

ECOLOGY OF THE EASTERN LARCH BEETLE,
(DENDROCTONUS SIMPLEX) LECONTE
(COLEOPTERA: SCOLYTIDAE).
IN NEWFOUNDLAND

CENTRE FOR NEWFOUNDLAND STUDIES

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DAVID W. LANGOR

Ecology of the Eastern Larch Beetle, *Dendroctonus simplex*
LeConte (Coleoptera: Scolytidae), in Newfoundland

by

© David William Langor, B.Sc (Honours)

A thesis submitted to the School of Graduate
Studies in partial fulfillment of the
requirements for the degree of
Master of Science

Department of Biology
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Abstract

The ecology of the eastern larch beetle, *Dendroctonus simplex* LeConte, was studied in Newfoundland. Overwintered beetles emerged in May. One generation and two broods were produced in both 1983 and 1984. Females initiated attacks and males arrived up to two days later. One to four pairs of beetles used each entrance hole but each pair constructed a different gallery.

Egg galleries were vertical, slightly sinuous and averaged 41 cm in length. Females laid zero to four eggs per niche averaging 1.4. The average number of eggs per gallery and per cm of gallery was 39 and 1.0, respectively. Mean brood density was 49 individuals per 100 cm².

About 90% of all parents reemerged and a small proportion of them attacked a second group of trees and produced a second brood. Galleries in second brood trees averaged 26 cm in length and 27 eggs per gallery. Mean brood density averaged 23 individuals per 100 cm². Following brood production 61% of parents reemerged and likely died.

Development from egg to adult averaged 60 and 70 days for first and second broods, respectively.

During egg gallery construction and oviposition *D. simplex* flight muscles degenerated. Flight muscles were completely regenerated in only 17% of 96 reemerged beetles in 1984. No reemerged beetles were observed to fly.

Emergence, host attack and reemergence occurred between 10:30 and 17:00 hours and at temperatures of 4 °C or higher. Peaks of attack, which reflects flight peaks, occurred at temperatures of 10 °C or higher.

Only adults overwintered. Freezing temperatures caused high mortality among immature stages of the second brood.

Thirty-four percent of new brood adults emerged in the fall and reentered galleries at the base of trees for hibernation.

The fourth larval instar had the highest mortality, at 29.2%, and pupae the lowest, at 7.6%. Total mortality was 79% and 82% for first and second broods, respectively. Pathogens caused the largest proportion of mortality among eggs, second instar larvae and pupae, resinosis among first instar larvae and parasitoids among third and fourth instar larvae. Overwintering mortality was 7.8%.

Fifty-two species of insects, spiders, mites and nematodes were associated with *D. simplex* in 1983.

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1. INTRODUCTION

The family Scolytidae is comprised of beetles that are subcortical feeders - generally inhabiting the outer bark, phloem or xylem of trees. The phloem-feeding genus *Dendroctonus* contains 18 species, 13 of which are found in North America (Wood 1982). Several of these 13 species are among the most destructive of forest insects destroying in excess of 12.5 million m³ (5 billion board feet) of standing merchantable timber annually in North America (Bright 1976). Such severe losses have focused the attention of entomologists, foresters and the general public on this genus. Consequently most of the species, especially the more destructive ones, have been frequently studied. However, some of the less destructive species of *Dendroctonus* have received comparatively little attention and basic aspects of their biology and population dynamics have not been investigated. One such species is the eastern larch beetle, *Dendroctonus simplex* LeConte.

LeConte (1868) described *D. simplex* from adults collected on tamarack in Canada and the immature stages were described by Thomas (1965). The eastern larch beetle occurs across North America from Newfoundland and the northeastern states to British Columbia and Alaska. Its range is limited by the natural range of eastern larch or tamarack, *Larix laricina* (Du Roi) K.Koch, its principal host (Wood 1982). It will also attack exotic species of *Larix* planted within its

range, such as Siberian larch, *L. siberica* Ledebour (McGuffin and Barker 1946) and European larch, *L. decidua* Miller (Sippel et al. 1961). It was also reported on red spruce (Baker 1972) but this record is questionable.

Since the first recorded *D. simplex* infestation (probably in Ontario) by Harrington (1884) there have been many reports of localized larch beetle infestations in various parts of Canada (Annual Reports of the Forest Insect and Disease Survey - 1939, 1946, 1960 to 1963, 1965, and 1967 to 1969; Drouin and Turnock 1967; Grisdale and MacLeod 1962), Alaska (Baker et al. 1975) and the northeastern states (Schwarz 1888).

The first widespread outbreak of *D. simplex* began about 1977 and has killed large numbers of larch in eastern Canada (Annual Reports of the Forest Insect and Disease Survey - 1977 to 1983) and the northeastern states (Lanier 1981; 1984 - personal communication).

Relatively little is known about the biology of the larch beetle. General seasonal life history and egg gallery patterns were first described by Hopkins (1909) who reported that weakened, dying or felled tamarack were attacked by emerging beetles in May and June. Only one generation was produced per year and the progeny overwintered in the adult stage. Swaine (1911) reported two larch beetle generations in one year in Quebec although his 'second generation' may have been a second brood established by parents reemerged

from first brood trees. Egg gallery formation and structure as well as oviposition were also described by Swaine (1911; 1918). Larch beetle egg galleries were described as vertical and sinuous containing turning niches, ventilation holes and egg niches in which one to four eggs were laid. Simpson (1929) studied the life history of *D. simplex* in caged larch billets in New Brunswick. He reported that parent beetles established only one brood/year in 1925 and 1926, three in 1927 and two in 1928. All progeny overwintered as adults except for the third brood of 1927 which overwintered as larvae. These died in the spring before reaching maturity. Only one generation occurred per year. Prebble (1933) reported an average developmental time, from egg to adult, of 46 days for *D. simplex* in New Brunswick. He also used head capsule widths to determine that there were four larval instars.

Recorded predators of *D. simplex* are the clerid beetle, *Phyllobaenus dislocatus* Say, (Blackman and Stage 1918) and larvae of the dolichopodid fly, *Medetera aldrichii* Wheeler, (Furniss 1976). Recorded parasitoids of larch beetle larvae are the braconids, *Cosmophorus dendroctoni* Viereck, *Spathius tomici* Ashmead (Bushing 1965) and *Coeloides rufovariegatus* (Provancher) (Mason 1978) and the chalcid, *Heydenia unica* Cook and Davis, (Bushing 1965). Furniss (1976) recorded four species of nematodes that parasitized adults - *Ektaphelenchus obtusus* Massey, *Aphelenchoides* sp., *Nebcephalobus* sp. and *Neoditylenchus* sp. .

An aggregation pheromone of *D. simplex* has not been demonstrated, though it no doubt exists. There are two reports of strong attraction of females to Seudenol (3 - methyl - 2 - cyclohexen - 1 - ol), an aggregation pheromone of *Dendroctonus pseudotsugae* Hopkins (Baker et al. 1977; Werner et al. 1981).

Most Scolytidae attack and kill physiologically weak trees. Such trees are usually few and widely scattered (Raffa and Berryman 1980) keeping beetle populations at relatively constant and low levels. However, a sudden abundance of susceptible trees or recently cut logs enables species of some bark beetle genera, including *Dendroctonus*, to reach population levels of outbreak proportions (Berryman 1973, 1982). These species may then successfully attack and kill apparently healthy mature and overmature trees (Berryman 1982; Rudinsky 1962). Drought and defoliation are two forms of stress that commonly weaken trees and make them susceptible to bark beetle attack (Dewey et al. 1974; Miller and Keen 1960; Wickman 1978; Wright et al. 1984).

The spruce budworm, *Choristoneura fumiferana* (Clem.), outbreak in Newfoundland in the mid to late 1970's was at times so severe that larch trees were also severely defoliated, even though the spruce is not usually seriously damaged by the spruce budworm (Otvos and Moody 1978). Cumulative effects of two to three years of defoliation included extensive bud mortality and, thereby, reduced

foliage on trees (Raske 1984 - personal communication). This presumably reduced tree vigor and wood production but caused little mortality. Weakening of larch trees by budworm defoliation from 1974 to 1977 in western Newfoundland and from 1976 to 1978 in central and eastern Newfoundland may have predisposed them to attack by the larch beetle enabling beetle populations to reach outbreak levels by 1976 (Raske *et al.* 1978). During the following eight years this larch beetle outbreak caused much mortality of larch all across Newfoundland with the severest infestation occurring in the central region. Each year from 1978 to 1984 groups of up to sixty trees were attacked and killed and others injured at many locations across the island. Although larch beetle infestations in central Newfoundland are reported to be declining (Hudak *et al.* 1983), abrupt collapse of the outbreak did not occur in 1984.

Coincident outbreaks of *D. simplex* with that in Newfoundland were also reported in Nova Scotia and Prince Edward Island (Magasi 1977), southern New Brunswick (Magasi 1979), southern Quebec (Lachance *et al.* 1981) and the northeastern states of the United States (Lanier 1981; Teillon *et al.* 1980). The larch beetle outbreak in eastern Canada has been associated with the larch sawfly, *Pristiphora erichsonii* (Htg.), which likely predisposed trees to beetle attack in the maritime provinces (Magasi 1977) and in Quebec (Lachance *et al.* 1982). It is thought that some predisposing agent fostered the larch beetle

outbreak in parts of the northeastern United States but the nature of this agent is not known (Lanier 1984 - personal communication; Snowden 1984 - personal communication).

Although large populations of *D. simplex* have been associated with larch decline in Vermont and parts of New Hampshire in recent years (Snowden 1984 - personal communication; Teillon *et al.* 1980; 1981), there is some uncertainty as to whether the decline was caused by *D.*

simplex or some other factor (Bergdahl 1983; Snowden 1984 - personal communication). Bergdahl (1983) has isolated the pinewood nematode, *Bursaphelenchus xylophilus* (Steiner and Buhrer), from newly killed tamarack in Vermont. This species might be responsible for the extensive larch mortality that has occurred in Vermont and possibly other regions of the northeastern states and southern Canada too.

Approximately 50% of the trees attacked and killed by the larch beetle during the spring and summer are detectable in late summer and early fall because their needles turn yellow before those of healthy larch trees (Raske *et al.* 1978). On a yearly basis damage by the larch beetle may not seem great, however, cumulative mortality over several years may be economically and silviculturally very important. A survey in Newfoundland in 1981 estimated the volume of larch killed by the larch beetle at 18,500 m³ (Hudak *et al.* 1982). Many other trees have been killed since 1981. Surveys in New Brunswick, Nova Scotia and Prince Edward Island in 1981 reported larch mortality by the eastern larch beetle of 24%,

64% and 13% representing 314,000 m³, 972,000 m³ and 11,600 m³ of dead larch in each province, respectively (Magasi 1982).

Although larch has relatively little current economic importance, some believe it may become more valuable in the future because of its high biomass per unit area and its high energy value per unit of weight (Hall 1984). Widespread mortality of larch by *D. simplex* has caused some concern as to the feasibility of growing larch for wood production. It has also helped us realize how little we know about the bionomics of an important forest pest, the eastern larch beetle. Hence, this study was initiated to investigate the basic biology of *D. simplex* (i.e. seasonal life history, population dynamics, fecundity, brood development and mortality) in Newfoundland. Such information will be of value to the Newfoundland forest industry.

2. MATERIALS AND METHODS

2.1 GENERAL FIELD PROCEDURES

2.1.1 Site and tree characteristics

The study site was located approximately 8 km west of St. John's near the junction of Manuals River and the Trans Canada Highway. Forest composition at the site was mainly black spruce, *Picea mariana* (Mill.), and balsam fir, *Abies balsamea* (L.), with a large number of eastern larch scattered in the forest and bordering the river and bogs. The larch beetle had been active in the area for four to five years and had killed 75 to 100 trees that may have been weakened by mechanical injury, flooding or defoliation by the spruce budworm. In October 1982, approximately twenty trees at the study site contained overwintering brood adults which could attack uninfested trees in the area in 1984.

Five unattacked trees were girdled each in early April and mid-June, approximately one month before expected first and second attacks, respectively, to weaken and hence predispose them to attack by the larch beetle. The following parameters were measured for each tree used in the study: total height, height to top of infested bole, diameter and phloem thickness at each sample height and tree diameter at breast height (DBH).

Weather data (daily mean temperature, precipitation) for the study period was obtained from meteorological

services at Torbay Airport approximately 20 km from the study site.

2.1.2 Sampling techniques

Field populations of all life stages occurring beneath the bark of host trees were sampled by removing 100 cm² bark disks with a circular bark punch (Fig. 1) modified from the design outlined by Furniss (1962). The punch consisted of a circular cutting head of 11.3 cm inside diameter (=100 cm²) attached to a 12 cm long handle, both constructed from solid steel and kiln hardened using standard techniques. Hammer blows were used to drive the cutting head of the punch through the bark into the wood severing the phloem. While sampling, a 30 cm x 40 cm rectangular cloth apron was attached to the tree below the punch to catch specimens that fell from the bark samples. The apron was reinforced with stiff wire around three sides, bent to form a lip extending 20 to 25 cm from the tree trunk (Fig. 2). The remaining side was hemmed with twine to fasten the apron to the tree. Specimens caught in the apron were added to other specimens from the sample.

Adult emergence and reemergence was sampled with emergence traps (Fig. 3) similar to those described by McClelland *et al.* (1978). Each trap consisted of three parts: base plate, net and collection unit. The base plate consisted of a 15 cm x 15 cm sheet of 28-gauge galvanized metal with a 11.3 cm diameter hole (=100 cm²) cut in the

Figure 1. Bark punch used to cut 100 cm² circular bark samples. A/ cutting head (11.3 cm inside diameter), B. handle.

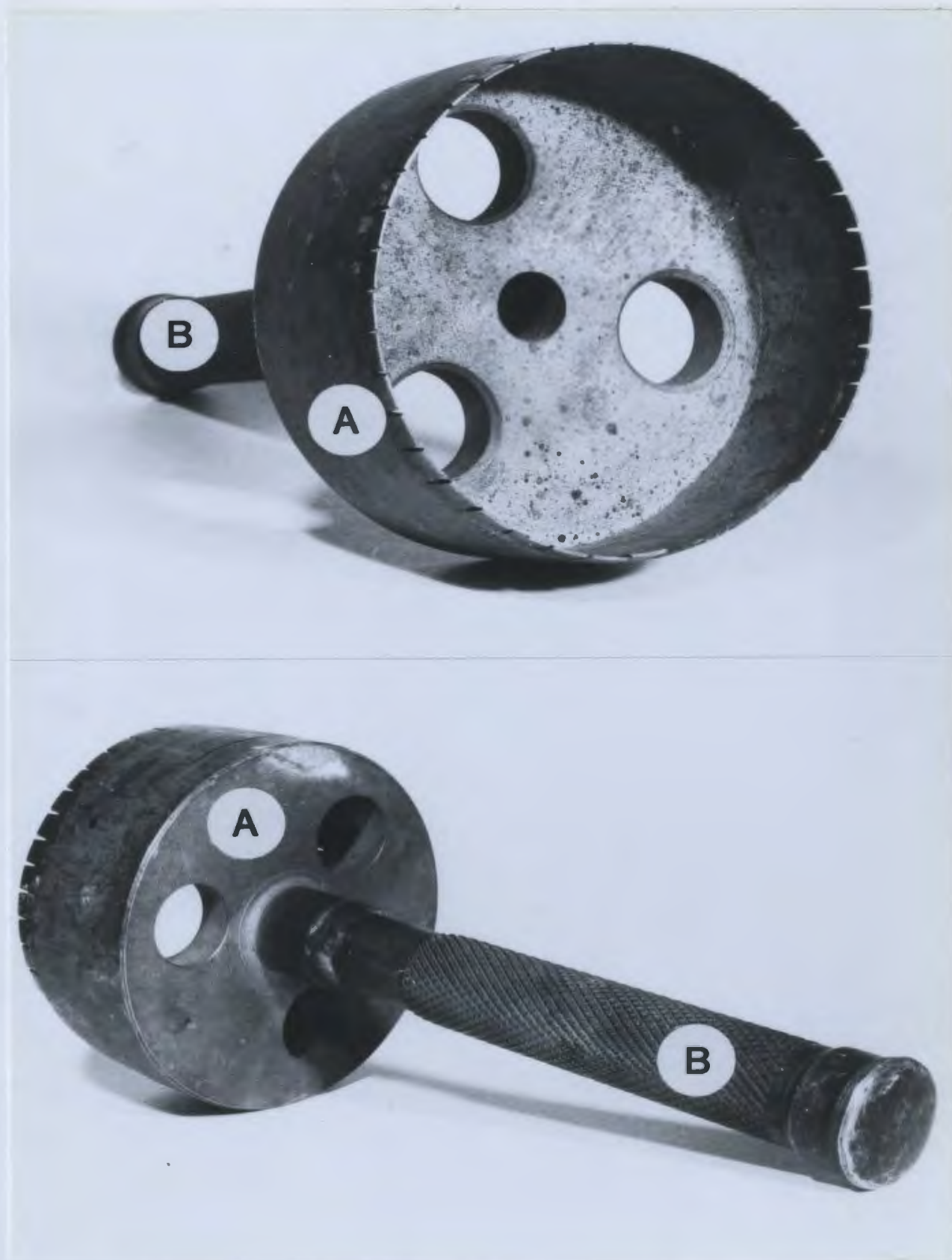




Figure 2. Cloth apron used to catch bark beetle specimens that fell from bark samples removed from trees.

