends with hot paraffin wax to delay desiccation, and placed in emergence cages held at 23-28° C on a photoperiod of 16:8 (L:D). Infested logs not immediately used were waxed and maintained in cold chambers at 4° C for up to eight months. Emerged beetles were collected within two days, sexed using the two median tubercules on the frons of the male (Bright 1976), and maintained at 4° C on moist tissue paper in glass jars.

Field Attraction Studies

In 1983 and 1984, studies were conducted in a black spruce stand near Miguels Lake in the Northwest Gander River watershed, in central Newfoundland. Emerged beetles were sexed and then allowed to infest fresh logs of black spruce measuring 40 cm long. To obtain sufficient numbers a few brood adults in the process of emerging were excised from host tissue.

Attraction studies were carried out using "greenhouse" cages on which glass barrier traps were erected (Chapman 1966; Nijholt 1970). Each replicate comprised 5 treatments within the

greenhouse cages: a spruce log with 50 males; a spruce log with 50 females; a spruce log with 50 males and 50 females; a fresh, green spruce log; and no stimulus (empty cage). To minimize variation in host quality all logs for a given replicate were cut from the same black spruce tree. Most beetles placed on logs immediately bored into the phloem tissue. If they failed to establish readily, additional beetles were added. Following successful beetle attack, each log was wrapped with saran screening to prevent further attack by *P. rufipennis* or by parasites and predators. Cages were randomly placed 20 m apart in a beetle-infested black spruce stand, and to minimize positional effects each treatment was rotated twice weekly to a different position.

One replicate was run from 1-12 June and a second from 13-23 June, 1983, and four replicates were run from 5 June to 12 August, 1984 (Table 3.2). In 1984, the four replicates ran for 21, 25, 23, and 25 days respectively.

Collection and Preparation of Frass and Abdominal Extracts for Laboratory Bioassays

Frass, composed of excrement and bark tissue from beetle feeding, was obtained by allowing newly-emerged beetles to bore freely into fresh spruce logs or by placing them into preformed entrance holes. Gelatin capsules (size 000) were used to confine feeding beetles; frass was collected from the capsules and stored at -40° C until it was used in bioassay experiments. In British Columbia and Newfoundland, beetle emergence and frass production was highly variable. Accordingly, for most experiments frass from different collection dates was combined to obtain sufficient quantities. To investigate the effects of mating on the attractiveness of frass, 3 female beetles were added to galleries colonized for 2-3 days by single males. Extracts of frass and phloem tissue were prepared by pulverizing the material with a mortar and pestle in double distilled pentane or hexane (1.0 mL/0.1 g material) over dry ice. Abdominal extracts were

prepared by excising beetles from logs in which they had been boring, removing the abdomen, and crushing it in either chilled pentane or hexane (10 μl/beetle abdomen).

Laboratory Bioassays

From June 1984 to October 1986, the responses of *P. rufipennis* to frass, frass extract, and abdominal extract were tested in an open-arena, air-stream olfactometer (Wood and Bushing 1963; Stock and Borden 1983). Ten experiments were performed as outlined in Table 3.3. Experiment I utilized beetles that emerged from black spruce logs transported from Newfoundland to British Columbia in fall 1983. Beetles began emerging in December and were fed on uninfested Newfoundland black spruce. Experiments II and III were carried out in British Columbia in 1984 and 1985 and utilized beetles reared on black and white spruce respectively. Experiments IV-X were conducted in 1985 and 1986 with beetles reared on black spruce in Newfoundland. In 1985, Experiments IV-VI were conducted using the same group of 80 beetles to test crude frass on 26 July and abdominal and frass extracts on 27 July.

In 1986 one additional experiment was carried out to investigate the response of beetles to frass produced by males that had colonized logs for 2, 4, 8 and 12 days. On 5 August 200 male beetles were placed on 5 black spruce logs from the same tree. After 2 days frass from 40 beetles was collected, weighed and hexane extracts of frass and beetle abdomens were prepared, sealed in a vial, and maintained at -40° C. This procedure was repeated with 40 males after each of 4 and 8 days of feeding. Following 12 days of feeding, frass, frass extracts and abdominal extracts were obtained from 24 beetles.

On 15 October the material was bioassayed at a stimulus level of 0.1 g of frass with 8 replicates of 5 beetles of each sex. On 17 and 21 October, frass and abdominal extract stimuli

were bioassayed at a concentration of 0.002 g equivalents and 2 male equivalents, respectively. Control bioassays tested the response to air and to phloem shavings removed from the logs before beetle introduction and stored at -40° C before use.

In all laboratory bioassays, frass stimuli were placed in a small plastic dish positioned just below the olfactometer air outlet. For extract stimuli a clear glass tube containing a rolled-up filter paper impregnated with the stimulus was slipped onto the air nozzle. Medical air was passed over the stimulus at 0.5 L/min or 1.0 L/min using a compressed air cylinder. Tests were run with full background lighting at 22-25° C.

Beetles for bioassay were removed from holding jars 30 min prior to bioassay and placed on filter paper in petri dishes maintained at 4° C. With 2 exceptions, stimuli were tested with 8 replicates of 5 beetles of each sex. Experiment I utilized 3 male replicates and 6 female replicates of 5 beetles of each sex and Experiment II was run with 6 replicates of 5 beetles of each sex. A clean stimulus tube was used for each treatment and the filter paper arena floor (18.5 cm diameter) was changed for each new stimulus. Beetles were released in rotation 9.0 cm downwind of the stimulus source. Beetles were considered to be responding if they walked upwind and only if within 2 min entered a 1 x 3 cm area in front of the air outlet. Beetles that walked off the filter paper outside this area were removed and considered nonresponders, as was any insect that had not reached the designated response area within 2 min. Any insect that appeared maimed or dead was replaced at the start of each bioassay. After use all beetles were returned to their petri dish which was placed at the end of the rotation. Bioassays were usually completed within a 5 hour period without interruption. Control bioassays were conducted for the response to air and to fresh host phloem.

Collection of Beetle and Host Volatiles

Volatiles from living adults boring in fresh host logs were collected by aeration and adsorption on Porapak Q^{R} (50-80 mesh, Applied Sciences Division, Milton Roy Laboratory Group, State College, Pa.) (Byrne *et al.* 1975). The Porapak Q was thermally conditioned and packed into metal (15.5 cm x 6.4 mm O.D.) or glass traps (12.0 cm x 6.0 mm O.D.).

Aerations were carried out in Newfoundland in the laboratory at 21°C under full background lighting. Fresh logs were infested with newly-emerged beetles and placed in a 120 L container made from food grade high density polyethylene modified after that used by Peacock *et al.* (1975). Air was drawn with a vacuum pump at 1.8 L/min through a charcoal filter, over a log and through a Porapak Q-filled metal trap. Beetles were allowed to feed before aerations for 24-48 hr on logs to ensure gallery establishment and were checked for evidence of frass production; uninfested control logs received 50 holes made with a number 5 cork borer to simulate beetle feeding. Eleven aerations of fresh spruce logs yielded a total of 792 lhr (1 lhr=amount of volatiles collected from 1 log for 1 hr); ten aerations of male-infested logs yielded a total of 41,142 bhr (1 bhr=amount of volatiles collected from 1 beetle boring in a log for 1 hr); one aeration of a female-infested log yielded a total of 3750 bhr; six aerations of logs infested with 1 male and 2 female beetles per gallery yielded a total of 18,732 bhr from mated males.

Logs from the same tree were used for each aeration experiment, to minimize possible effects of host variation. Within each experiment, uninfested control logs were aerated first, followed by male-infested logs and logs infested by males and females. The odor-laden Porapak Q was extracted after 72 hr in 5.0 mL of redistilled hexane or pentane and ethyl ether (95:5) and

stored in a teflon-lined vial at -40°C. Between treatments, the aeration container was wiped clean with acetone and the glass wool and the activated charcoal filter was replaced. Filters were flushed with double-distilled pentane and ethyl ether followed by a 2 hr nitrogen purge.

Aerations in British Columbia utilized a water aspirator with an airflow rate of 1-2 L/min. Single beetle collections were made using an on-tree collection device (Gries *et al.* 1988), consisting of a Porapak Q trap connected to an expanded glass tube placed over the entrance hole of the beetle's gallery. Aerations were carried out in the laboratory at 21°C on a photoperiod of 16:8 (L:D). Treatments included aeration of single males, one male and three females, a control vial filled with finely ground phloem tissue, and an empty, control vial. Six males boring in white spruce were individually aerated for 60 hr in each of three experiments. Three females were added to each male gallery in experiments 1 and 2, and the 60 hr aeration was repeated. The third female refused to enter four male galleries in experiment 1. Beetle establishment and frass production were recorded for each experiment. Logs from experiment 1 were dissected three weeks following aeration to verify that females had established broods. Trapped volatiles were extracted in 0.5 mL pentane and ethyl ether (95:5), and stored at -40°C in a vial with a teflon-lined cap.

Collection and Preparation of Frass and Abdominal Extracts for Chemical Analysis

Phloem tissue was obtained by removing samples of bark from fresh black spruce with a No. 5 cork borer. Frass was collected after allowing newly-emerged beetles to bore freely into fresh spruce logs or by confining them with gelatin capsules in preformed entrance holes. To prepare extracts, phloem and frass were pulverized in redistilled pentane or hexane and ethyl ether (95:5) (1.0 mL/0.1 g material) over dry ice. Abdominal extracts from 500 male and 250

female beetles were prepared by excising beetles from logs, and crushing the abdomens in either chilled pentane or hexane and ethyl ether (95:5) (10 μL/abdomen) in a vial held on dry ice. The vials were sealed with a teflon-lined cap and stored at -40°C.

Analysis of Trapped Volatiles

Volatiles were analyzed in a Hewlett-Packard 5830A gas chromatograph (GC) equipped with a 18835B capillary inlet system and a flame ionization detector (FID). Helium was the carrier gas and the injection port and detector temperatures were 260 and 270°C, respectively. Mass Spectroscopy (MS) was done with a Hewlett-Packard 5985 coupled GC-MS. Captured volatiles were concentrated to 5 μL by evaporation over gentle heat or with a stream of nitrogen at -10°C and analyzed on a 60 m x 0.32 mm I.D. DB-1 fused silica column with temperature programming from 30 to 130 °C at 1°C per min. Abdominal and frass extracts were analyzed on a 30 m x 0.25 mm I.D. fused silica column coated with SP-1000 (Supelco, Inc., Bellafonte, PA), with temperature programming from 70 to 180°C at 2°C per min. To identify beetle-produced compounds, chromatograms of volatiles produced by the attacking virgin males were compared with chromatograms of host volatiles and with those following the addition of the females. Drs. G. Gries, Dept. of Biology, and H.D. Pierce Jr., Dept. of Chemistry, assisted in the analysis of volatiles and extracts and with the identification of beetle-produced compounds.

Field Bioassays

The candidate pheromone was tested in 1987 and 1988 in black spruce stands near Powderhorn Lake and Crooked Bog 5.0 and 8.0 km, respectively, north of Badger, Newfoundland. Volatiles (Table 3.1) were released from 400 μL polypropylene Eppendorf® tubes (Brinkman Instruments, Rexdale, Ontario) suspended in 8-unit multiple-funnel traps (Lindgren

Table 3.1 Source, purity and release rates of volatile materials used in *P. rufipennis* field-trapping and tree-baiting experiments.

Compound	Abbreviation	Source	Purity (%)	Approximate release rate (μg/day)[a]
3-Methyl-3-buten-1-ol	Mb	Aldrich Chem. Co., Milwaukee, WI	97	4390 (open Eppendorf tube) 200 (capped Eppendorf tube) 6 (Conrel fibre)
α-Pinene	αP	Aldrich Chem. Co., Milwaukee, WI	99	100
β-Pinene	βP	Aldrich Chem. Co., Milwaukee, WI	98	100
3-Carene	C	Albany Int'l Co., Columbus, OH	95	150
Myrcene	M	Sigma Chem Co., St. Louis, MO	98	300
Bornyl acetate	Ba	Aldrich Chem Co., Milwaukee, WI	97	100

[a] Eppendorf tubes loaded with 200 μl of 3-methyl-3-buten-1-ol or terpene. For 3-methyl-3-buten-1-ol at lowest release rate, Conrel fibres were 3-cm long, sealed at one end, and placed inside a capped Eppendorf tube. Release rates determined in the laboratory at 20°C, values represent means for 2 measurements.

1983) or affixed at 1.3 m height to the north side of a black spruce bole. Open and capped tubes released 3-methyl-3-buten-1-ol at rates of 4390 and 200 μg per day, respectively. For an ultra-low rate of 6 μg per day the candidate pheromone was released from 3 cm long and 0.2 mm I.D., polyester Conrel fibres (Albany International Co., Needham, Mass.) placed inside a closed Eppendorf tube. Terpene hydrocarbons were released from an open Eppendorf tube. Vapona No-Pest Strip (Boyle-Midway Can. Ltd., Toronto Ont.) was used to kill captured beetles in multiple-funnel traps. Trap baits were replaced at weekly intervals. Traps were monitored twice weekly and captured beetles were removed, placed in 75% ethanol, and separated by species and sex.

Six trapping experiments were conducted (Tables 3.4-3.7). Experiments 1 and 2 tested the candidate pheromone at two release rates, with treatments randomly assigned to 30 traps spaced at least 20 m apart. Experiment 1 was run during the beetle's spring flight and experiment 2 during the summer flight. Experiments 3 and 4 tested the candidate pheromone alone and in binary combination with each of the major terpenes identified in twigs of black spruce (von Rudloff 1975) in a randomized complete block design. Because the Powderhorn stand was located on a gentle slope, blocks were laid on contours to minimize within-block variability. Blocks were 20 m apart and traps 15 m apart. Experiment 5 compared the candidate pheromone at two different release rates to a fresh spruce log infested with 50 newly-emerged male beetles. The logs were wrapped with saran screening to prevent further attack and tied to the side of multiple-funnel traps spaced 20 m apart in a linear sequence. Treatments were randomly assigned to traps at the beginning of each replicate. Experiment 6 was similar to experiment 5, but was laid out in a randomized complete block design and replaced the low-dose

pheromone stimulus with an uninfested log.

The effectiveness of the candidate pheromone in inducing attack on black spruce was evaluated in two tree-baiting experiments (Experiments 7,8). Experiment 7 was a 10-replicate experiment laid out in a completely randomized design with at least 20 m between trees. Treatments included an empty (control) Eppendorf tube, and the candidate pheromone released at a rate of 6 μg per day from a 0.2-mm I.D. Conrel fibre inside a tube, or released at 200 μg per day from a closed tube.

Treatments for experiment 8 included: an empty (control) tube, and the candidate pheromone at 200 μg per day alone or with either alpha-pinene, bornyl acetate, beta-pinene, 3-carene, myrcene, or a mixture of the above five terpenes released from separate tubes at rates given in Table 3.1. Treatments were assigned at random to 5 blocks spaced 20 m apart and with baited trees spaced 15 m apart.

All baited trees had $\geq$ 10 cm diameters at breast height and had light damage ($\leq$ 30% cumulative defoliation) from *C. fumiferana* in the previous 10 years. Baits were placed on trees at breast height on 3 June at the beginning of the spring flight; they were replaced on 1 July at the beginning of the summer flight. The incidence of attack on baited trees and the nearest four trees $\geq$ 10 cm dbh surrounding each baited tree was assessed on 2 September by counting attacks, represented by frass piles and resin flow, on areas of bark surface within two 16.7 x 30 cm open frames 1.3 m high on the north and south aspects of the tree. Attacks with fresh frass were considered successful and attacks with copious resin flow in the entrance holes were considered unsuccessful. The number of successful and unsuccessful attacks on the north and south aspects of attacked trees were combined and expressed as attack density per square meter

of bark surface.

Data were analysed using the SAS statistical package version 6.0 (SAS Institute Inc., Cary, NC). Data were transformed by $\log_{10}(X + 1)$ to remove heteroscedasticity prior to analysis of variance. Duncan's multiple range test was used to examine differences among treatment means. Proportional data from laboratory experiments were subjected to an arc sine transformation to promote equality of variances and analyzed by a Newman-Keuls test modified for testing frequencies (Zar 1984). The Chi-square statistic was used to examine differences in the attack frequencies of unbaited and baited trees. Differences in the mean attack density on unbaited and baited trees was tested using a two-sample t-test.

The Pearson product-moment correlation statistic was calculated to describe the intensity of association between *L. intricatus* and *P. rufipennis* captured in summer 1987 and spring 1988. In all tests, the maximum probability of a Type-I error was set at 0.05.

RESULTS

Field Attraction Studies

In 1983, significantly more female beetles responded to male-infested logs than to logs infested by females, males and females, uninfested logs or unbaited traps (Table 3.2). The response by males to male-infested logs was high but did not differ significantly from other treatments. A total of 1720 beetles was captured from 24 June to 19 August to traps left in place after the completion of replicate 2; 72.7% were caught at the trap with the male-infested log. In 1984, beetles of both sexes responded significantly to male-infested logs and more than twice as many females as males entered the traps over the male-infested logs. The sex ratios of beetles responding to the male-infested logs were 2.3 : 1 and 2.2 : 1 in favor of females in 1983 and 1984, respectively. In both years the response to female-infested logs was low as was the response to uninfested logs and empty cages. Also, the response to logs infested by beetles of both sexes was higher than but not significantly different from control or female treatments.

Laboratory Bioassays

Laboratory experiments corroborated field tests and added supporting evidence for the existence of a male-produced aggregation pheromone. Females responded significantly to male-produced frass in all experiments except Experiment II, and with the exception of Experiments I and II there was a consistent and significant response by males (Table 3.3). On only 3 occasions, however (Exps. I, V and X) did the response exceed 50%.