Figure 3. Bark beetle emergence trap for sampling a
100 cm² circular bark area. A. base plate (15 X 15
cm), B. net, C. funnel, D. collecting vial.



center. Eight small holes were drilled at equal intervals around the perimeter of the plate to accomodate screws. Foam padding (carpet underlay) was cemented to the back of the metal plate to ensure snug fit of the trap to the bark surface. The trap net was a 20 cm length of nylon stocking stapled to a 15 cm x 15 cm piece of waterproofed cardboard (300 weight illustration board) and cemented to the metal base plate. The other end of the net was glued around the mouth of a 10 cm diameter plastic funnel. A collecting vial cap with a hole drilled through its center was glued to the funnel shaft and a collecting vial containing 70% ethanol attached. Traps were fastened to trees with screws and washers. Vials were anchored with elastic bands to nails embedded in the tree boles.

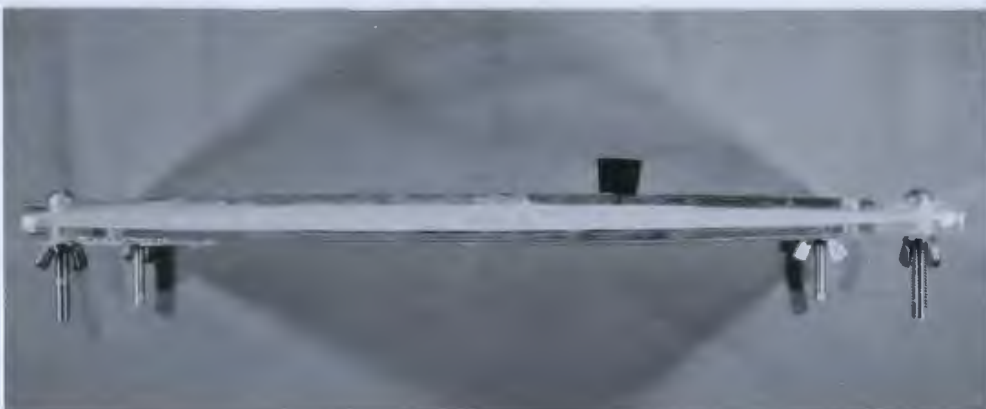
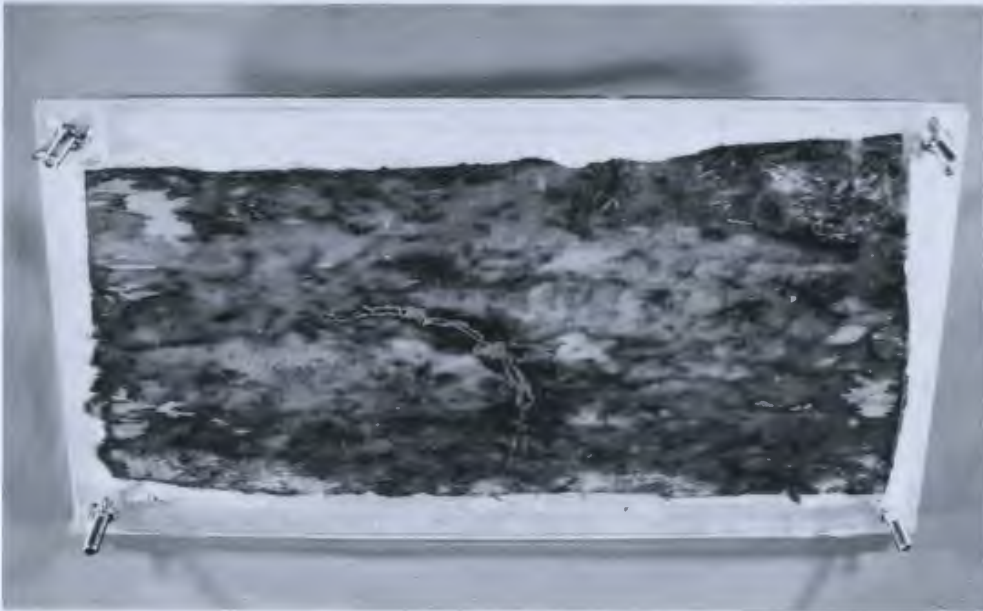
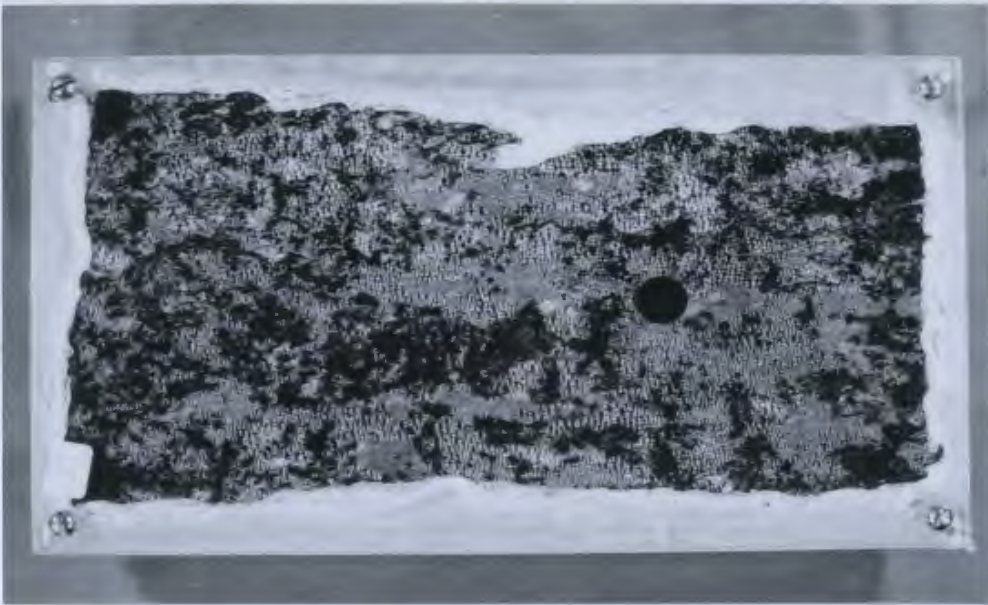
2.2 LABORATORY PROCEDURES

2.2.1 Rearing chamber studies

Mating and oviposition behaviour, gallery construction as well as brood development and behaviour were observed by use of 'bark-sandwich' rearing chambers (Fig. 4) similar to that described by Schmitz (1972). Each chamber consisted of a 15 cm x 30 cm piece of bark and phloem sandwiched between a pair of rectangular, transparent sheets of plexiglass, 20 cm x 35 cm. A 1.5 cm diameter hole, through which beetles were introduced to the bark surface, was drilled through the centre of one sheet. The unit was fastened together by

Figure 4. Bark-sandwich rearing chamber (20 X 30 cm).

Top. top view, Center. bottom view, Bottom. side
view.



screws in each corner and the edges were sealed with paraffin to retard dessication.

A female beetle was introduced through the central hole which was then plugged with a rubber stopper. After successful attack by the female a male was added. Two chambers were stored vertically at each of three temperatures: 12 °C, 18 °C and 24 °C, and observed daily. In addition to observations of behaviour the following data were recorded: gallery elongation rates at each temperature, the developmental time of each instar of each individual and the number of larval instars for each individual. The developmental time of each instar and total developmental time from egg to adult was averaged for all individuals reared at the same temperature.

2.2.2 Larch bolt studies

Four pairs of beetles were introduced into each of seven larch bolts, 50 cm long and 20 to 25 cm in diameter, two days after they were cut from living trees. The ends of the bolts were sealed with paraffin to slow dessication. Holes of 2 to 3 mm diameter were drilled at a 45° angle approximately 5 mm into the bark at equal intervals around the perimeter of each bolt, 8 to 10 cm from the base. A female beetle was introduced into each hole which was then covered with a gelatin capsule secured to the bolt with an insect pin. This prevented escape of beetles yet allowed frass to be expelled. The presence of frass in the capsules

indicated successful attack. A female that did not initiate attack was replaced. One day after attack initiation a male was added. If frass continued to be expelled after male introduction, attack was considered successful, whereupon, gelatin capsules were removed. Each bolt was placed in a screened rearing chamber of 40 cm x 40 cm x 55 cm and stored outdoors. After beetle reemergence the bark was removed from all bolts, each gallery system individually examined and the following data recorded: gallery length and shape and number of live and dead progeny of each instar.

2.3 LIFE HISTORY

2.3.1 Spring emergence

In late April 1983 emergence traps were placed on four trees containing overwintered adults. A trap was placed on each of north and south aspects at each height of 0.5 m, 1 m, 2.5 m and 5 m. Traps were checked every second morning and emerged beetles removed, counted and sexed (males possess stridulating teeth on abdominal tergite seven which are lacking on females). Each specimen was dissected to examine gonad and flight muscle size and gut contents. After emergence was completed the 100 cm² bark area covered by each trap was removed and checked for remaining adults.

2.3.2 Host attack and reemergence

Three trees of 25 to 30 cm DBH and 8.5 to 10 m in height that were girdled in early April were used to

investigate host attack and reemergence. One nail was embedded in each cardinal direction of the bole at 0.5 m from ground level and at 1 m intervals along the length of the bole to a height of 7 m. Every second morning after start of host attack, a wire loop of 11.3 cm inside diameter ($=100 \text{ cm}^2$) was hung on each nail and the number of entrance holes encircled by the loop tallied.

When host attack was nearly complete, four emergence traps were placed at each height of 0.5 m, 3 m and 6 m on two of the three trees. When parent adults began to reemerge, traps were monitored at two day intervals and reemerged adults tallied and sexed. When reemergence was complete the 100 cm^2 bark area covered by each trap was removed and the number of live and dead residual adults counted and sexed.

The above procedures were repeated for the second attack and reemergence periods using two trees that were girdled in mid-June.

2.3.3 Mating and egg gallery construction

Behaviour during mating and egg gallery formation as well as gallery elongation rates at various temperatures were observed using bark-sandwich rearing chambers. Rates of gallery formation by females were compared before and after male introduction. These observations were supplemented with observations of egg gallery lengths and shapes in the field.

2.3.4 Oviposition

Field data pertinent to this study were collected from bark samples used for the brood development study which is discussed in the next section. Samples containing only eggs were used. The following data were collected from each sample: phloem thickness, total egg gallery length, number of egg niches and number of eggs per niche. The number of eggs produced per pair of beetles per egg gallery was estimated by substituting the length of each egg gallery measured in infested trees in the field into the equation obtained from the regression of number of eggs per 100 cm² sample on the total egg gallery length in the sample.

Behaviour of adults during oviposition was observed in bark-sandwich rearing chambers.

In 1983 changes in flight muscle, fat body and gonad size were investigated in adults collected: during spring emergence and attack initiation; from two to three, four to five and eight to twelve day old galleries; and at reemergence. In 1984 reemerged beetles were collected with emergence traps at Pynn's Brook in western Newfoundland and examined for condition of flight muscles. Also, cut larch bolts (1 m long, 20 to 25 cm diameter) were placed at various distances from three infested larch trees to attract reemerging beetles. A bolt was placed lengthwise on the ground 2 m from the base of each tree, another 4 m from the base on the opposite side of the tree and a third bolt was

suspended in the air from the ground 3 m from the tree bole and at a 90° angle to the other bolts. Additionally, three larch, approximately 25 to 30 m from the infested trees, were girdled before beetle reemergence. Bolts and girdled trees were examined each day during the reemergence period and attacking adults were collected. All specimens used in flight muscle studies were fixed in alcoholic Bouin's solution and examined for flight muscle, gonad and fat body condition. The metathoracis medianus and lateralis medius muscles were selected for study of flight muscle size changes because they were distinct, easily recognizable and varied greatly in size between the flying and non-flying condition.

2.3.5 Brood development and behaviour

Two girdled trees containing brood were selected for study of the development of the first brood in the field. One tree (Tree 1) was located in a sheltered site and constantly shaded by neighbouring trees, whereas, the other (Tree 2) was in a clearing and sun-exposed. Each tree was sampled at five day intervals from commencement of attack until completion of brood development. Sampling consisted of removing two 100 cm² bark disks from each tree at each sample height of 0 to 1 m, 2.5 to 3.5 m and 5 to 6 m. The following data were collected from each disk: number of brood in each instar, head capsule widths of larvae (to the nearest 0.02 mm) and the number of dead larvae in each

instar and apparent causes of mortality.

Sampling of the second brood consisted of removing two 100 cm² bark disks every five days from a height of 0.5 to 2 m of each of two infested, girdled trees.

Developmental time of each instar was estimated as the number of days between the date of first appearance of one instar in samples to the date of first appearance of the next instar. Instar developmental times were compared between successive broods in the field as well as to that of brood reared at various temperatures in the laboratory. Developmental time from egg to adult was estimated as the number of days between the first appearance of eggs in the samples to the first appearance of brood adults.

A development index, similar to the one used by Dyer (1969), was used to describe brood development at each sampling date numerically. Eggs; first, second, third, fourth instar larvae; pupae and brood adults were assigned the values one to seven, respectively. The development index of brood at each sampling date was calculated by multiplying the proportion of all live brood in each development stage by the numeric value assigned to that stage and summing for all stages present in the samples, thus giving a value between one and seven.

Brood behaviour during development and feeding was observed in bark-sandwich rearing chambers.

2.3.6 Overwintering behaviour

In early August 1983, four emergence traps were placed at each height of 0.5 m, 2.5 m and 5 m on each of two trees containing the first brood of 1983 and on 1 October four traps were placed at a height of 1.5 m on each of two trees containing the second brood of 1983 to determine if brood adults emerged from the upper regions of infested boles before winter to hibernate in galleries at the bole base. Traps were checked every five days and emerged beetles removed, counted and sexed. In late October the 100 cm² bark area covered by each trap was removed and the number of residual adults (live and dead) were counted and sexed. Flight muscle condition of emerged beetles was examined. On 3 December 1983 two 100 cm² bark samples were removed from each height of 0 to 20 cm, 40 to 60 cm and 80 to 100 cm of the two first brood trees previously used for winter emergence studies and three other trees containing overwintering first brood adults. All live and dead beetles in each sample were counted and sexed. Also on 3 December four duff samples, 0.1 m² and 20 cm deep, were collected near the base of each of the two first brood trees previously sampled for winter emergence and examined for overwintering larch beetles.

2.4 MORTALITY

2.4.1 Brood mortality

The two trees used for brood development studies were also used for brood mortality studies. The number of dead brood of each instar was counted in each phloem sample and an attempt was made to determine the cause of death.

Cadavers that were bloated, brown to black in color and without apparent physical injury were assumed to have been killed by pathogens. The type of pathogen, ie. fungal, bacterial, viral or protozoan, was not determined. Brood covered in resin and exhibiting no other apparent injuries were assumed to have been killed by resinosis. Cadavers fed upon by insect predators and hymenopterous larvae were classified as killed by predators and parasitoids, respectively. Larvae and pupae killed by cold temperatures were a darker color than live individuals and contracted longitudinally. If cause of death could not be determined or if doubtful it was credited to unknown causes.

Total mortality within each instar (ie. instar specific mortality) was estimated using samples in which all live individuals were of later instars than the one for which mortality was being calculated. Instar specific mortality (M_x) was calculated for each instar as follows:

$M_x = D_x / (D_x + N)$ where D_x = number of dead of instar X and N = total number of live and dead in later instars. Total

mortality from egg to adult was estimated in two ways: (1) instar specific mortality was multiplied by the proportion of the original number of individuals that lived to reach that instar and summed for all instars (2) the difference between the average density of eggs in brood trees and the average density of new brood adults after brood maturation.

2.4.2 Overwintering mortality and cold tolerance

Four non-girdled trees of 25 to 30 cm DBH, 8 to 10 m in height and containing overwintering larch beetle brood were sampled by removing a 100 cm² bark disk from the north and south aspects of the bole at each height of 0.5 m, 2.5 m and 5 m. Trees were sampled before winter, on 19 November 1982, and again after winter, on 21 April 1983. All live and dead specimens were counted and overwintering mortality was calculated as the change in mortality between the two sampling periods. Overwintering mortality was not determined for the winter of 1983/84.

To determine cold tolerance, overwintering adult larch beetles were collected from host trees at the study site and transported to the laboratory, where fifty live adults were placed into each of 31 petri dishes filled with moistened softwood sawdust. Six petri dishes with beetles were stored at each temperature of 5 °C, 0 °C, -5 °C and -10 °C; four dishes at -15 °C and three at -20 °C. All petri dishes were placed in plastic bags to prevent dehydration. One dish was removed from storage at each temperature after 2, 4, 8, 16,

32 and 64 days, or until all dishes at a given temperature were exhausted, at which time pronotal width and sex of individual was recorded and percent mortality calculated. The entire treatment was repeated for beetles collected on 6 October 1983, 11 November 1983 and 2 January 1984.

To determine if acclimated beetles were more tolerant to cold than non-acclimated ones, some beetles collected from the field on 6 October were acclimated to temperatures of -15°C and -20°C . This was accomplished by decreasing the storage temperature of the beetles from 5°C to the desired temperature by intervals of 5°C every two days. Four groups of fifty beetles each were acclimated to -15°C and three groups to -20°C .

2.5 ASSOCIATED ORGANISMS

All organisms associated with the larch beetle were collected and preserved in 70% ethanol and the following data collected: date, developmental stage(s), height of tree bole at which collected and instar(s) of *D. simplex* present.

2.6 DATA ANALYSIS

One way analysis of variance was used to make comparisons between data. All tests were performed at the 95% level of significance unless otherwise noted.

The data were allowed to determine the intercept of regression equations and no attempts were made to force equations through the origin. Forced equations result in substantially higher r^2 because the r^2 in forced equations does not subtract out sums of squares due to the mean as is done in non-forced equations. Forced equations also result in extrapolation outside the range of the data and thus may mask biological phenomena.

3. RESULTS

3.1 LIFE HISTORY

3.1.1 Spring emergence

Emergence of overwintered *D. simplex* from trees in 1983 lasted from 7 May to 19 June and peaked on 19 to 21 May when 30% of total emergence occurred (Fig. 5). All live beetles that had overwintered in trees emerged. Peaks of emergence coincided with periods of high daily mean air temperature (Fig. 5) and no beetles emerged on days when mean air temperature was 4 °C or less.

Diurnally, emergence was observed to occur between 10:30 and 17:00 hours.

There was a sex ratio of 0.4 males: 1 female among emerged beetles during the first eight days of emergence (Fig. 5) as compared to a 1.4:1 ratio for the remainder of the emergence period and 1.2:1 for the entire emergence period.

Of the beetles that emerged during the first ten days, 77% came from the south aspect of the trees (Fig. 6) compared to 34% for the remainder of the emergence period and 47% for the entire emergence period.

Peak emergence occurred on 19 to 21 May at each sample height (Fig. 7) but differences occurred in total number and sex ratio of emerged adults with sample height (Table 1).

Figure 5. Total number of emerged overwintered *Dendroctonus simplex* adults from four larch in Newfoundland and daily mean air temperatures from 7 May to 19 June 1983 (n= 32 emergence traps for all trees combined).

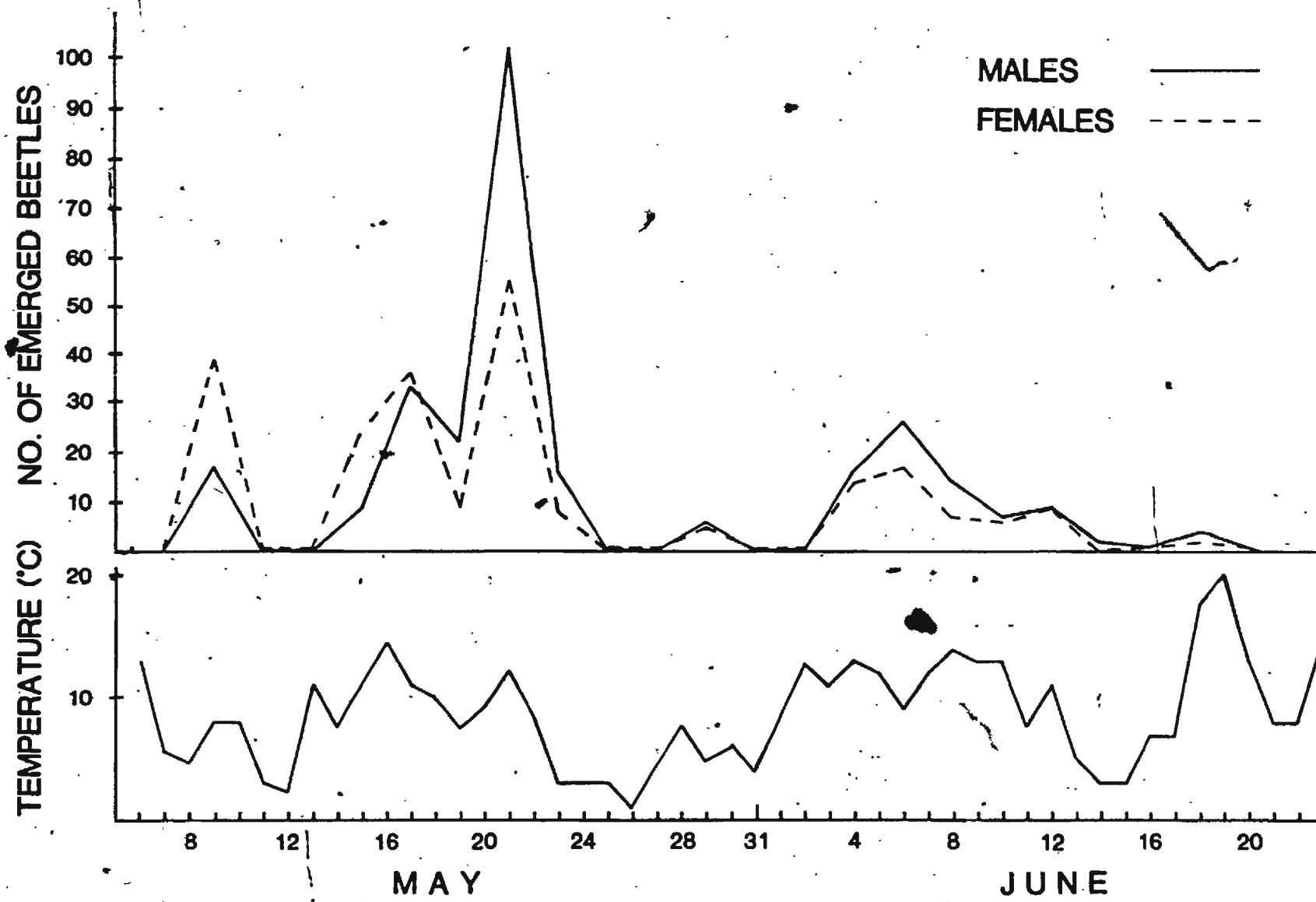


Figure 6. Total number of emerged overwintered
Dendroctonus simplex adults from north and south
aspects of boles of four larch in Newfoundland
from 7 May to 19 June 1983 (n= 16 emergence traps
per aspect for all trees combined).

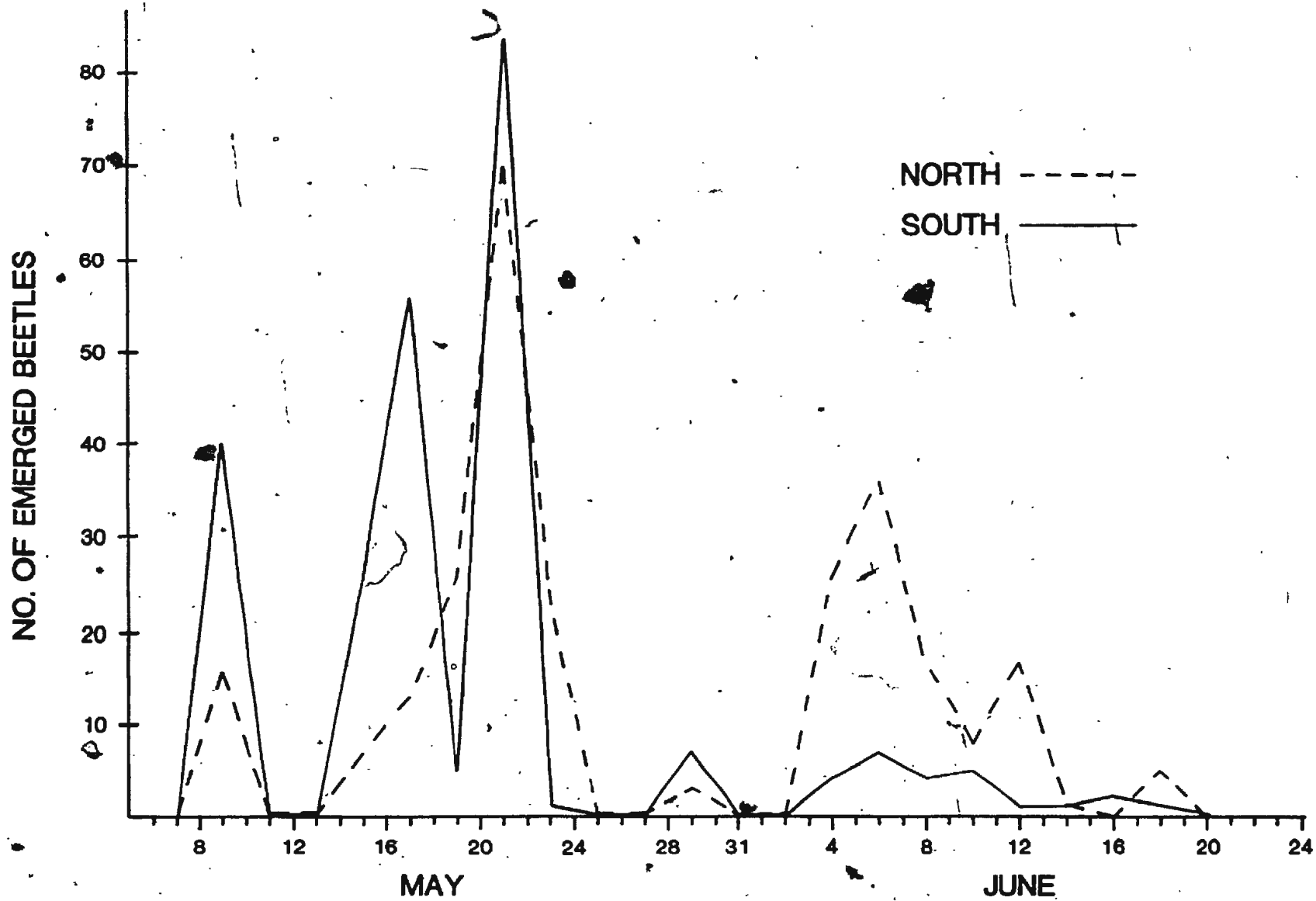


Figure 7. Total number of emerged overwintered
Dendroctonus simplex adults at four sample heights
of four larch in Newfoundland from 7 May to 19
June 1983 (n= eight emergence traps per height for
all trees combined).

NO. OF EMERGED BEETLES

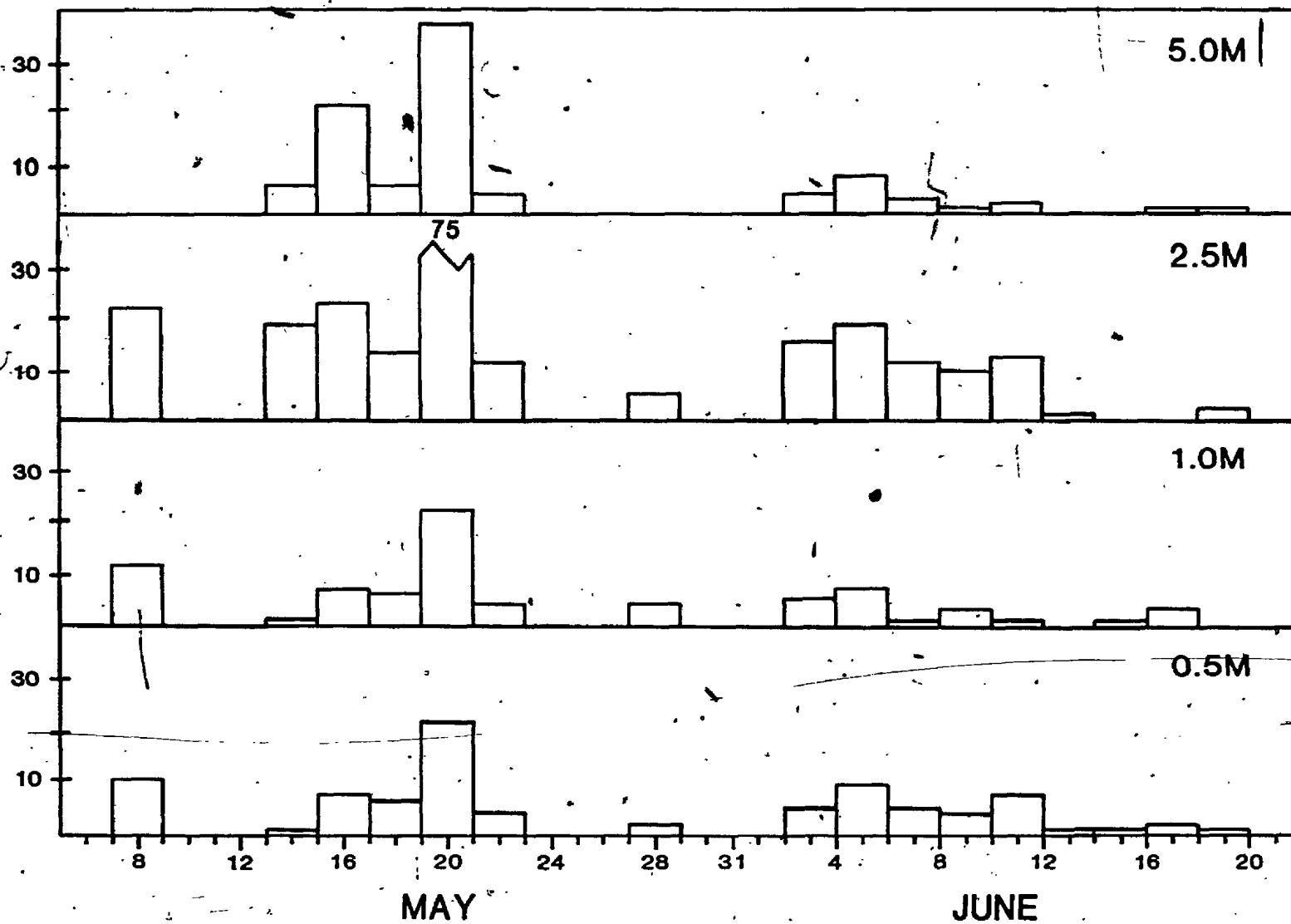


Table 1. Total number, sex ratio and density of overwintered Dendroctonus simplex adults emerged from four sample heights of four infested larch in Newfoundland from 7 May to 19 June 1983 (n=8 emergence traps per height for all trees combined).