In walking bioassays, *P. rufipennis* exhibited alterations in locomotory mode. Responding beetles often walked upwind towards the stimulus source in a straight line. Many responders

Table 3.2 Numbers of *P. rufipennis* captured in glass barrier traps over "greenhouse" cages containing logs infested by *P. rufipennis*.

Date	Treatment	Number of Beetles Captured ($\bar{x}$ ± SE)[a]		
		Males	Females	Total
June 1-23, 1983	No log	11.0 ± 5.0 a	11.0 ± 6.0 a	22.0 ± 11.0 a
N = 2	Unattacked log	20.5 ± 10.5 a	18.5 ± 5.5 a	39.0 ± 16.0 a
	Log + 50 males	57.0 ± 6.0 a	65.5 ± 4.5 b	122.5 ± 10.5 a
	Log + 50 females	12.5 ± 3.5 a	9.0 ± 3.0 a	21.5 ± 6.5 a
	Log + 50 prs.	38.0 ± 32.0 a	28.0 ± 19.0 a	66.0 ± 51.0 a
June 5 - August 12, 1984	No log	0.5 ± 0.5 a	2.2 ± 1.4 a	2.7 ± 1.9 a
N = 4	Unattacked log	4.5 ± 2.9 a	6.7 ± 4.8 a	11.2 ± 7.7 a
	Log + 50 males	175.5 ± 58.9 b	392.7 ± 119.5 b	568.2 ± 177.1 b
	Log + 50 females	2.5 ± 1.2 a	8.0 ± 2.5 a	10.5 ± 3.1 a
	Log + 50 prs.	56.5 ± 33.1 a	114.0 ± 60.4 a	170.5 ± 92.7 a

[a] Totals, within columns for each experiment, followed by same letter not significantly different, Neuman-Keul's Test, $P \leq 0.05$.

Table 3.3 Responses of *P. rufipennis* in laboratory bioassays to beetle-produced frass, frass extracts, and abdominal extracts.

Exp. No., date and beetle source	Stimulus description	Amount or concentration	% Responders[a] Male	% Responders[a] Female
I.	Airstream	1.0 L/min	6.7 a	10.0 a
19 Feb. 1984	Phloem tissue	0.5 g	20.0 a	20.0 a
Newfoundland	Female frass	0.5 g	20.0 a	33.3 a
Black spruce[b]	Male frass	0.5 g	46.7 a	70.0 b
	Male + female frass	0.5 g	46.7 a	66.7 b
II.	Airstream	1.0 L/min	13.3 a	8.0 a
28 March 1984	Phloem tissue	0.25 g	0a	12.0 a
British Columbia	Female frass	0.25 g	6.6 a	12.0 a
Black spruce[c]	Male frass	0.25 g	6.6 a	36.0 a
	Male + female frass	0.25 g	13.3 a	24.0 a
III.	Airstream	0.5 L/min	0.0 a	2.5 ab
2 May 1985	Pentane	20 $\mu\ell$	5.0 a	5.0 ab
British Columbia	Phloem tissue ext.	0.002 g equiv.	7.5 a	0.0 a
White spruce[d]	Female frass ext.	0.002 g equiv.	2.5 a	7.5 ab
	Male frass ext.	0.002 g equiv.	15.0 ab	15.0 b
	Male frass	0.25 g	35.0 b	42.5 c
IV.	Airstream	0.5 L/min	12.5 a	5.0 a
26 July 1985	Phloem tissue	0.25 g	10.0 a	12.5 a
Newfoundland	Female frass	0.25 g	5.0 a	7.5 a
Black Spruce[c]	Male frass	0.25 g	45.0 b	45.0 b

Exp. No., date and beetle source	Stimulus description	Amount or concentration	% Responders[a] Male	% Responders[a] Female
V.	Airstream	0.5 L/min	5.0 a	12.5 a
27 July 1985	Pentane	20 $\mu\ell$	12.5 a	2.5 a
Newfoundland	Phloem tissue	0.25 g	15.0 a	5.0 a
Black spruce[e]	Female abd. ext.	2 beetle equiv.	7.5 a	5.0 a
	Male abd. ext.	2 beetle equiv.	12.5 a	15.0 a
	Male frass	0.25 g	47.5 b	52.5 b
VI.	Airstream	0.5 L/min	2.5 a	5.0 a
27 July 1985	Pentane ext.	20 $\mu\ell$	15.0 a	7.5 a
Newfoundland	Phloem tissue ext.	0.002 g equiv.	10.0 a	7.5 a
Black spruce[e]	Female frass ext.	0.002 g equiv.	12.5 a	15.0 a
	Male frass ext.	0.002 g equiv.	17.5 a	15.0 a
VII.	Airstream	1.0 L/min	5.0 a	5.0 a
6 Aug. 1986	Phloem tissue	0.13 g	7.5 a	5.0 a
Newfoundland	Female frass	0.13 g	5.0 a	7.5 a
Black spruce[f]	Male frass	0.13 g	35.0 b	37.5 b
VIII.	Airstream	1.0 L/min	7.5 a	2.5 a
6 Aug. 1986	Hexane	40 $\mu\ell$	2.5 a	0.0 a
Newfoundland	Phloem tissue ext.	0.004 g equiv.	2.5 a	5.0 a
Black spruce[f]	Female frass ext.	0.004 g equiv.	10.0 a	2.5 a
	Male frass ext.	0.004 g equiv.	10.0 a	5.0 a

Table 3.3.

Exp. No., date and beetle source	Stimulus description	Amount or concentration	% Responders[a] Male	% Responders[a] Female
IX.	Airstream	1.0 L/min	0.0 a	5.0 a
7 Aug. 1986	Hexane	40 $\mu\ell$	5.0 a	2.5 a
Newfoundland	Phloem tissue ext.	0.004 g equiv.	5.0 a	2.5 a
Black spruce[f]	Female abd. ext.	4 beetle equiv.	7.5 a	2.5 a
	Male abd. ext.	4 beetle equiv.	5.0 a	17.5 a
X.	Airstream	1.0 L/min	7.5 a	2.5 a
14 Aug. 1986	Phloem tissue	0.25 g	12.5 a	2.5 a
Newfoundland	Female frass	0.25 g	10.0 a	7.5 a
Black spruce[g]	Male frass	0.25 g	52.5 b	27.5 b
	Male + female frass	0.25 g	45.0 b	17.5 ab

[a] Percentages followed by the same letter are not significantly different, Neuman-Keul's Test modified for testing proportions (Zar 1984), $P \leq 0.05$.

[b] Female frass from 21 December - 19 February male frass from 2 December - 19 February, male + female frass from 1-19 February 1984 combined for bioassay.

[c] Beetle frass from 15-22 March 1984 combined for bioassay.

[d] Beetle frass from 26 April - 2 May 1985 combined for bioassay.

[e] Beetle frass from 24 June - 13 July 1985 combined for bioassay.

[f] Beetle frass from 15 July - 6 August 1986 combined for bioassay.

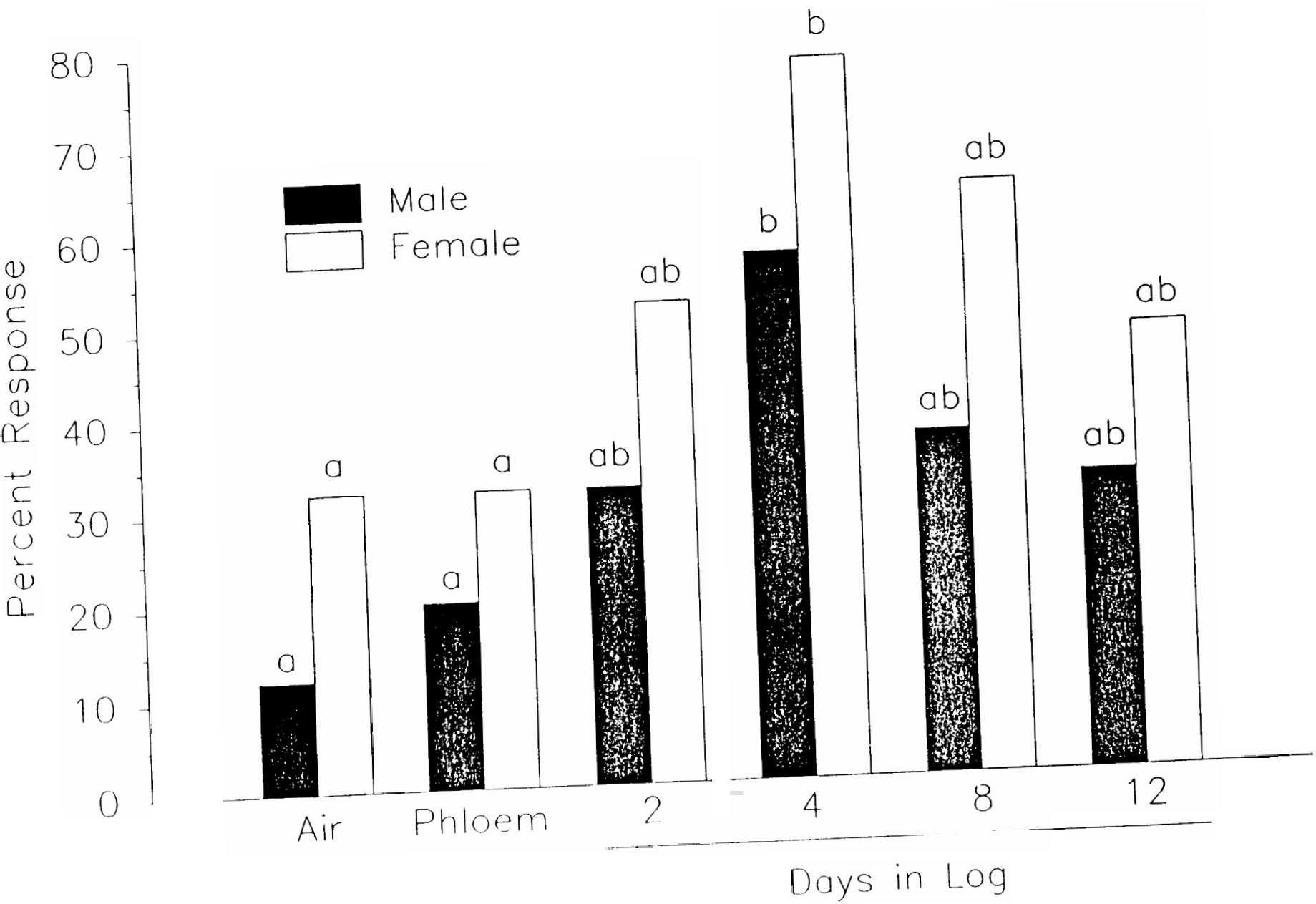
[g] Beetle frass from 30 July - 14 August 1986 combined for bioassay.