	SAMPLE HEIGHT (m)				TOTAL / AVERAGE
	0.5	1.0	2.5	5.0	
No. of emerged beetles (% of total)	90 (17)	104 (20)	233 (45)	93 (18)	520 (100)
Sex ratio (male : female)	1.3 : 1	1 : 1	1.2 : 1	1.9 : 1	1.2 : 1
Density of beetles (per 100 cm ²)	11	13	29	12	16

The highest density of emergence was 29 beetles per 100 cm² at 2.5 m. About 45% of the total number of beetles caught in emergence traps emerged from 2.5 m. Average density of emerged beetles and percent of total emergence was similar between the other three sample heights, at about twelve per 100 cm². The ratio of males to females among emerged beetles was nearly 2:1 at 5 m and about 1:1 at the other three sample heights (Table 1).

Overwintered beetles collected from larch on 25 April, 12 days before commencement of emergence, possessed empty guts, whereas, more than 90% of emerged beetles had food in their guts. The gonads and fat body of emerged beetles appeared slightly larger than those of beetles collected from trees on 15 to 25 April, 12 to 22 days before start of emergence. Also, the flight muscles of emerged beetles were much larger than those of beetles collected on 25 April and were judged capable of sustaining flight.

Emerging beetles constructed their own exit holes, used nearby exit holes constructed by other individuals or used previously constructed entrance or ventilation holes. Upon emergence beetles tended to walk over the bark surface for several minutes before attempting to fly with the wind. If there was little or no wind beetles generally tended to fly southward towards the sun. Most beetles observed to emerge from the lower 2 m of boles flew to the ground within 3 m of the tree base.

3.1.2 Host attack and reemergence

Overwintered beetles that emerged in 1983 produced two broods, one in late May and early June (Brood I) and one in July and August (Brood II). Hence, there were two attack and two reemergence periods (Fig. 8). There was an interval of eight days from start of emergence, on 7 May to start of the first attack period, on 15 May. The interval from the first reemergence, on 25 June, to the first day of the second attack period, 4 July, was nine days.

The average time that parent beetles spent in trees, the interval between the midpoint of the attack period to the midpoint of the following reemergence period, was 30 and 32 days in Brood I and Brood II trees, respectively. Average temperature during Brood I and Brood II production was 13 °C and 16 °C, respectively.

Attack

The number of attacks by overwintered *D. simplex* adults on host trees during the first attack period varied greatly between 15 May and 25 June (Fig. 9). During the 42 day attack period, peaks of attack coincided with peaks in mean daily air temperature. All but one attack peak occurred when mean air temperature was above 10 °C (Fig. 9). There were no attacks on days when mean air temperature was 4 °C or less. Trees were observed to be attacked between 11:00 and 17:00 hours with no discernable peak during that time.

Figure 8. Emergence, attack and reemergence periods of *Dendroctonus simplex* in Newfoundland in 1983. Width of bars indicate general quantitative changes in the adult population for the duration of each activity. Dotted lines mark the midpoint of each period.

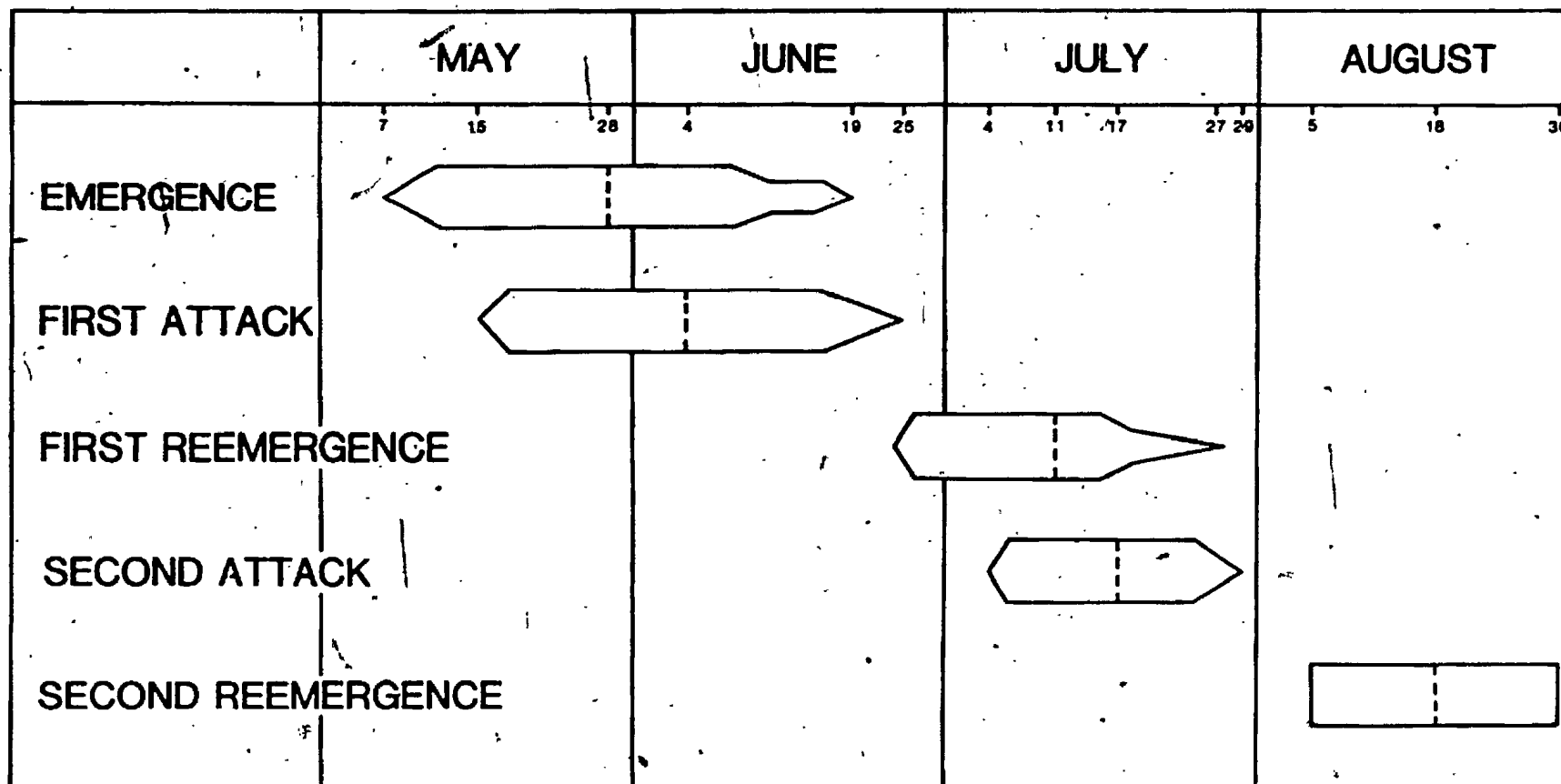
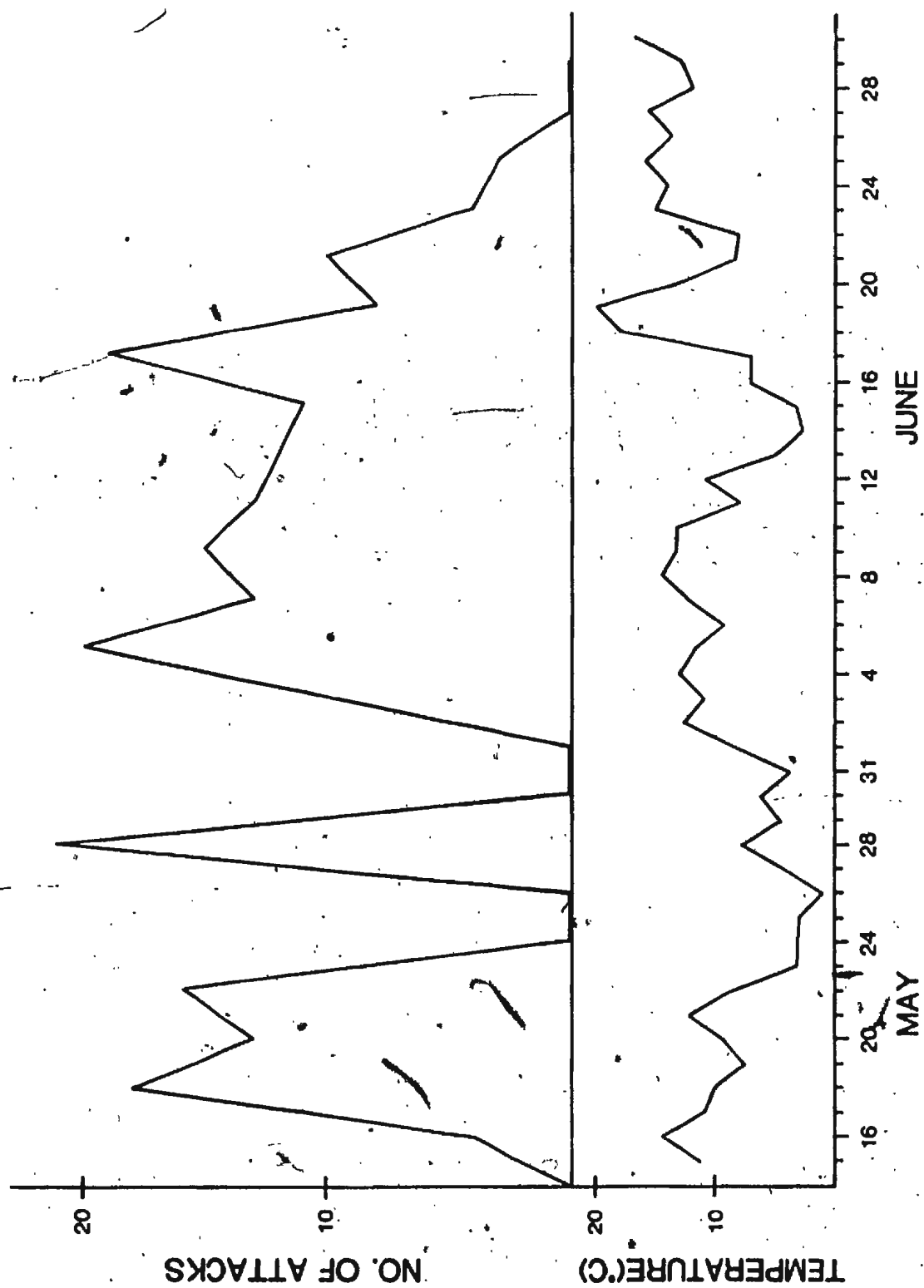


Figure 9. Total number of attacks by overwintered
Dendroctonus simplex adults on three larch in
Newfoundland and daily mean air temperature from
15 May to 25 June 1983 (n= 96 100 cm² samples for
all trees combined).



The number of attacks at 1 m intervals along the boles of three girdled larch varied with time and height (Fig. 10). Tree boles, 10 to 11 m in height, were attacked from ground level to a height of approximately 8 m. Large exposed roots and limbs were also attacked. The central portion of the bole, from 2.5 to 5 m, was generally attacked first with attacks on the lower portion occurring two days later and those on the higher portion 12 to 18 days later.

Mean attack density was lowest in the upper part of the infested bole, from 6.5 to 8 m, where phloem thickness and bole diameter were smallest (Table 2). There was no significant difference in attack density between the two lower sample heights. Average attack density for the entire infested bole was 2.4 ± 1.2 attacks per 100 cm^2 . No successful attacks occurred in areas where phloem was thinner than 2 mm, although some abandoned attack holes that extended inward to the wood surface were found. There was no significant difference in attack density between the four cardinal directions of tree boles or between sample trees.

All trees in the study plot that were attacked in 1983 died the same year. However, two trees that were attacked by a few pairs in 1982 survived and were attacked again in 1983 and killed.

I observed only four beetles that were 'pitched-out', ie. killed by resinosis, at the study site in 1983. There appeared to be more resin production by Brood II trees than

Figure 10. Total number of attacks by overwintered *Dendroctonus simplex* adults at 1 m intervals along the boles of three larch in Newfoundland from 15 May to 25 June 1983 (n= twelve 100 cm² samples per height for all trees combined).

NO. OF ATTACKS

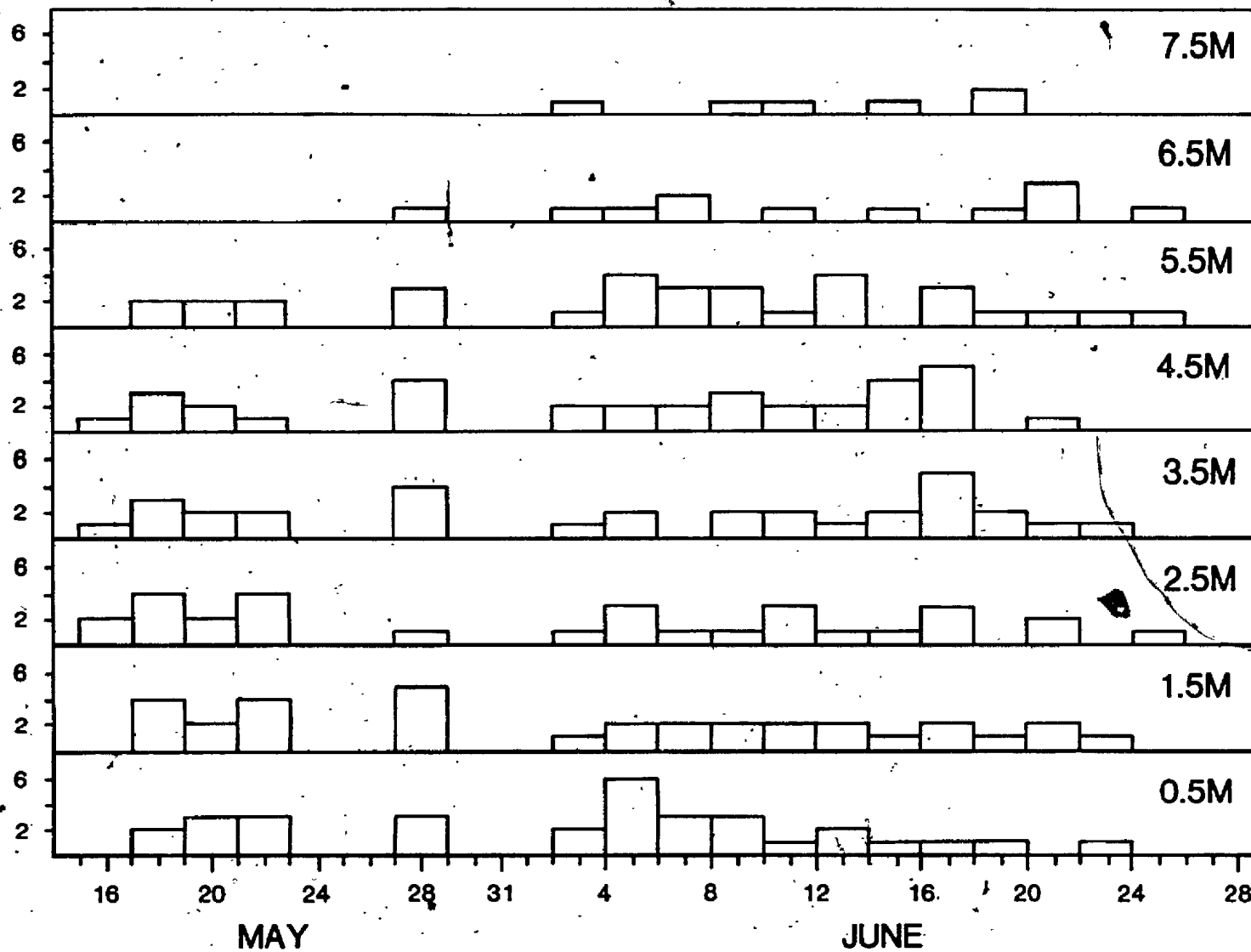


Table 2. Mean (\pm standard deviation) phloem thickness, tree diameter and attack density by Dendroctonus simplex at 1 m intervals along the infested boles of three girdled larch during the first attack period in Newfoundland in 1983 (n= 12 100 cm² samples at each height for all trees combined).

HEIGHT OF BOLE (m)	MEAN (\pm SD) PHLOEM THICKNESS (mm)	MEAN (\pm SD) DIAMETER (cm)	MEAN (\pm SD) ATTACK DENSITY PER 100 cm ²
7.5	2.5 \pm 0.4	16.1 \pm 3.9	0.8 \pm 0.7
6.5	2.5 \pm 0.4	17.2 \pm 4.9	1.5 \pm 0.8
5.5	3.0 \pm 0.5	20.3 \pm 4.7	2.7 \pm 1.6
4.5	4.0 \pm 0.5	21.7 \pm 5.5	2.8 \pm 1.5
3.5	4.5 \pm 0.4	22.9 \pm 4.7	2.6 \pm 0.8
2.5	5.0 \pm 0.5	24.7 \pm 5.5	2.5 \pm 0.9
1.5	5.5 \pm 0.7	29.2 \pm 7.9	2.8 \pm 0.9
0.5	6.0 \pm 0.9	36.0 \pm 9.7	2.7 \pm 0.8
AVERAGE	---	---	2.4 \pm 1.2

by Brood I trees in 1983.

Beetles were observed to land on trees other than larch and on larch that, subsequently, were not attacked.

The second attack period lasted 25 days, from 4 to 29 July (Fig. 8). In the study plot in 1983 only two girdled trees were attacked from ground level to a height of 2.5 m. The total number of attacks on both trees was 40 to 50. The average number of attacks per 100 cm² was 2.0, 1.0 and 0.25 at 0.5 m, 1.5 m and 2.5 m, respectively. In 1984, only three girdled trees and cut larch bolts were attacked during the second attack period at Pynn's Brook. Trees were attacked from ground level to a height of 3 m and the total number of attacks was 15 to 20. No ungirdled, standing trees were attacked during the second attack periods of both years.

Females initiated attack. After landing on a larch tree she moved around the surface apparently searching for a suitable area in which to commence boring. Many bark scales and crevices were usually examined before boring commenced. Some beetles arriving at hosts late in the day were observed to remain in bark crevices overnight to commence boring the next day. Females avoided smooth areas and bored under bark scales or in bark crevices. Attack sites were easily discernible by the accumulation of reddish-brown boring dust or frass on bark scales beneath the boring site. Beetles tended to bore into the bark at an oblique angle which resulted in attack holes being oval in shape.

Males usually arrived up to two days after start of boring by females. After landing on a host a male moved around the bark surface. When an entrance hole was found he waited outside for two to ten minutes, occasionally stridulating, before entering the gallery. If the male arrived early and the gallery was not long enough for him to enter he waited outside until the female elongated it. Sometimes a male left an attack site after a brief period of stridulation and looked for another on the same tree.

Up to four pairs of beetles used a single entrance hole but each pair constructed their own egg gallery in a direction away from that of the other pair(s). Use of a single entrance hole by one, two or three to four pairs of beetles occurred approximately 60%, 30% and 5% of the time, respectively. The ratio of number of pairs of attacking adults to number of entrance holes was approximately 1.6:1.

Reemergence

Reemergence of parent adults from trees in which they established their first brood lasted 32 days, from 25 June to 27 July (Fig. 11), without a distinct peak. Most reemergence peaks and declines coincided with temperature increases and decreases, respectively. Diurnally, reemergence occurred between 11:00 and 16:00 hours.

Reemergence at 6 m started four days later than at lower sample heights (Fig. 12). Beetle density was lowest at

Figure 11. Total number of reemerged *Dendroctonus simplex* parents from two larch in Newfoundland and daily mean air temperatures from 25 June to 27 July 1983 (n= 24 emergence traps for all trees combined).

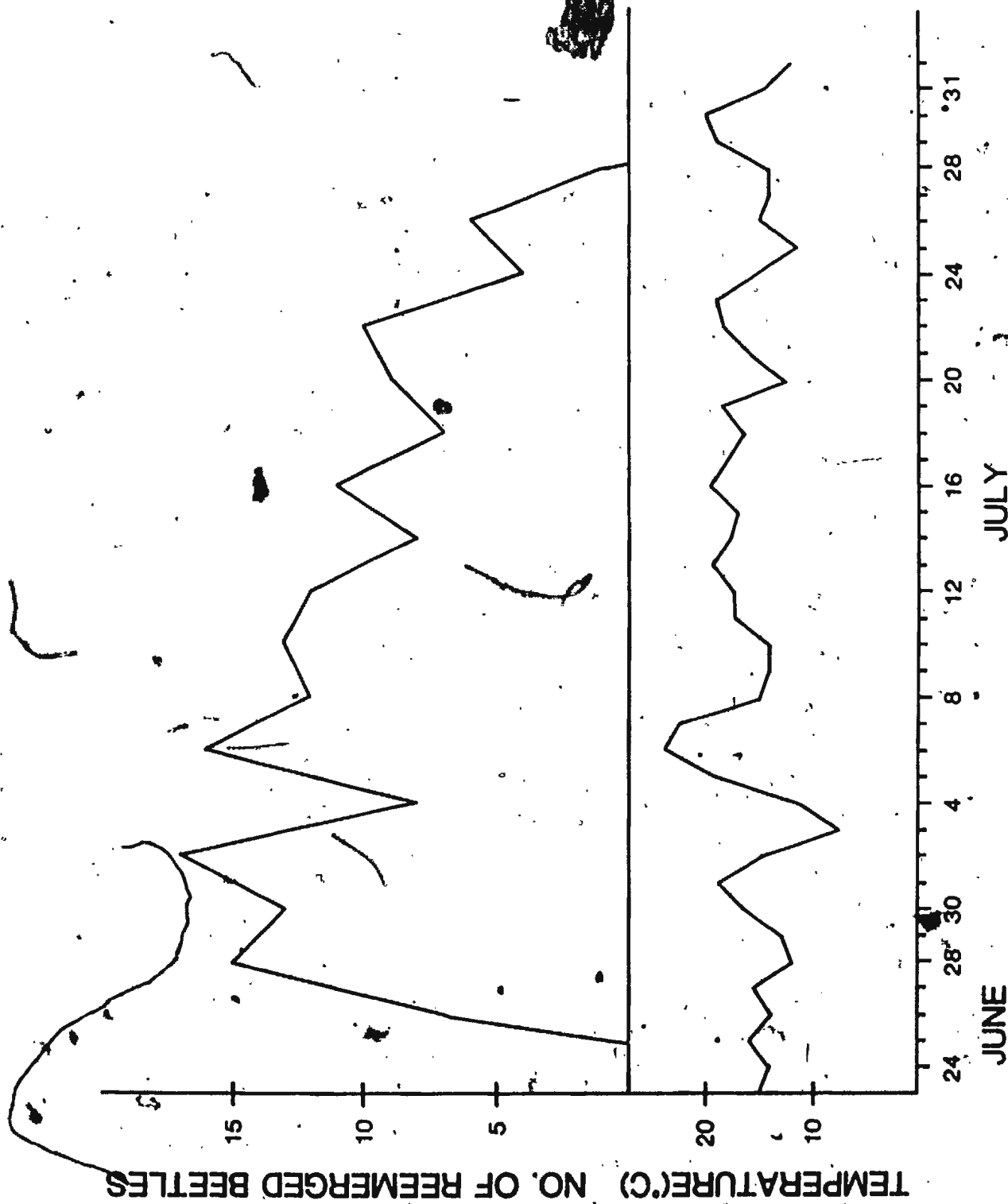
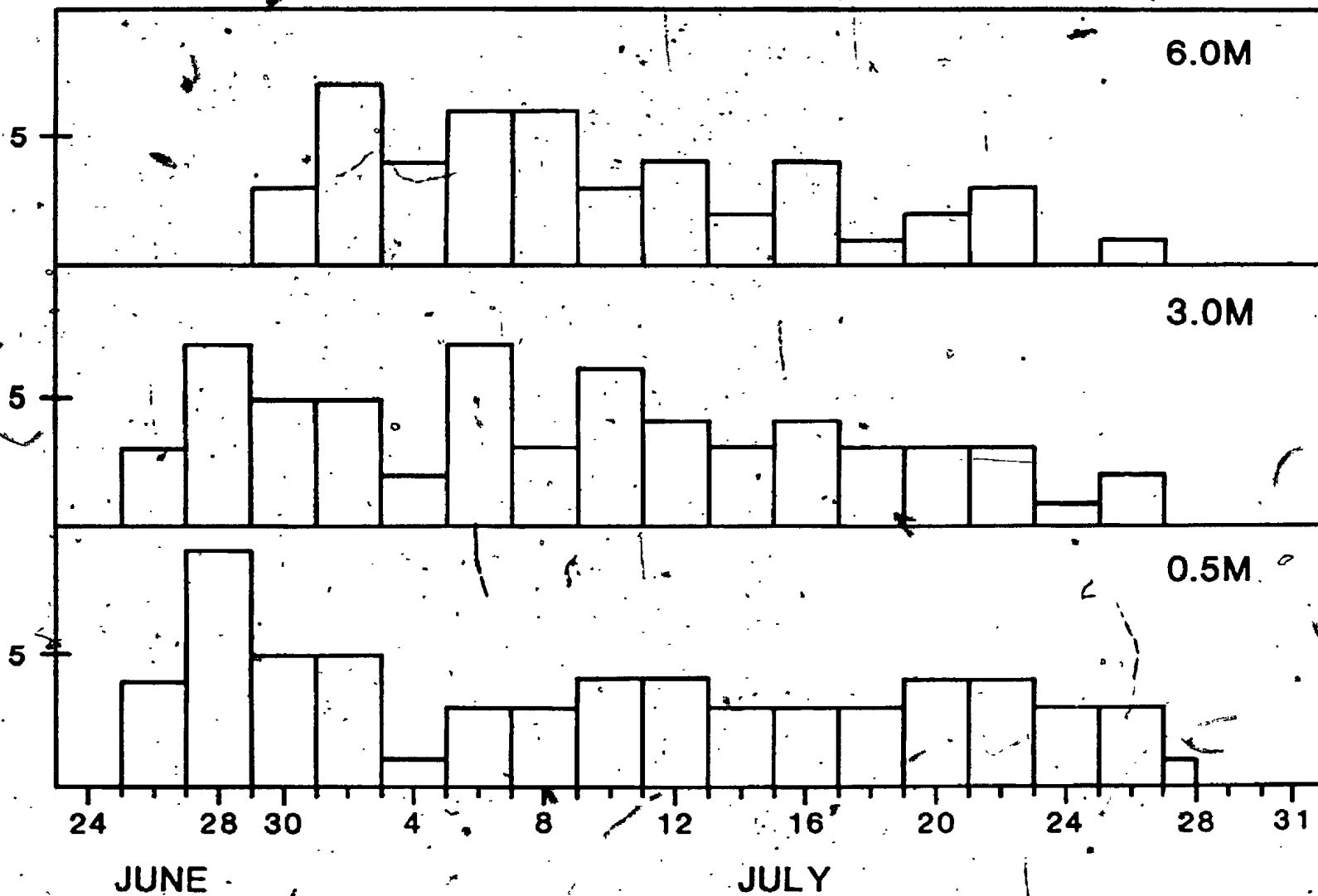


Figure 12. Total number of reemerged parent *Dendroctonus simplex* at three sample heights of two larch in Newfoundland from 25 June to 27 July 1983 (n = eight emergence traps per height for all trees combined).

NO. OF REEMERGED BEETLES



6 m, at 6.4 beetles per 100 cm², than at the two lower sample heights where density was 8.4 to 8.8 per 100 cm² (Table 3). Percent reemergence was similar for all heights, at 90%. Therefore, mortality of adults establishing their first brood was about 10%. There was an approximate 1:1 sex ratio among both reemerged adults and those that died before reemergence (Table 3). Number of reemerged beetles per 100 cm² did not differ significantly between the four cardinal directions of tree boles. Both sexes usually left the gallery at about the same time. Reemerged beetles fell to the ground at the base of trees. None were observed to fly.

The second reemergence period lasted 25 days, from 5 to 30 August (Fig. 8). There was 61% reemergence at 1 m. Therefore, mortality of beetles establishing second broods was 39%. Beetles that reemerged from Brood II trees died.

3.1.3 Mating and egg gallery construction

After the male joined the female in the egg gallery, the female continued to elongate the gallery either up or down the bole of the tree and the male followed close behind. Mating occurred after the adults were in the egg gallery.

Mating

Larch beetles were observed to mate only in the distal end of egg galleries. Mating occurred five to thirty minutes after the male entered the gallery. After entrance the male

Table 3. Total number of Dendroctonus simplex parents that reemerged and that died, percent reemergence and density of parent beetles at three sample heights of two infested larch in Newfoundland from 25 June to 27 July 1983 (n = 8 100 cm² samples at each height for all trees combined).

	SAMPLE HEIGHT (m)						TOTAL		GRAND TOTAL
	0.5		3.0		6.0				
	M	F	M	F	M	F	M	F	
No. of reemerged parent beetles	31	31	29	32	25	21	85	84	169
No. of dead parent beetles	3	2	4	5	3	2	10	9	19
Total	34	33	33	37	28	23	95	93	188
Percent reemergence	92.5		87.1		90.2		89.9		89.9
Density of beetles (per 100 cm ²)	8.4		8.8		6.4		7.8		7.8

M = male; F = female

proceeded to a location behind the female and started to jostle her with his head and front legs. To facilitate mating the male backed into a turning niche, turned around, and backed up the gallery toward the female where he continued courtship by stroking the tip of her abdomen with his hind legs for ten to thirty seconds before copulation occurred (Fig. 13). During copulation the male continued to stroke the female who remained inactive. On the average copulation lasted 92 seconds ($SD=29.5$, $n=14$) and none was longer than 180 seconds. Following copulation the female recommenced gallery construction while the male turned around and returned to a position behind the female. The average number of copulations per beetle pair and the average time interval between copulations was not determined. One pair was observed to mate four times within two days and the shortest interval between copulations was one hour. It was not determined whether a female required more than one mating to complete brood production. However, the male stayed in the egg gallery with the female until completion of brood production and mating was observed periodically until reemergence. It was not determined whether a female required a mate to produce a second brood in a different tree. However, females that produced second broods were accompanied by males. In the field, less than 1% of the galleries observed contained a female only and galleries with only a male were not encountered. Most galleries contained one male and one female. However, three