wandered out of and into the airflow through alternating left and right turns, as they proceeded to the designated area in front of the stimulus, characteristic of a klinotaxis (Borden and Wood 1966). Other beetles in the presence of male frass moved a short distance, stopped, and then proceeded to sit back and move the antennae up and down. In this state the beetles appeared to be arrested. This behavior, however, did not meet the criteria established for a positive response.

As in the field studies, females in the laboratory generally exhibited a higher level of response than males to male-produced stimuli (Table 3.3). In only one bioassay (Exp. X) was the female response lower than the male response. Comparison of bioassays conducted in winter and summer indicated that females were attracted to male-produced frass in both winter (except in Exp. II) and summer. Males, however, did not respond to male-produced frass in the winter (Exps. I, II), but did so in spring and summer (Exps. III-X). The response to female frass and to phloem tissue was low in all bioassays. Furthermore, abdominal extracts, as well as extracts of frass and phloem tissue, did not elicit a significant response by either sex. Both sexes responded to as little as 0.13 g of male-produced frass (Exp. VII), but strengths of extracted stimuli were apparently too low to induce a response (Exps. III, V, VI, VIII and IX). Beetles assayed against male frass produced for 2, 4, 8 and 12 days demonstrated a clear preference for frass produced during the first 4 days (Fig. 3.1). The response of male and female beetles was 56.7 and 76.7%, respectively.

Responses to frass produced by presumably mated beetles paired in logs disclosed no striking trends. In Experiment I, frass produced by mated beetles was attractive to females but not to males. In Experiment X, frass produced by mated beetles was attractive to males but not to females.

Fig. 3.1. Responses of *P. rufipennis* in laboratory bioassays to frass produced by male beetles feeding on black spruce logs for 2, 4, 8 and 12 days, 1986. Bars within each sex topped by the same letter are not significantly different, Newman-Keul's Test, $P \leq 0.05$.


Percent Response
80
70
60
50
40
30
20
10
0
Male
Female
a
a
a
a
ab
ab
b
b
ab
ab
ab
Air
Phloem
2
4
8
12
Days in Log

Analysis of Trapped Volatiles

Analyses of volatiles from *P. rufipennis* males, females and hosts disclosed an unknown compound produced by males; this compound was produced in a lesser amount after males were joined by females (Fig. 3.2). The unknown volatile was produced by males in both black and white spruce. Comparison of host volatiles with volatiles from female-infested logs did not disclose any female-specific compounds. There was no chromatographic evidence for more than one male-produced compound.

The mass spectrum of the unknown compound indicated major fragments of mass *m/z* 41(100), 56(88), 68(69), 31(65), and 86(20) This fragmentation pattern matched the mass spectrum of the primary alcohol, 3-methyl-3-buten-1-ol (Heller and Milne 1978). GC-MS comparison of the beetle-produced compound with an authentic sample of 3-methyl-3-buten-1-ol indicated identical retention and mass spectral characteristics. Chromatograms of hindgut extracts from male and female *P. rufipennis* disclosed no sex-specific volatiles. However, 3-methyl-3-buten-1-ol was detected by GC-MS in extracts of frass from males but not females, boring in black spruce (Fig. 3.3). The compound was not present in extracts from phloem tissue.

Field Bioassays

Bioactivity of 3-methyl-3-buten-1-ol was demonstrated in field-trapping and tree-baiting experiments. Traps baited with 3-methyl-3-buten-1-ol released at 200 μg per day in the spring caught significantly higher numbers of both male and female beetles than unbaited traps or those baited with 3-methyl-3-buten-1-ol released at 6 μg per day (Table 3.4, Exp. 1). Attraction of males and females to 3-methyl-3-buten-1-ol released at 6 μg per day did not differ significantly from unbaited traps. Catches during the summer were low and there was no significant

Fig. 3.2. Representative chromatograms of airborne volatiles collected from (A) a black spruce log, (B) from an individual *P. rufipennis* male boring in black spruce, and (C) the same male following addition of three females. Arrow denotes retention time of 3-methyl-3-buten-1-ol. Temperature programming: 30-130°C at 1°C/min.

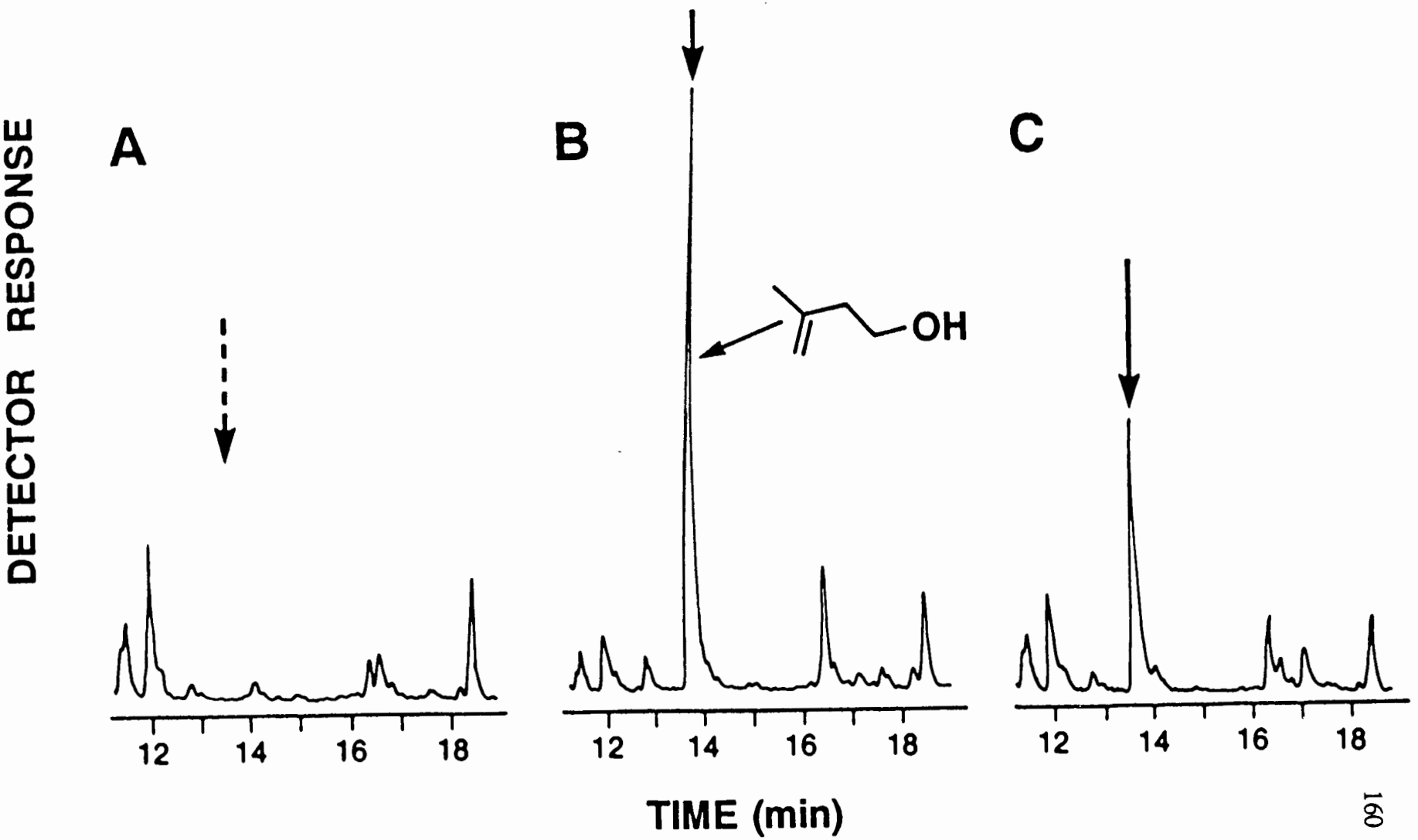

DETECTOR RESPONSE
A
B
C
OH
12
14
16
18
12
14
16
18
12
14
16
18
TIME (min)

Fig. 3.3. Gas chromatograms of (A) synthetic 3-methyl-3-buten-1-ol, compared with (B) male frass extract, (C) female frass extract, and (D) extract of fresh phloem tissue. Arrow denotes retention time of 3-methyl-3-buten-1-ol. Temperature programming: 70-180°C at 2°C/min.