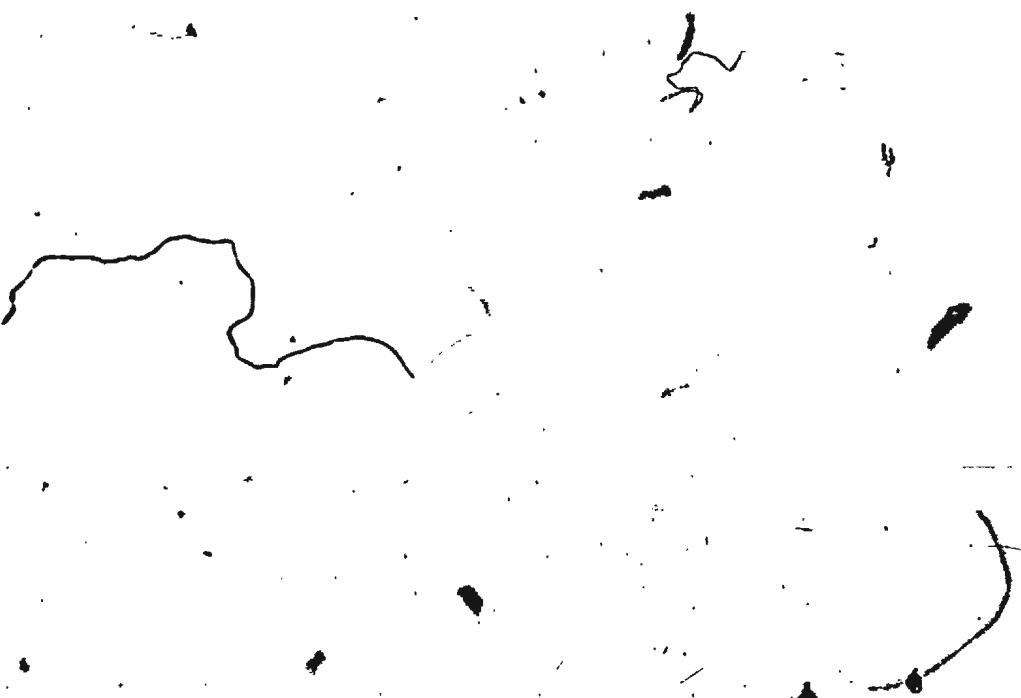
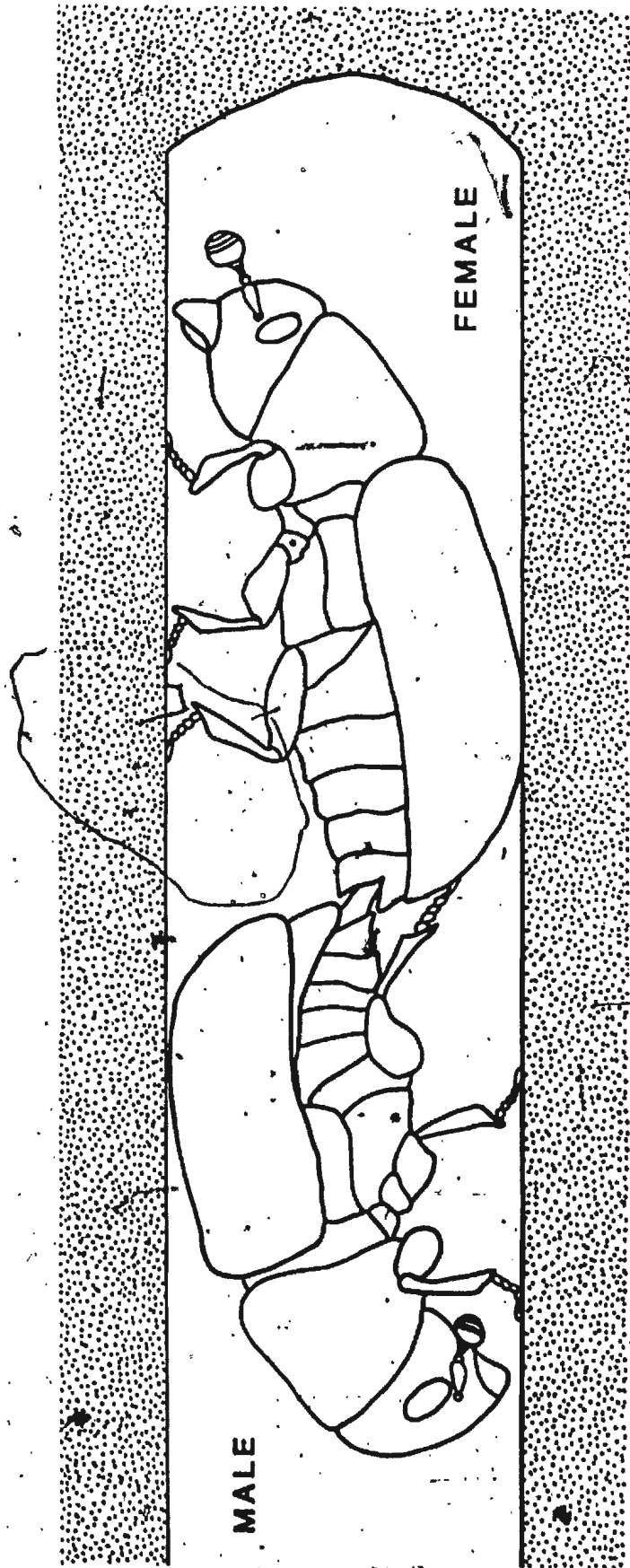


Figure 13. Position of male and female *Dendroctonus simplex* during copulation.



galleries were observed to contain two males with one female.

Egg gallery construction

Only the female contributed to egg gallery elongation. She bit off small pieces of phloem from the distal end of the gallery, ate some of it, and pushed the rest of the phloem bits (frass) behind her where the male gathered it into a pile with his legs and pushed it out of the entrance hole. Before male arrival females kept galleries clear by pushing the frass out of the entrance holes. No males were observed to ingest frass. When 4 to 6 cm of gallery was constructed the male packed the frass in the lower portion of the gallery. Thus, 4 to 8 cm of the distal end of the gallery was kept clear.

Egg galleries were slightly sinuous and vertical (Fig. 4), i.e. parallel to the grain. They extended upward from the entrance hole approximately 80% of the time and downward the other 20%. Galleries were constructed primarily in the phloem, continuously in contact with the cambium and very lightly scoring the wood in areas where phloem was thin. Average egg gallery diameter was approximately 3 mm but varied according to the diameter of the beetle that constructed it. From the entrance hole approximately 75% of all egg galleries ascended (or descended) diagonally before turning directly upward (or downward). There was no diagonal portion in the other 25%. Branch galleries extending from



Figure 14. Egg gallery patterns of *Dendroctonus simplex* in the phloem of eastern larch, *Larix laricina*, in Newfoundland (magnification= .3X).

the main gallery were relatively uncommon. When branches did occur they rarely exceeded 8 cm in length but did contain egg niches and eggs. Turning niches, approximately 3 mm wide and 3 to 5 mm long, were cut by males into the sides of egg galleries at irregular intervals, which averaged 5 cm. Males also constructed ventilation holes leading to the outside at irregular intervals, which averaged 4 cm, along the gallery. Ventilation holes were constructed only after the entrance hole was plugged with frass. Ventilation holes appear smaller and more circular in shape than entrance holes when viewed from the external surface of the tree. Many ventilation holes were covered by bark scales. Males were observed to ingest phloem bitten off during turning niche and ventilation hole construction.

When a pair of beetles entered an attack hole used by another pair(s) they constructed an egg gallery away from or parallel to the other gallery(s). Less commonly a pair would walk for a short distance along a gallery constructed by another pair before branching off and starting a gallery of their own. Intersection of galleries was fairly common (Fig. 14) especially in densely attacked trees. This made measurement of length of individual galleries difficult. Only 31 galleries were measured in the field (Table 4). All were at heights of 0.5 to 2.5 m in trees thus preventing a comparison of gallery lengths between tree heights. Galleries in Brood I trees (mean = 41 cm) were significantly longer than those produced in Brood II trees (mean = 26 cm).

Table 4. Mean (\pm standard deviation) and range of egg gallery lengths of Dendroctonus simplex in Brood I and Brood II trees in Newfoundland field populations in 1983 and in caged larch bolts.

SOURCE OF EGG GALLERIES	N	MEAN (\pm SD) LENGTH OF GALLERIES (cm)	RANGE
Brood I trees	24	41 \pm 13.8	20 - 85
Brood II trees	7	26 \pm 7.6	16 - 36
Caged larch bolts	21	35 \pm 14.9	14 - 78

but not significantly different from those in caged larch bolts (mean = 35 cm), nor were the latter significantly different from those in Brood II trees (Appendix A).

Egg gallery elongation rates by *D. simplex* in bark sandwich rearing chambers increased with increasing temperature (Table 5). Between 12 °C and 18 °C gallery elongation rate doubled. However, the difference in rate between 18 °C and 24 °C was relatively small. Before males were introduced to the chambers females elongated galleries at average rates of 0.5, 1.0 and 1.1 cm/day at 12 °C, 18 °C and 24 °C, respectively. After male introduction the respective gallery elongation rates doubled to 1.0, 2.0 and 2.3 cm/day.

3.1.4 Oviposition

Females commenced oviposition approximately three to five days after start of egg gallery construction and stopped two to three days before reemergence. Eggs were deposited at irregular intervals along both sides of galleries except for the first and last 2 to 4 cm. Before ovipositing the female excavated a small rounded depression, 1.5 to 2 mm deep, into one side of the gallery at the distal end. This depression became the egg niche. The female then backed down the gallery to a previously constructed turning niche, reversed, backed to the distal end of the gallery and laid an egg(s) in the niche. She then repeated the turning

U

Table 5. Mean (\pm standard deviation) egg gallery elongation rates by Dendroctonus simplex females* in bark-sandwich rearing chambers at three temperatures.

TEMPERATURE (°C)	NUMBER OF DAYS OF GALLERY ELONGATION	MEAN (\pm SD) GALLERY ELONGATION RATE (cm / day)
12	31	1.0 \pm 0.24
18	23	2.0 \pm 0.44
24	22	2.3 \pm 0.52

* males were present

process, returned to the distal end and continued to elongate the gallery before excavating another niche. The beetles appeared to not pack the egg niches with frass deliberately but this soon was done incidentally by the male during the process of frass clearing. Of 1273 egg niches examined 17%, 42%, 26%, 11% and 4% contained zero, one, two, three and four eggs, respectively. The mean number of eggs per niche (E/N) and mean number of niches per centimeter of gallery length (N/cm) were approximately 1.4 and 0.7, respectively, and varied little with tree height or between first and second broods (Table 6). Differences in E/N and N/cm between Brood I sample trees, between sample heights of Brood I trees and between first and second broods were not significant (Appendices B and C).

The mean number of eggs per centimeter of gallery length (E/cm) was near 1.0 for each height and both broods (Table 7). However, E/cm in caged large bolts, which averaged 2.0, was significantly higher than for Brood I trees for all heights combined (Appendix D). Additionally, there was a significant difference in E/cm between the two Brood I sample trees (Appendix D). The tree with the higher E/cm ratio also had significantly thicker phloem and lower egg gallery length per 100 cm² of phloem area (GL). The differences in E/cm with tree height and between Brood I and Brood II trees were not significant (Appendix D), although there were significant differences in phloem thickness with tree height and Brood II trees had significantly lower GL.

Table 6. Mean (\pm standard deviation) number of Dendroctonus simplex eggs per niche (E/N) and niches per cm of gallery length (N/cm) in 100 cm² phloem samples from each height of Brood I and Brood II trees in Newfoundland field populations in 1983.

BROOD	SAMPLE HEIGHT (m)	E / N		N / cm	
		NUMBER OF NICHES SAMPLED	MEAN \pm SD	NUMBER OF 100 cm ² SAMPLES	MEAN \pm SD
I	0 - 1	400	1.46 \pm 1.07	24	0.78 \pm 0.31
	2.5 - 3.5	443	1.42 \pm 0.98	24	0.63 \pm 0.22
	5 - 6	328	1.44 \pm 1.01	20	0.69 \pm 0.31
	Average	1171	1.44 \pm 1.02	68	0.70 \pm 0.28
II	0 - 2	102	1.40 \pm 0.94	8	0.84 \pm 0.29

Table 7. Mean (\pm standard deviation) number of Dendroctonus simplex eggs per cm of gallery length (E/cm) in 100 cm² phloem samples from each sample height of Brood I and Brood II trees in Newfoundland field populations in 1983 and for galleries in caged larch bolts.

BROOD	SAMPLE HEIGHT (m)	NUMBER OF 100 cm ² SAMPLES	MEAN (\pm SD) E / cm
I	0 - 1	64	1.0 \pm 0.33
"	2.5 - 3.5	64	0.9 \pm 0.26
"	5 - 6	58	1.0 \pm 0.28
"	Average	186	1.0 \pm 0.30
II	0 - 2	50	1.0 \pm 0.20
Bolt	—	21*	2.0 \pm 0.39

* number of galleries

than Brood I trees. Multiple regression of E/cm on GL and phloem thickness ($N=186$) yielded an R^2 value of 0.04, ie. only 4% of the variation in E/cm was accounted for by the two predictors.

Regression of number of eggs per 100 cm^2 sample (E) on GL yielded the regression equation: $E = 5.09 + 0.833 GL$, where $N = 236$ and $r = 0.91$. The equation was considered satisfactory for estimating number of eggs from gallery length because 82% (r^2) of the variation in number of eggs was explained by the regression.

The total number of eggs produced by each pair of beetles in an egg gallery was estimated by substituting the length of each of the 31 galleries measured in the field into the above regression equation. The number of eggs produced by each pair of beetles in caged larch bolts was obtained directly by counting all live and dead progeny in each gallery. The number of eggs per gallery was significantly different between Brood I trees (mean = 39) and Brood II trees (mean = 27) and between Brood I trees and caged larch bolts (mean = 70) (Appendix E). Pairs of beetles produced an average of 44% more eggs in their first egg galleries than in their second galleries and pairs of beetles in caged larch bolts produced 79% more eggs in their first egg galleries than were produced in first egg galleries by beetles in the field (Table 8).

Table 8. Mean (\pm standard deviation) and range of number of eggs laid per pair of Dendroctonus simplex adults per gallery (E/P) in Brood I and Brood II trees in the field and in caged larch bolts.

	NUMBER OF GALLERIES	MEAN (\pm SD) E / P	RANGE
Brood I trees*	24	39 \pm 11.5	22 - 76
Brood II trees*	7	27 \pm 6.3	18 - 35
Caged larch bolts**	21	70 \pm 33.3	21 - 160

* E/P was estimated with the regression equation: $E = 5.09 + 0.833 \text{ GL}$; E = no. eggs; GL = length of each gallery measured in the field

** E/P was counted

Mean brood density, approximately 49 individuals per 100 cm² for all sample heights combined in Brood I sample trees, varied little with tree height (Table 9). Differences in brood density between sample heights of Brood I trees and between Brood I sample trees were not significant (Appendix F). However, Brood II trees had significantly lower brood densities (mean = 23 individuals per 100 cm²) than Brood I trees (Appendix F). Regression of brood density on phloem thickness resulted in an r^2 value of 0.02 (N = 186). Hence, phloem thickness is a poor predictor of brood density.

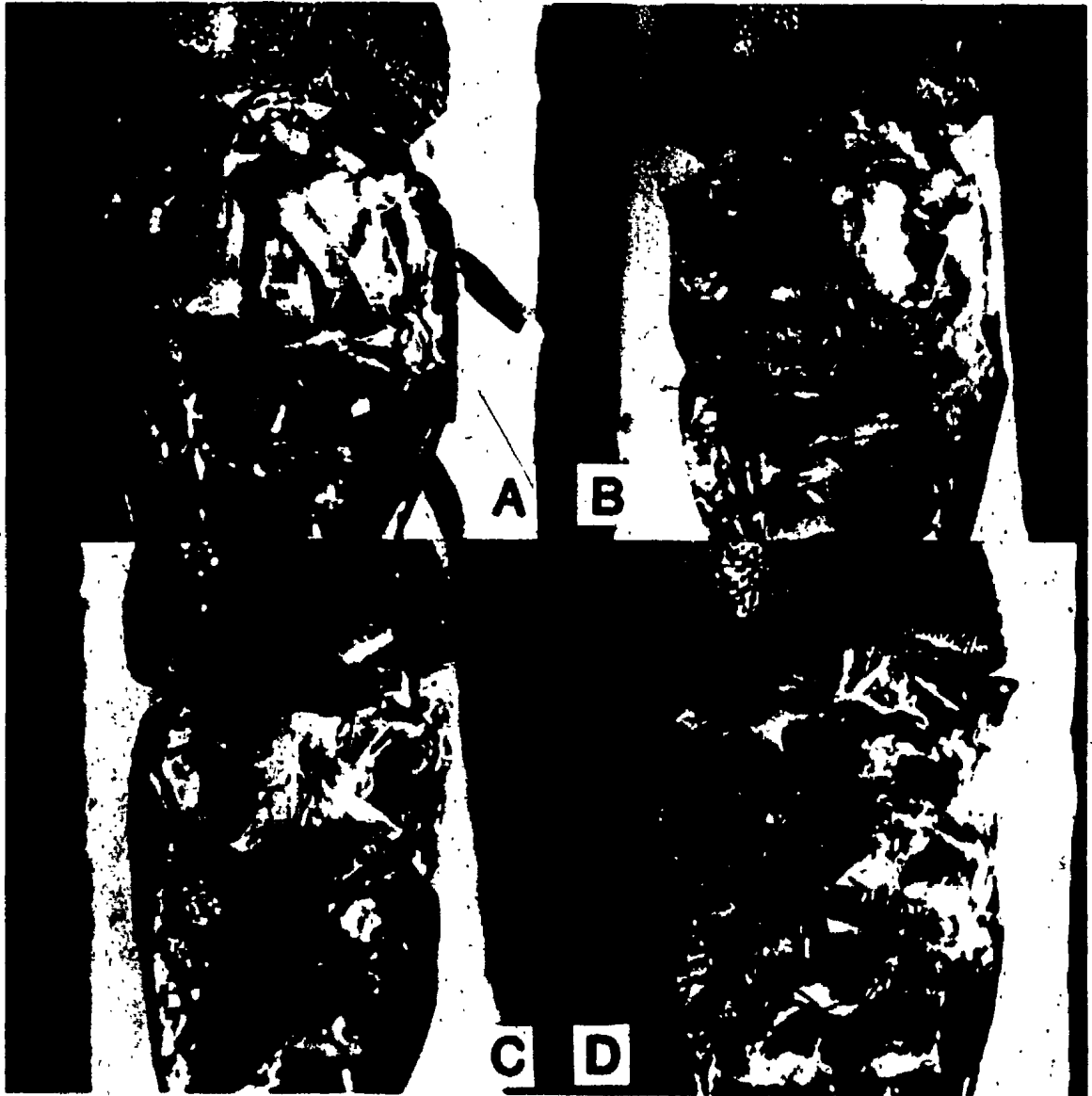
When overwintered adults emerged in the spring and commenced gallery construction in new trees they possessed large, fully developed flight muscles in their metathorax (Fig. 15A), a large fat body that occupied most of the space in the abdomen and reduced gonads that occupied relatively little space in the abdomen. Adults taken from two to three day-old galleries, before commencement of oviposition, had greatly reduced flight muscles (Fig. 15B), smaller fat body and enlarged gonads. Testes of males had increased only slightly in size but the ovarioles of females took up most of the abdominal space and protruded into the metathorax. The flight muscles of adults taken from four to five day-old galleries, just after commencement of oviposition, were much more reduced and had almost disappeared except for a few strands (Fig. 15C). Flight muscles were not visible in adults taken from eight to twelve day-old galleries (Fig. 15D). Gonads filled most of the space in the metathorax

Table 9: Mean (\pm standard deviation) and range of Dendroctonus simplex brood densities for each sample height of Brood I and Brood II trees in Newfoundland field populations in 1983.

BROOD	SAMPLE HEIGHT (m)	NUMBER OF 100 cm ² SAMPLES	MEAN (\pm SD) NO. BROOD / 100 cm ²	RANGE
I	0 - 1	59	47 \pm 18.0	7 - 97
"	2.5 - 3.5	55	52 \pm 17.5	9 - 90
"	5 - 6	54	50 \pm 18.4	3 - 95
"	Average	168	49 \pm 18.0	3 - 97
II	0 - 2	48	23 \pm 8.5	6 - 41

Figure 15. Degeneration of flight muscles (metathoracis medianus and lateralis medius) in *Dendroctonus simplex* adults. A. muscle condition at emergence and host attack, B. female taken from a two to three day-old gallery before start of oviposition, C. female taken from a four to five day-old gallery just after start of oviposition, D. female taken from an eight to twelve day-old gallery. (magnification= 28X)

M- metathoracis medianus, L- lateralis medius



formerly occupied by flight muscles.

There was no flight muscle regeneration in the twelve reemerged beetles (seven males, five females) examined in 1983. Of 96 reemerged beetles examined at Pynn's Brook in 1984 only 17% had fully developed flight muscles and were judged capable of flight, 33% had small flight muscles and 50% had no flight muscles. All live reemerged beetles, observed (about fifty to sixty) in both years fell to the ground without attempting to fly. The ovarioles of reemerged females contained no or a few small oocytes. Sixty reemerged beetles attempting to construct second galleries were collected from cut larch bolts placed at various distances from first brood trees at Pynn's Brook in 1984 and from three girdled trees at the same locality. Beetles with small or no flight muscles comprised 73% of the total of 16 beetles collected from bolts placed 2 m away from first brood trees. The six beetles collected from bolts 4 m away, the nine from suspended bolts 3 m away and the thirty from the girdled trees 25 to 30 m away all had fully developed flight muscles. Flight muscles of beetles that established second broods in the field in 1983 were not examined.

3.1.5 Brood development and behaviour

Like other species of *Dendroctonus*, *D. simplex* develops from the egg stage through four larval instars and a pupal stage to the adult (Fig. 16). Freshly laid eggs were ovoid

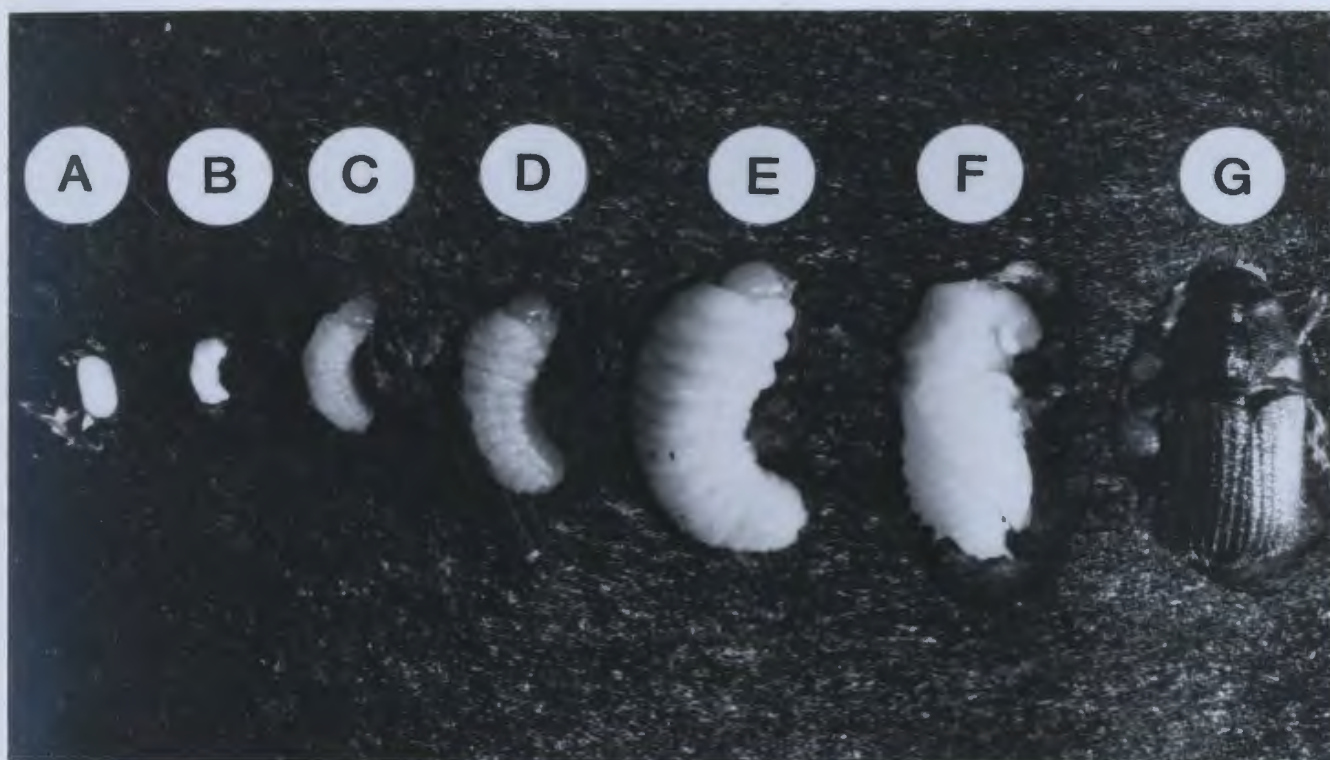


Figure 16. Developmental stages of *Dendroctonus simplex* (magnification= 9X). A. egg, B to E. larval instars one to four, F. pupa, G. adult.

in shape, 1.0 to 1.1 mm long, 0.6 to 0.7 mm wide and white in color. Eggs passed through several recognizable phases during development. They were evenly milky white for the first day and then showed a slight solidification in the center and transparency around the margins and ends as the embryo developed. The egg stayed this way until about two days before eclosion when chitinized mandibles became visible through the chorion. One day before eclosion other head appendages became visible as well. During eclosion the chorion was cut with the mandibles and the larva crawled out. Freshly emerged larvae had pointed abdomens and white head capsules. Some were observed to eat part of the chorion. Newly emerged larvae began feeding after three to six hours by tunneling away from the egg gallery. With the first intake of food the alimentary canal turned a red-brown color which was visible through the transparent larval cuticle. During feeding larvae often reversed directions to pack loose frass behind them leaving one to two body lengths at the distal end of the feeding gallery free of frass. Larvae were also observed to ingest nematodes, fungal hyphae and their own excrement. Although feeding galleries sometimes intersected and larvae came into close contact, no antagonistic behaviour was observed. No ingestion of dead or live eggs, larvae or pupae by other larvae and adults was observed.

The width of larval feeding galleries increased with each successive instar (Fig. 17) and varied in total length

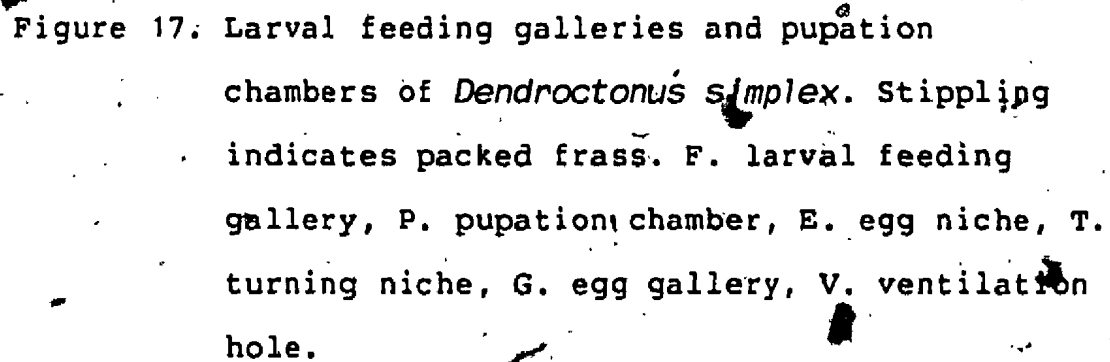
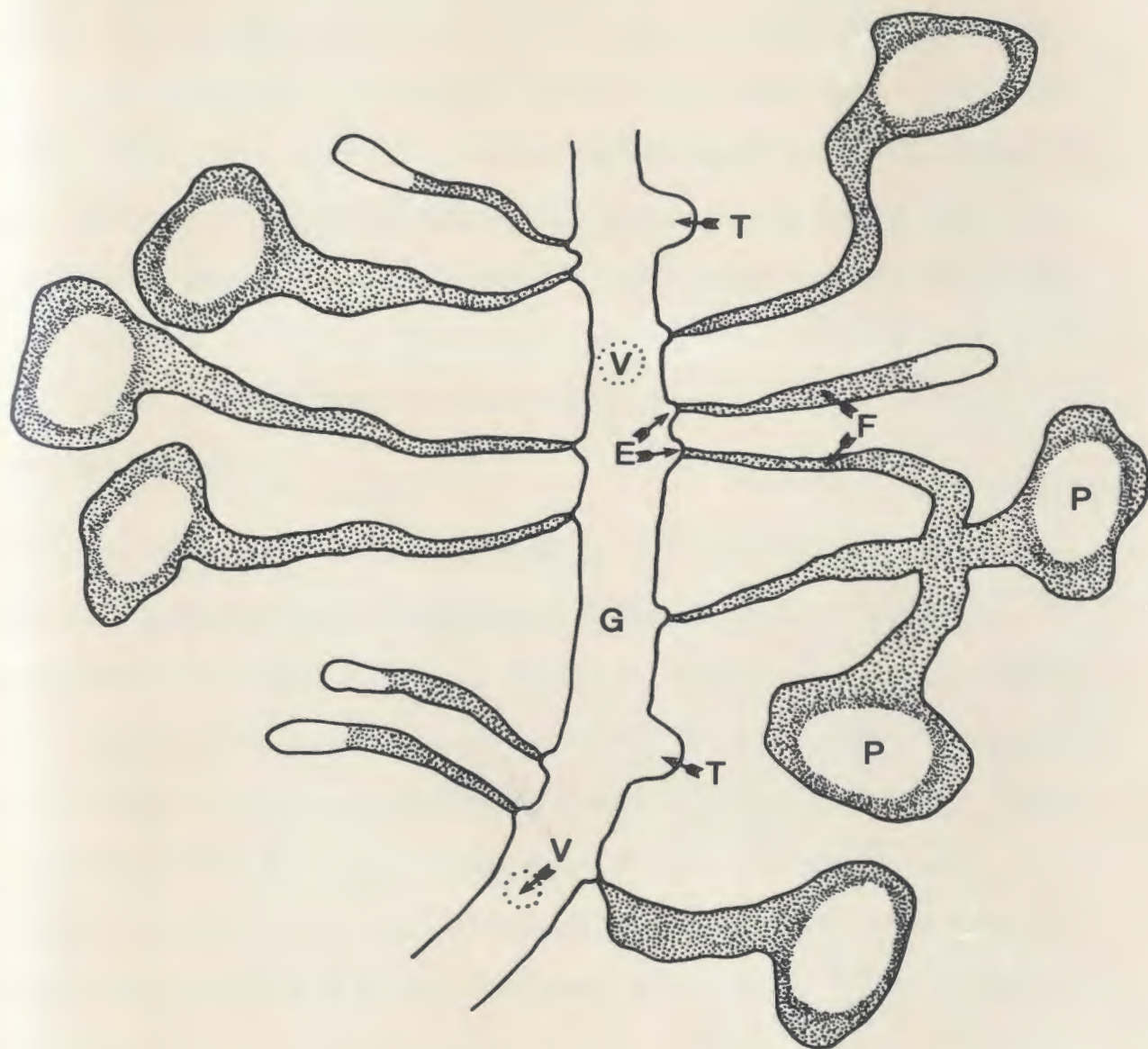


Figure 17. Larval feeding galleries and pupation chambers of *Dendroctonus simplex*. Stippling indicates packed frass. F. larval feeding gallery, P. pupation chamber, E. egg niche, T. turning niche, G. egg gallery, V. ventilation hole.



1 cm

from 2 to 12 cm.

Larvae moulted in the distal ends of feeding galleries. Newly moulted larvae possessed white head capsules which darkened to a light color within a day. Some larvae were observed to eat part of their exuvia but not the old head capsules. The last larval instar excavated an oval pupation chamber (Fig. 17) and blocked the tunnel entrance to the chamber with frass. Approximately two days before pupation larvae stopped feeding and their digestive tracts emptied. The larvae became inactive and were believed to have entered a prepupal stage.

A plot of head capsule widths of 492 Brood I larvae from field populations displayed four distinct peaks corresponding to four larval instars (Fig. 18). Mean head capsule widths of successive instars (Table 10) increased geometrically with an average growth factor of 1.33. Mean head capsule widths of *D. simplex* larval instars in Newfoundland were, on the average, 17% larger than those recorded by Prebble (1933) for New Brunswick populations (Table 10).

The pupa remained uniformly white for four to five days after which the compound eyes and mandibles began to darken. Approximately two days before adult emergence from the pupa the pupal cuticle turned a pale yellow color and the elytra acquired more distinct markings. The adult emerged from the pupa by rupturing the cuticle on the dorsal part of the head.

Figure 18. Larval head capsule widths of *Dendroctonus simplex* (n= 492) in Newfoundland.