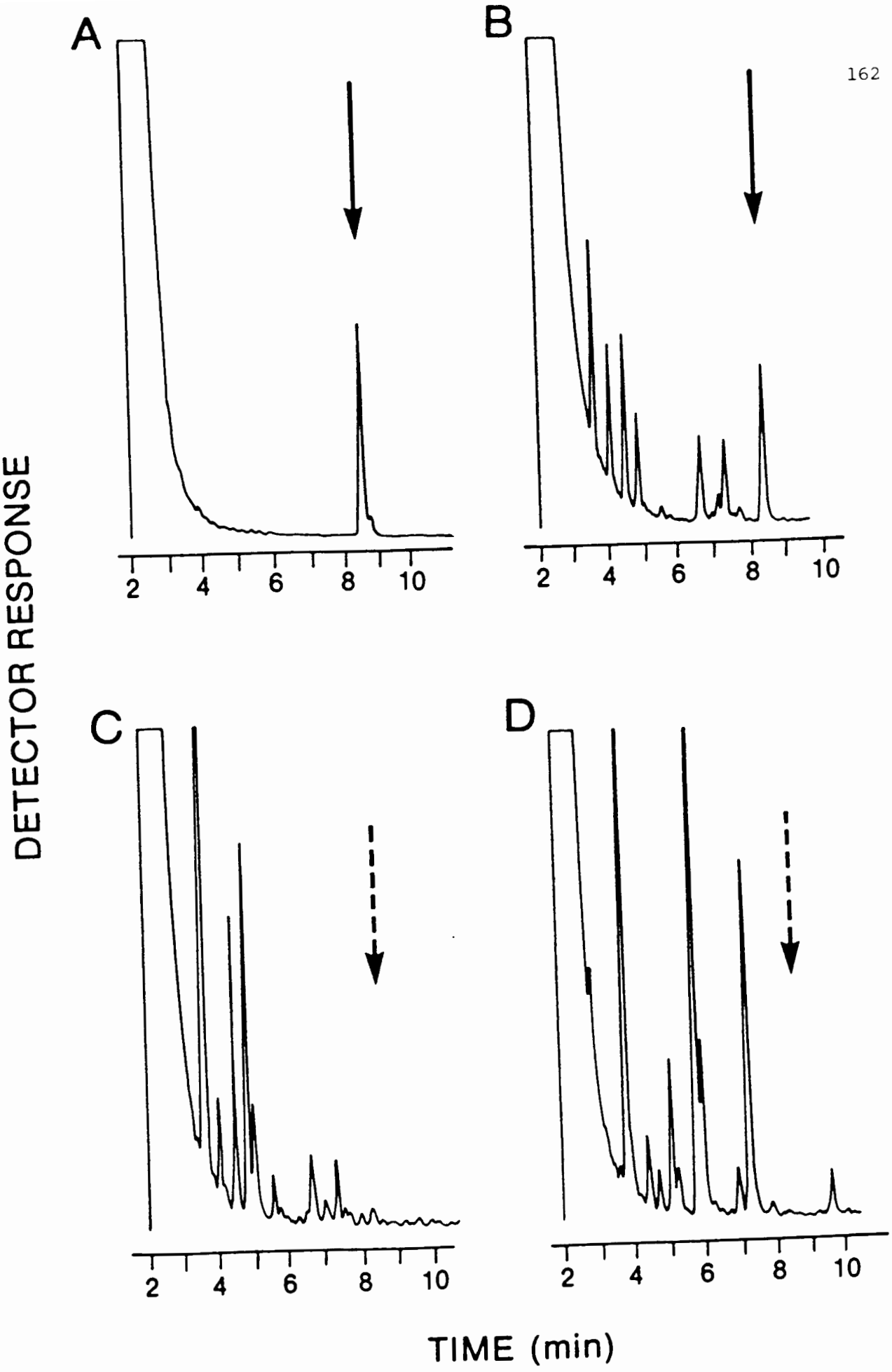

A
B
C
D
2
4
6
8
10
DETECTOR RESPONSE
TIME (min)

Table 3.4. Mean catches of *P. rufipennis* to multiple-funnel traps baited with 3-methyl-3-butten-1-ol (Mb), Crooked Bog, Newfoundland, 5-30 June (Experiment 1) and 1 July - 15 August (Experiment 2), 1987 (N=10).

Treatment	Released rate (μg/24 hr)	Mean ($\pm$SE) number per trap[a]			
		Experiment 1		Experiment 2	
		Male	Female	Male	Female
Unbaited trap		0.6 $\pm$ 0.3a	0.7 $\pm$ 0.3a	0.3 $\pm$ 0.2ab	0.2 $\pm$ 0.1a
Mb	6	1.2 $\pm$ 1.0a	0.9 $\pm$ 0.4a	0a	0.4 $\pm$ 0.2a
Mb	200	13.8 $\pm$ 6.1b	8.8 $\pm$ 4.3b	1.2 $\pm$ 0.5b	2.7 $\pm$ 1.6a

[a] Means within columns for each experiment, followed by same letter not significantly different ($P \leq 0.05$, Duncan's multiple-range test).

difference between treatments (Table 3.4, Exp. 2). Release of 3-methyl-3-buten-1-ol at 200 μg per day in combination with terpenes of black spruce did not improve beetle catch (Table 3.5, Exp. 3, 4). A significant increase in male and female response occurred when the release rate of 3-methyl-3-buten-1-ol was increased to 4390 μg per day (Tables 3.6, Exp. 5). Responses by beetles of both sexes in the summer to the male-infested logs were significantly lower than to 3-methyl-3-buten-1-ol at high release rates but significantly higher than to 3-methyl-3-buten-1-ol at low release rates (Table 3.6, Exp.5). Similarly, in spring responses by male and female beetles to male-infested logs were significantly higher than to unbaited traps and uninfested logs, but lower than to 3-methyl-3-buten-1-ol released at 4390 μg per day (Table 3.7, Exp. 6).

Forty-five percent of the black spruce trees baited with 3-methyl-3- buten-1-ol were attacked by *P. rufipennis* compared to 20% of the unbaited trees, but the difference was not significant (χ^2 test, $P > 0.05$). In contrast, significantly more trees surrounding baited trees were attacked than those surrounding unbaited trees. The rate of attack success was low for both control trees (10%) and baited trees (20%). No trees surrounding control trees were successfully attacked but 52.8% of the trees surrounding baited trees were successfully attacked. Analysis of mean attack density on unbaited and baited trees, or those surrounding them, disclosed no evident trend. Similarly, there was no indication that the major terpenes of black spruce significantly enhanced beetle response to baited trees or to trees surrounding them. Very few trees in this experiment were attacked, precluding detection of differences in attack density.

The attraction of *L. intricatus* to traps baited with synthetic 3-methyl-3-buten-1-ol at release rates of 6.00 μg per 24 h and 0.20 mg per 24 h was not significantly different from that to unbaited traps (Table 3.8, Exp. 1, 2). In Exp. 4, but not in Exp. 1-3 or 5, the response by

Table 3.5. Mean catches of *P. rufipennis* to multiple-funnel traps baited with 3-methyl-3-butten-1-ol alone and in combination with terpenes of black spruce, Powderhorn Lake, Newfoundland, 5-30 June (Experiment 3) and 30 June - 13 August (Experiment 4), 1987 (N=5).

	Mean (±SE) number per trap[a]			
	Experiment 3		Experiment 4	
Treatment[b]	Male	Female	Male	Female
Unbaited trap	0.2 ± 0.2a	0.6 ± 0.4a	0a	0.2 ± 0.2a
Terpene mixture	0.2 ± 0.2a	0.6 ± 0.4a	0.2 ± 0.2a	0.2 ± 0.2a
Mb, C	1.8 ± 1.2ab	2.0 ± 1.0a	0.4 ± 0.2a	1.0 ± 0.3a
Mb, BA	9.8 ± 4.5b	5.4 ± 1.6a	0.2 ± 0.2a	0.8 ± 0.4a
Mb, M	16.0 ± 6.8b	10.2 ± 4.8a	0.8 ± 0.6a	1.0 ± 0.3a
Mb, αP	20.4 ± 10.2b	12.2 ± 5.7a	5.0 ± 3.1a	7.4 ± 4.6a
Mb	28.4 ± 17.5b	14.8 ± 9.3a	1.6 ± 1.4a	3.8 ± 3.1a
Mb, βP	29.2 ± 15.2b	17.8 ± 11.2a	0.2 ± 0.2a	1.0 ± 0.6a

[a] Means within colums for each experiment, followed by same letter not significantly different ($P \leq 0.05$, Duncan's multiple-range test).

[b] Abbreviations and release rates for terpenes as in table 3.1. Mb released at 200 μg/day.

Table 3.6. Mean catches of *P. rufipennis* to multiple-funnel traps baited with synthetic 3-methyl-3-butten-1-ol (Mb), to male infested logs and unbaited traps, Crooked Bog, Newfoundland, 30 June - 13 August, (Experiment 5), 1987 (N=6).

Treatment	Release rate (μg/24 hr)	Mean ($\pm$SE) number per trap[a]	
		Males	Females
Unbaited trap		0a	0a
Mb	200	0a	0a
Mb	4390	322.5 $\pm$ 94.7c	435.7 $\pm$ 121.1c
Log + 50 males		12.2 $\pm$ 2.6b	13.7 $\pm$ 3.7b

[a] Means within columns for each experiment, followed by same letter not significantly different ($P \leq 0.05$, Duncan's multiple-range test).

Table 3.7. Mean catches of *P. rufipennis* to multiple-funnel traps baited with synthetic 3-methyl-3-butten-1-ol (Mb), uninfested host, and male infested logs, Crooked Bog, Newfoundland, 27 May - 4 July (Experiment 6), 1988 (N=5).

Treatment	Release rate (μg/24 hr)	Mean ($\pm$SE) number per trap[a]	
		Males	Females
Unbaited trap		0.8 $\pm$ 0.4a	1.2 $\pm$ 0.1a
Infested log		0.4 $\pm$ 0.1a	0.6 $\pm$ 0.2a
Mb	4390	685.6 $\pm$ 174.5c	879.2 $\pm$ 178.4c
Log + 50 males		34.4 $\pm$ 9.2b	38.6 $\pm$ 12.5b

[a] Means within columns for each experiment, followed by same letter not significantly different ($P \leq 0.05$, Duncan's multiple-range test).

Table 3.8. Catches of *Lasconotus intricatus* to multiple-funnel traps baited with the aggregation pheromone of *P. rufipennis*, 5-8 km north of Badger, Nfld. 1987-88.

Exp.	N	Date	Stimulus[a]	Number per trap[b] (Mean ± SE)
1	10	5-30 June	Unbaited trap	0.3 ± 0.1a
		1987	Mb (6.00 μg per 24 h)	0.5 ± 0.4a
			Mb (0.20 mg per 24 h)	2.6 ± 1.7a
2	10	1 July -	Unbaited trap	3.5 ± 2.4a
		15 August	Mb (6.00 μg per 24 h)	11.6 ± 7.6a
		1987	Mb (0.20 mg per 24 h)	3.0 ± 1.2a
3	5	5-30 June	Unbaited trap	0.4 ± 0.2a
		1987	Terpene mixture	0.4 ± 0.2a
			Mb (0.20 mg per 24 h), Ba (0.10 mg per 24 h)	2.1 ± 1.2a
			Mb (0.20 mg per 24 h), βP (0.10 mg per 24 h)	6.2 ± 5.0a
			Mb (0.20 mg per 24 h), C (0.15 mg per 24 h)	0.8 ± 0.4a
			Mb (0.20 mg per 24 h), M (0.30 mg per 24 h)	3.8 ± 2.6a
			Mb (0.20 mg per 24 h), αP (0.10 mg per 24 h)	1.6 ± 0.4a
			Mb (0.20 mg per 24 h)	1.2 ± 0.4a

Table 3.8. cont'd.

Exp.	N	Date	Stimulus[a]	Number per trap[b] (Mean ± SE)
4	5	30 June -	Unbaited trap	0.8 ± 0.4a
		13 August	Terpene mixture	1.0 ± 0.5a
		1987	Mb (0.20 mg per 24 h), Ba (0.10 mg per 24 h)	1.4 ± 1.2a
			Mb (0.20 mg per 24 h), βP (0.10 mg per 24 h)	2.0 ± 1.1a
			Mb (0.20 mg per 24 h), C (0.15 mg per 24 h)	12.8 ± 8.9ab
			Mb (0.20 mg per 24 h), M (0.30 mg per 24 h)	30.8 ± 27.8ab
			Mb (0.20 mg per 24 h), αP (0.10 mg per 24 h)	81.8 ± 78.3ab
			Mb (0.20 mg per 24 h)	209.2 ± 99.0b
5	6	30 June -	Unbaited trap	0 ± 0a
		13 August	Mb (0.20 mg per 24 h)	0.2 ± 0.2a
		1987	Mb (4.39 mg per 24 h)	742.8 ± 364.4c
			Log + 50 males	139.3 ± 109.0b

Table 3.8.

Exp.	N	Date	Stimulus[a]	Number per trap[b] (Mean ± SE)
6	5	27 May -	Unbaited trap	0.4 ± 0.2a
		4 July	Blank log	0.2 ± 0.2a
		1988	Mb (4.39 mg per 24 h)	560.0 ± 137.1c
			Log + 50 males	33.6 ± 17.0b

[a] Abbreviations, source, and chemical purity for terpenes are: α-pinene, αP, Aldrich Chem. Co. Milwaukee, Wis, ≥ 99%; β-pinene, βP, Aldrich, 98%; bornyl acetate, Ba, Aldrich, 97%; 3-carene, C, Albany Int'l Co., St. Louis, MO, 95%; myrcene, M, Sigma Chem. Co., St. Louis, MO, ≥ 98%. Abbreviation for 3-methyl-3-buten-1-ol, Mb.

[b] Means followed by same letter not significantly different, Duncan's Multiple Range Test, $P \leq 0.05$.

L. intricatus to 3-methyl-3-buten-1-ol released at 0.20 mg per 24 h was significant. In contrast, traps baited with fresh logs infested with male *P. rufipennis* (Table 3.8, Exp. 5, 6) caught significantly greater numbers of *L. intricatus* than unbaited traps, or traps baited with uninfested, control logs. When 3-methyl-3-buten-1-ol was released at 4.39 mg per 24 h, large catches of *L. intricatus* occurred. The terpenes bornyl acetate and beta-pinene significantly reduced the response of *L. intricatus* to 3-methyl-3-buten-1-ol during the beetle's summer flight in 1987 and 3-carene, myrcene, and alpha-pinene appeared to have a partial inhibitory effect (Table 3.8, Exp. 4). The ratios of captured *L. intricatus* to *P. rufipennis* were 1 : 1.03 (summer 1987) and 1 : 2.75 (spring 1988).

DISCUSSION

My results demonstrate that the isoprene alcohol, 3-methyl-3-buten-1-ol, is produced by male *P. rufipennis* and mediates the host selection process. Furthermore, this secondary attractant is produced by males and is probably released through the frass. Such pheromones are widely reported among scolytids and are considered to be instrumental in aggregating conspecifics to a suitable resource (Shorey 1973; Borden 1977). Exploitation of these chemicals would confer a selective advantage (Alcock 1981) on individual *P. rufipennis* foraging for budworm-defoliated black spruce with low resistance but with acceptable nutritive value.

The differential response of male and female beetles to male-infested logs and male-produced frass is similar to that for other polygamous scolytids including *Dryocoetes confusus* Swaine (Stock and Borden 1983), *Ips paraconfusus* Lanier (Wood 1962; Pitman *et al.* 1965; Borden 1967; Birch *et al.* 1977), *Ips tridens* (Mann) (Moeck *et al.* 1985), and *Ips typographus* (L.) (Tomescu *et al.* 1979; Schlyter and Löfqvist 1986). Sources of variation in response (Tables 3.1, 3.2) could be: the physiological condition of the beetle and duration of exposure to the stimulus (Borden 1967), exercise (Atkins 1969), and environmental conditions including atmospheric pressure, temperature, cloud cover, relative humidity, wind, and precipitation (Coster *et al.* 1978; Lanier and Burns 1978). My data suggest that *P. rufipennis* females have a lower threshold of response than males, particularly in winter when the beetle is in diapause (Hilton 1968).

These findings are consistent with previously reported pheromones for polygynous bark beetles where pioneer males produce and release aggregation pheromones (Wood *et al.* 1966;

Bakke 1975, 1976; Harring and Mori 1977; Francke *et al.* 1977; Stoakley *et al.* 1978; Baader 1989). Although the drop in response to mated males in the field was significant, logs with mated males attracted considerably more beetles than the control logs or the female-infested log. In the laboratory as well, frass from mated beetles tended to remain attractive. Therefore, while tending its first arriving female the polygamous male appears to reduce pheromone production rather than to terminate it. Alternatively, either or both sexes may release an epideictic (spacing) pheromone (Prokopy 1981) which would reach repellent levels when the polygamous males have been joined by their full complement of up to 6 females.

The lack of response to extract stimuli was unexpected. I hypothesize that the strengths of such stimuli were too low, especially given the highly volatile and evanescent characteristics of 3-methyl-3-buten-1-ol. However, such a compound would confer a selective advantage to individuals in boreal habitats where even mid-summer temperatures are often low. The insignificant responses to phloem tissue and to unattacked logs suggest further that *P. rufipennis* probably does not rely exclusively on host odours in detecting and selecting its hosts.

Although there was no direct evidence for more than one pheromone, the high release rate of 3-methyl-3-buten-1-ol required to elicit attraction in the field suggests other pheromones may be necessary to effect a maximum response. Knowledge that insects generally use multicomponent pheromones (Silverstein and Young 1976) and recent advances on the pheromone system of the six-spined spruce bark beetle, *Pityogenes chalcographus* (L.), (Byers *et al.* 1989, 1990) support the existence of additional pheromones. The presence of 3-methyl-3-buten-1-ol as a pheromone in *P. rufipennis* is of ecological interest. Isoprene alcohols have been reported in only two bark beetle species of the Scolytinae: 2-methyl-3-buten-2-ol in males of the spruce bark beetle, *Ips*

typographus L. (Bakke *et al.* 1977), and 3-methyl-3-buten-1-ol in males of the larch engraver, *Ips cembrae* Heer (Stoakley *et al.* 1978). Like *P. rufipennis*, both European species feed mainly on weakened trees but will attack healthy standing trees during epidemics (Postner 1974). Although phylogenetically different, *P. rufipennis* exploits the same highly volatile methylbutenol as *I. cembrae* to further its individual reproductive success. Use of such a compound may be of selective advantage to individuals in northern habitats where mid-summer temperatures are often low. Dickens (1981) and Birgersson *et al.* (1984) suggested that methylbutenol compounds may be short-range orientation or arrestment substances which act to concentrate pioneer beetles on a resistant host tree. Similarly, Schlyter *et al.* (1987) inferred from field trials that 2-methyl-3-buten-2-ol functions primarily as a landing stimulus for *I. typographus*. We have no definite knowledge as to the effective range of 3-methyl-3-buten-1-ol.

As for other polygynous members of the tribe Polygraphini, *P. rufipennis* appears to have a Eurasian-African origin. It is closely allied to *P. poligraphus* (L.) of Europe and northern Asia, and reached North America in recent geologic time (Wood 1982). Both species have similar ecological habits but are geographically isolated. However, the pheromone system of *P. rufipennis* shows no apparent relationship to that of the closely related European species, *P. poligraphus* (L.), that also attacks spruce. Male *P. poligraphus* produce three sex specific compounds, *trans*-4-thujanol, *cis*-4-thujanol and terpinen-4-ol (Francke and Vité 1983). *P. rufipennis* was previously treated as a synonym of *P. poligraphus* (Schedl 1957); however my findings support Wood (1982) who separated the two species on the basis of statistical differences in pronotal punctures and tubercles at the bases of the elytra.

The presence of 3-methyl-3-buten-1-ol in male frass is consistent with both male and

female positive responses to male-produced frass in laboratory bioassays. The absence of pheromone in the hindgut is surprising. It is possible that another biosynthetic site may be responsible for its production. For example, (E,Z)-MD, a major component of the pheromone of *Pityogenes chalcographus*, is found predominantly in the head and thorax of the male beetle. Furthermore, contents of hindguts and the composition of the released pheromone are known to differ (Peacock *et al.* 1975, Silk et al. 1982). For these reasons it cannot be assumed that a released pheromone will always be detected in the hindgut.

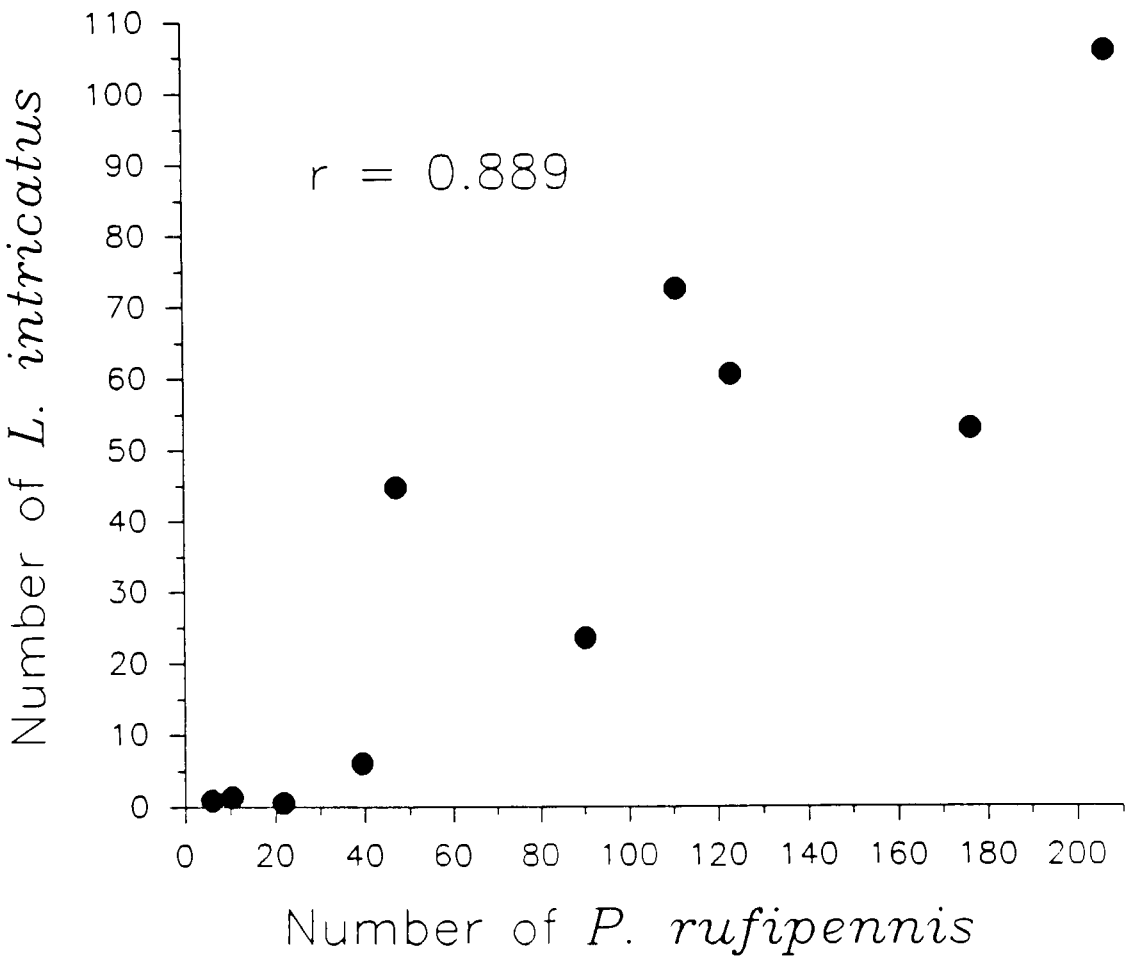
The magnitude of the response to traps releasing 3-methyl-3-buten-1-ol at 4390 μg per day suggests that the 200 μg per day release rate used in tree-baiting experiments may not have been optimal, and that a stronger response to baited trees would occur with higher release rates. It is also possible, as hypothesized above, that an additional pheromone may be required to effect an optimal response.

Although host terpenes often enhance response to beetle-produced pheromones (Hughes *et al* 1976; Lanier *et al.* 1977) no such enhancement was evident for *P. rufipennis*, and 3-carene even appeared to inhibit aggregation (Table 3.5, Exp. 3). The low response to fresh uninfested logs suggests that *P. rufipennis* does not rely exclusively on major host terpenes in searching for and exploiting quality resources. However, it is possible that minor host constituents may be involved in *P. rufipennis* host selection. Tømmerås and Mustaparta (1987) reported that minor host constituents stimulated single olfactory receptor cells of *I. typographus* and probably reveal qualitative differences between individual host trees. Moreover, computer-simulated searching strategies (Gries *et al.* 1989) suggested that random search alone is unlikely to maintain an *I. typographus* population.

Virtually nothing is known about the biogenesis of 3-methyl-3-buten-1-ol in *P. rufipennis*. Production probably occurs from acetate via the mevalonic acid pathway. Hackstein and Vité (1978) and Renwick and Dickens (1979) suggested that in *I. typographus* and *I. cembrae* the compound occurs *de novo* and is under hormonal control.

Several colydiids are listed as bark beetle associates (Thatcher 1960; Overgaard 1968; Moser et *al.* 1971; Rohlfs and Hyche 1981), but the biology of the Colydiidae has received scant attention. Various and contradictory feeding habits have been reported but most reports indicate some predatory behavior (Rohlfs and Hyche 1981; Stevens *et al.* 1982). *Lasconotus subcostulatus* Kraus is known to prey on *Ips paraconfusus* (LeConte) larvae and is considered an important mortality agent in bark beetle populations (Hackwell 1973). In field investigations and laboratory predation trials, Rolfs and Hyche (1983) demonstrated that *Lasconotus pusillus* LeConte consumed eggs, larvae, and pupae of bark beetles. Furthermore, Dixon and Payne (1980) reported attraction of *L. pusillus* to traps baited with frontalin and loblolly pine turpentine, suggesting a kairomonal response of a predator to host semiochemicals. Similarly, *Lasconotus complex* LeConte is attracted to the pheromone, ipsdienol, and a kairomone, β-phellandrene, used by the pine engraver, *I. pini* (Say) in stands of lodgepole pine in British Columbia (Miller and Borden 1990). My results demonstrate clearly that *L. intricatus* responded to the aggregation pheromone of *P. rufipennis* and we hypothesize a predator-prey relationship between these two species. Such a strategy by *L. intricatus* would minimize search time and distance and increase foraging efficiency. Moreover, analysis of beetle catches in summer 1987 and spring 1988 (Fig. 3.4) disclosed a high degree of temporal coincidence between the two species, except for the 1st week in 1987 in which the numbers of *L. intricatus* far exceeded

Fig. 3.4. Relationship between numbers of *P. rufipennis* and *L. intricatus* captured in trapping experiments in 1987 and 1988, 5-8 km north of Badger, Nfld. Outlier of 277 *L. intricatus* and 63 *P. rufipennis* captured during first week of July, 1987 deleted from the correlation analysis. Each point represents the number of beetles captured per trap per day for 5 collection periods in 1987 and 5 collection periods in 1988.


r = 0.889
Number of L. intricatus
Number of P. rufipennis
0
10
20
30
40
50
60
70
80
90
100
110
0
20
40
60
80
100
120
140
160
180
200

those of *P. rufipennis*. This close relationship suggests *L. intricatus* may track *P. rufipennis* during the flight season. Similar findings have been reported by Rohlfs and Hyche (1981) who reported direct correlations in flight patterns between the colydiid *L. pusillus* and *Ips* adults in Alabama. Combination of 3-methyl-3-buten-1-ol released at 0.20 mg per day with host terpenes released at rates indicated in Table 3.3 disclosed that terpenes inhibited attraction of *L. intricatus* in summer. It is probable that *L. intricatus* exploits information on the quantity or quality of plant constituents to determine that a host tree is too vigorous and thus contains few viable *P. rufipennis* on which to prey.

The level of the kairomonal response observed in black spruce stands in Newfoundland suggests that *L. intricatus* may have an important impact on beetle populations. Accordingly, management practices designed to reduce losses in black spruce stands should consider the potential impact on *L. intricatus* populations.

SUMMARY

The four-eyed spruce bark beetle, *P. rufipennis*, is a phloeophagous bark beetle restricted to Abietineae hosts in northern and mountainous areas of North America. Until recently, the bionomics and ecology of *P. rufipennis* in black spruce stands were largely unknown. However, projected wood shortages in Newfoundland have focused attention on the bark beetle and its role in contributing to black spruce mortality.

My findings disclosed that colonization on felled and standing trees by *P. rufipennis* followed the typical host selection sequence of scolytids, notably, emergence, dispersal, selection and establishment. All brood stages except eggs overwintered in black spruce, however, the majority of overwintering stadia consisted of larvae and callow adults. Adult mortality was significant during winter, especially in standing severed and felled trees. *P. rufipennis* has 1 generation and produces a Spring and Summer brood in Newfoundland and the total development time from egg to callow adult was estimated to be approximately 60 days. The time interval between overwintering brood adult emergence and parent adult re-emergence is 4 weeks. Peaks in flight activity corresponded strongly to patterns of spring emergence and re-emergence. There was a greater tendency for attack and nuptial chamber construction to be initiated by males than by females. Following copulation, males stay with the females and exhibit guarding behaviour by occupying the entrance hole. Attack density on felled and standing severed trees varied little but was nearly twice that found on standing unsevered trees. Significantly higher numbers of galleries were established on trees felled in shade than in full sunlight.

Two scolytids closely associated with *P. rufipennis* on black spruce included *D. Affaber*

Two scolytids closely associated with *P. rufipennis* on black spruce included *D. affaber* and *C. borealis*. Trees attacked by the four-eyed spruce beetle were often invaded by both species after *P. rufipennis* became established. Other associates included *Medetera* sp. (Diptera: Dolichopodiidae), the cylindrical bark beetle, *L. intricatus* (Coleoptera: Colydiidae), and *C. piceaperda*, a fungus that was associated with all phases of the colonization sequence of *P. rufipennis*.

Populations of *P. rufipennis* increased rapidly when the availability of breeding material increased. Brood productivity was prolific in damaged and recently killed black spruce, and attack on live trees occurred principally as a result of increased populations on dead and weakened material. Significant relationships between *P. rufipennis* attack and cumulative budworm damage in mature stands of black spruce were evident in both time and space. The highest incidence of beetle attack occurred in severely damaged stands in 1983 with 32.6% of the trees successfully attacked. In 1984 and 1985 the proportion of newly attacked trees in severely damaged stands decreased to 16.6 and 6.0%, respectively. In stands of moderate budworm damage the proportion of trees attacked by *P. rufipennis* decreased from 13.5% in 1983 to 6.7% in 1984 to 5.1% in 1985. The proportion of trees attacked by the beetle in lightly damaged stands varied little over time with 2.1, 2.9 and 2.2% of the trees attacked in 1983, 1984 and 1985, respectively. A significant trend between attacked trees and time was evident in moderate and severe damage, coupled with a significant dependency of beetle attack on stand damage level. The results of baited-tree experiments confirmed *a priori* expectations of greater attack success on trees in the higher damage classes.

Semiochemical-based communication in *P. rufipennis* was demonstrated in the laboratory

and in the field and 3-methyl-3-buten-1-ol was identified as the pheromone responsible for attraction. The aggregation pheromone was evident in the response of *P. rufipennis* to male-produced frass and male-infested logs and its bioactivity was demonstrated in field-trapping and tree-baiting experiments. There was no indication that the major terpenes of black spruce significantly enhanced beetle response to baited traps or trees. The cylindrical bark beetle, *L. intricatus*, responded to the aggregation pheromone of *P. rufipennis*. The high degree of temporal coincidence between the two species supports the hypothesis that *L. intricatus* is a predator of *P. rufipennis*.

The foregoing findings allow for a number of conclusions that have important implications for the management of secondary pests of black spruce in Newfoundland and elsewhere:

1. Increased population levels of *P. rufipennis* were symptomatic of a severely damaged spruce forest. Consequently, pest management systems for defoliators such as the spruce budworm should include components that address the role of host predisposition to secondary insect attack.

2. I conclude that the optimum management strategy against *P. rufipennis* is to reduce the susceptibility and vulnerability of fir-spruce forests by maintaining stand vigor, because outbreaks of *P. rufipennis* requires a means of predisposition to overcome tree resistance.

3. Long-term management and policy responses to outbreaks of *P. rufipennis* should be made in the context of pest management systems designed for spruce budworm, which should incorporate knowledge of the effects of *P. rufipennis* on black spruce mortality, on salvage schedules and on black spruce successional patterns that originate following fire.

4. Knowledge of the colonization sequence of *P. rufipennis*, including estimates of overwintering

mortality, attack density on felled and standing trees, and information describing harem dynamics, provide a basis to construct within-tree estimates of *P. rufipennis* populations and facilitate an understanding of how the beetle utilizes its black spruce host.

5. The propensity of *P. rufipennis* for weakened and dead trees, especially in shade, implies that as forest management intensifies, sanitation and salvage practices should be considered as prescriptions to minimize the risk of beetle outbreaks.

6. Immediate responses to *P. rufipennis* should focus on early detection and monitoring of populations, taking into account that semiochemical-based communication in *P. rufipennis* has been elucidated; this knowledge provides a reliable means of early detection. Also, because the flight period of *P. rufipennis* is established for Newfoundland, there is potential to mass trap or to disrupt mating.

7. The high degree of temporal coincidence between *L. intricatus* and *P. rufipennis* during the flight season implies that *L. intricatus* may be an important predator of the four-eyed spruce bark beetle. Management practices designed to reduce losses in black spruce stands should consider the potential impact on *L. intricatus*.

8. Several predators including *Medetera* spp. and clerid larvae probably help maintain *P. rufipennis* populations below the epidemic threshold level and therefore offer potential as biocontrol agents.

9. The fungus, *C. piceaperda* was associated with *P. rufipennis* during all phases of the colonization sequence. Future studies should investigate whether the fungus is a pathogen of black spruce.

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