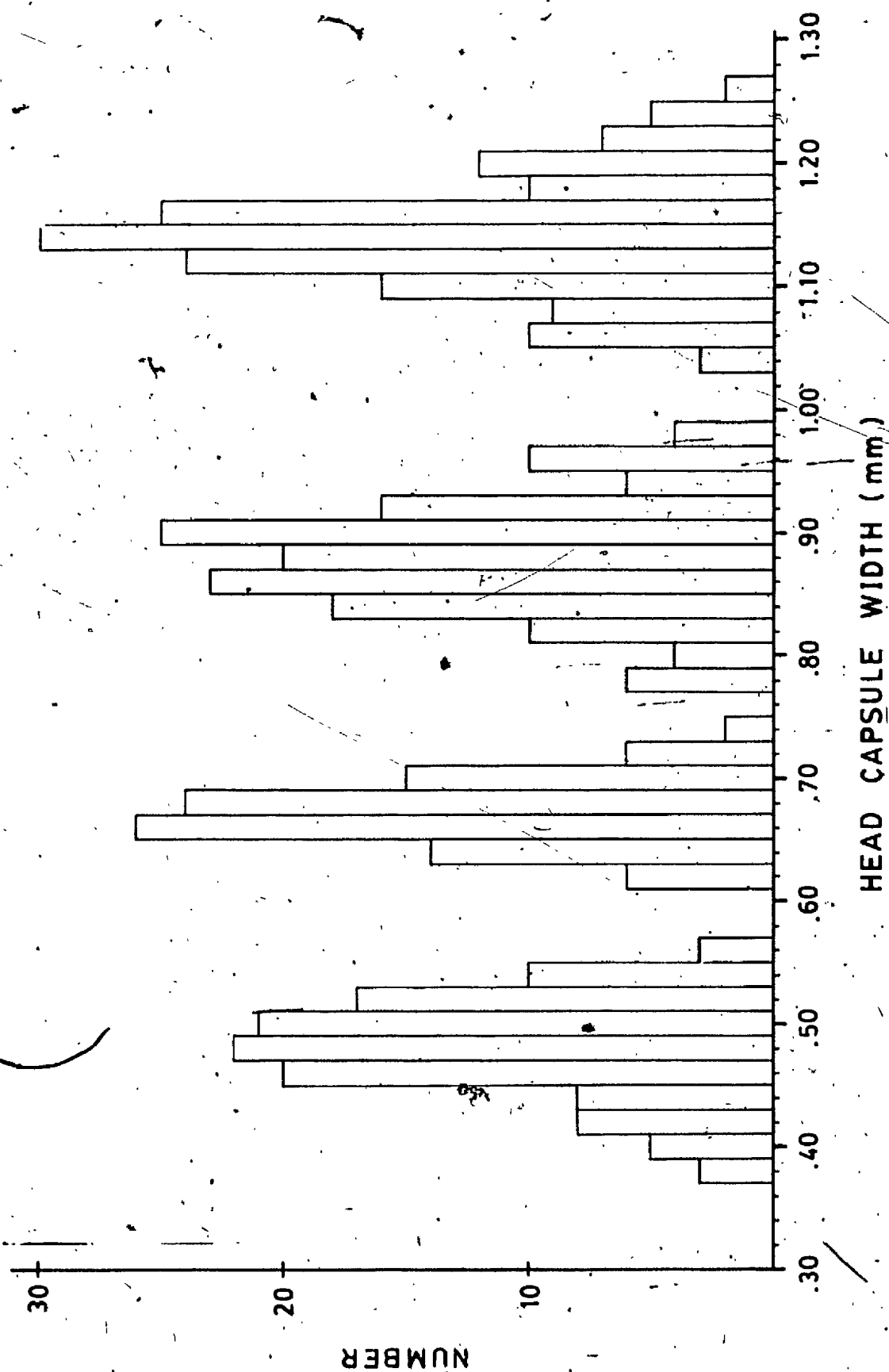


Table 10. Mean (\pm standard deviation) head capsule widths of Dendroctonus simplex larval instars in Newfoundland and New Brunswick (Prebble 1933).

LOCALITY		INSTAR			
		1	2	3	4
Newfoundland	Mean (\pm SD)	0.48 \pm 0.04	0.67 \pm 0.028	0.88 \pm 0.049	1.13 \pm 0.041
	Number of larvae measured	17	93	142	140
New Brunswick	Mean (\pm SD)	0.41 \pm 0.027	0.56 \pm 0.003	0.76 \pm 0.038	0.99 \pm 0.036
	Number of larvae measured	19	38	36	66

and thorax. Upon emergence adults were light yellow in color and the cuticle was soft. These callow adults remained in the pupal chambers for two to three days until the cuticle hardened and turned a light brown color. They then extended the larval feeding galleries at a rate of less than 5 mm per day. After seven to eight days adult cuticle had turned black with reddish elytra. Examination of 14 brood adults at this time indicated that they had poorly developed flight muscles incapable of sustaining flight.

Sexual dimorphism of adult body size was evident. Pronotal width was used as an index of body size. Pronotal widths of males averaged 1.8 mm (SD= 0.13, N= 244) and were significantly smaller than those of females which averaged 1.9 mm (SD= 0.12, N= 198).

The seasonal life history of *D. simplex* consisted of one generation and two broods per year in 1983 (Fig. 19) and 1984. The two broods were produced in different trees. Brood adults overwintered in brood trees and emerged the following spring. No immature instars overwintered. Duration of third and fourth larval instars and pupae in Brood II was much longer than in Brood I (Fig. 19).

The mean developmental times of *D. simplex* instars reared in bark sandwich chambers generally decreased with increase in temperature (Table 11). The greatest difference was between 12 °C and 18 °C. Developmental times of the egg and first and second larval instars of Brood I in field

Figure 19. Seasonal life history of *Dendroctonus simplex* in Newfoundland in 1983. Heights of peaks correspond to percentage composition of total population in sample trees at that date.

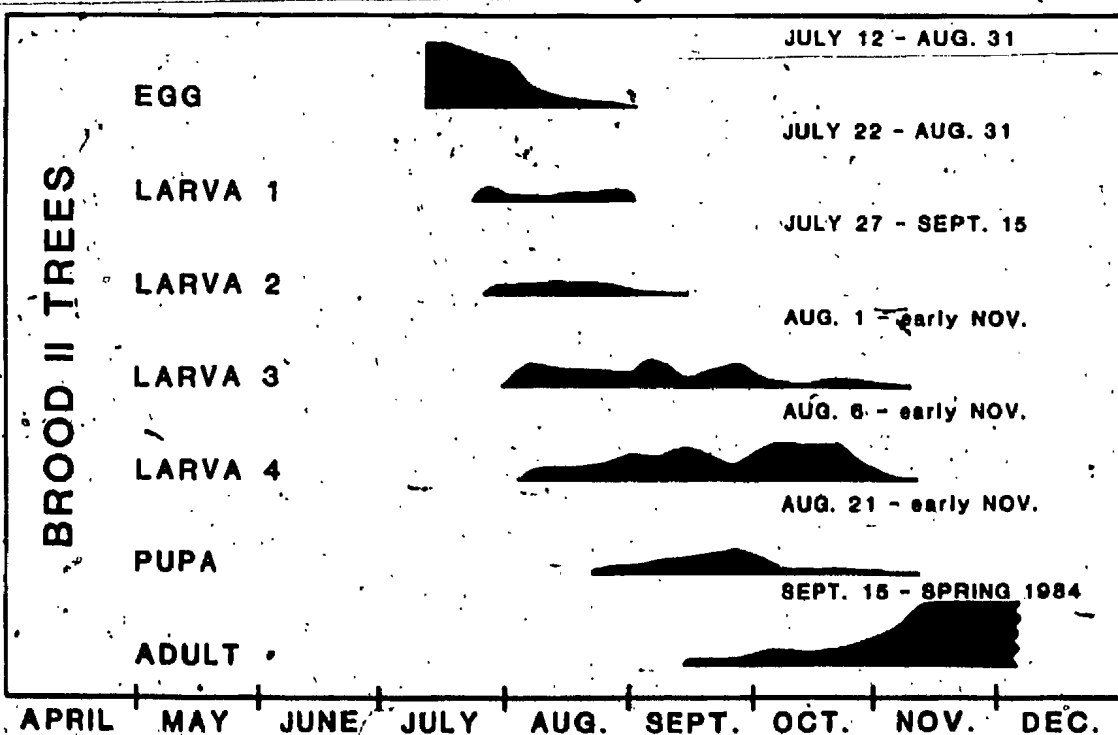
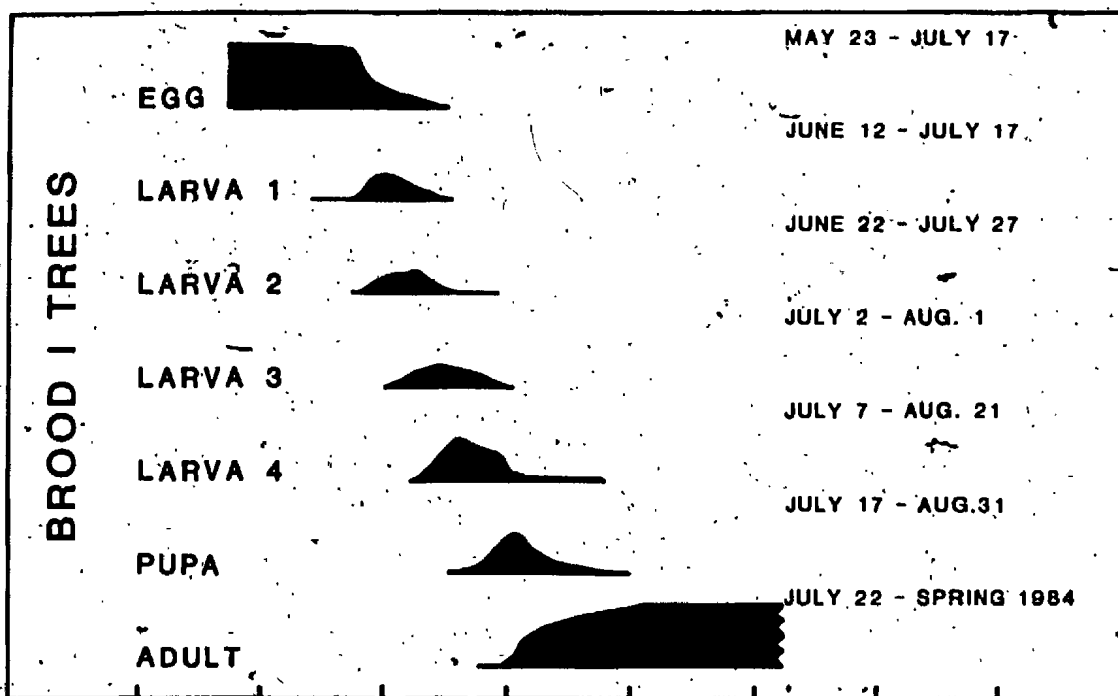
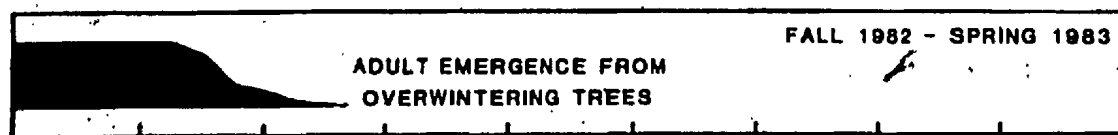


Table 11. Mean (\pm standard deviation) developmental time of each Dendroctonus simplex instar at three temperatures in the laboratory and regression of developmental time (Y) of each instar on rearing temperature (X).

INSTAR	DEVELOPMENTAL TIME (days) \pm SD (n)			N	r ²	REGRESSION EQUATION
	12 °C	18 °C	24 °C			
Egg	19.8 \pm 5.0 (40)	9.9 \pm 0.5 (40)	6.9 \pm 1.0 (26)	106	69.0	Y= 32.3 - 1.13X
Larva I	10.7 \pm 2.8 (16)	4.2 \pm 1.0 (20)	3.6 \pm 0.5 (29)	65	62.9	Y= 16.0 - 0.546X
Larva II	8.6 \pm 1.2 (18)	3.9 \pm 0.8 (18)	4.2 \pm 0.9 (21)	57	58.4	Y= 12.0 - 0.354X
Larva III	13.4 \pm 1.9 (17)	4.3 \pm 0.6 (15)	6.7 \pm 1.4 (12)	44	48.3	Y= 19.1 - 0.613X
Larva IV	17.3 \pm 2.3 (11)	11.0 \pm 0.7 (13)	11.2 \pm 2.2 (14)	38	48.1	Y= 21.8 - 0.482X
Pupa	13.1 \pm 1.7 (12)	8.5 \pm 0.5 (15)	6.7 \pm 0.7 (16)	43	83.9	Y= 19.2 - 0.554X
Life	79.7 \pm 3.3 (13)	41.9 \pm 1.6 (14)	39.2 \pm 3.0 (16)	43	77.1	Y= 113 - 3.28X

populations (Table 12) were similar to developmental times of the same instars at 12 °C in the laboratory (Table 11), whereas, developmental times of the other instars of Brood I were approximately equal to developmental times at 18 °C. Developmental times of the egg and first three larval instars of Brood II (Table 12) were close to those of the same instars at 18 °C in the laboratory (Table 11), whereas, the fourth larval instar of Brood II had a developmental time close to that obtained at 12 °C. The Brood II pupal developmental time was much longer than that at 12 °C. The instar developmental times for New Brunswick field populations (probably first brood) recorded by Prebble (1933) (Table 12) were comparable to those obtained at 18 °C in the laboratory (Table 11).

Regression of developmental times of each instar on rearing temperature yielded r^2 values not less than 0.48 (Table 11). Hence, the regression equations (Table 11) were considered satisfactory for estimating instar developmental time from rearing temperature.

Average air temperature for the duration of the egg and the first and second larval instars in field populations was roughly the same for both broods (Table 12). However, average air temperature for the duration of the third and fourth larval instars and pupal stage of Brood II was about 6 °C lower than for the same instars of Brood I.

Table 12. * Estimated developmental times* (DT) and mean air temperature (MT) for the duration of each Dendroctonus simplex instar in Brood I and Brood II in Newfoundland field populations in 1983 and mean developmental times for field populations in New Brunswick in 1929** (Prebble 1933).

INSTAR	NEWFOUNDLAND				NEW BRUNSWICK
	BROOD I		BROOD II		DT (days)
	DT (days)	MT (°C)	DT (days)	MT (°C)	
Egg	20	12.0	10	15.1	11
Larva I	10	14.0	5	14.5	5
Larva II	10	15.7	5	13.8	6
Larva III	5	16.3	5	10.0	6
Larva IV	10	16.2	15	9.9	10
Pupa	5	14.7	30	8.8	7
Life	60	13.2	70	11.1	45

* interval between the date of the first appearance of succeeding instars

** likely first brood

The development index for *D. simplex* brood at each sample height in Brood 1 trees was generally constant, at 1.0, from 23 May to 22 June but then increased rapidly until brood development was complete at all three sample heights on 5 September (Fig. 20). At each sampling date the brood development index was similar for the lower two sample heights of 0 to 1 m and 2.5 to 3.5 m. However, brood development at 5 to 6 m generally lagged behind that at the other sample heights and was not completed until 15 days after completion of development at the other two heights (Fig. 20).

The development index for brood in each Brood 1 sample tree (all heights combined) was constant, at 1.0, from 23 May to 22 June but increased rapidly until completion of development on 5 September (Fig. 21). Brood development in Tree 1 generally lagged behind that in Tree 2 and was not completed until at least five days after completion of development in Tree 2.

3.1.6 Overwintering behaviour

During the winters of 1982/83 and 1983/84 *D. simplex* overwintered only in the adult stage. Many larvae and pupae were killed by cold as temperatures decreased in October and early November. Live larvae and pupae were absent from field populations by mid-November in 1983 and 1984. It is likely that no parent adults overwintered. Overwintering occurred

Figure 20. Development index of *Dendroctonus simplex* brood at three sample heights of two Brood I trees in Newfoundland field populations from 23 May to 5 September 1983 (n= four 100 cm' samples per height per sample period for all trees combined).

DEVELOPMENT INDEX

- O 0-1M
- X 2.5-3.5M
- 5-6M

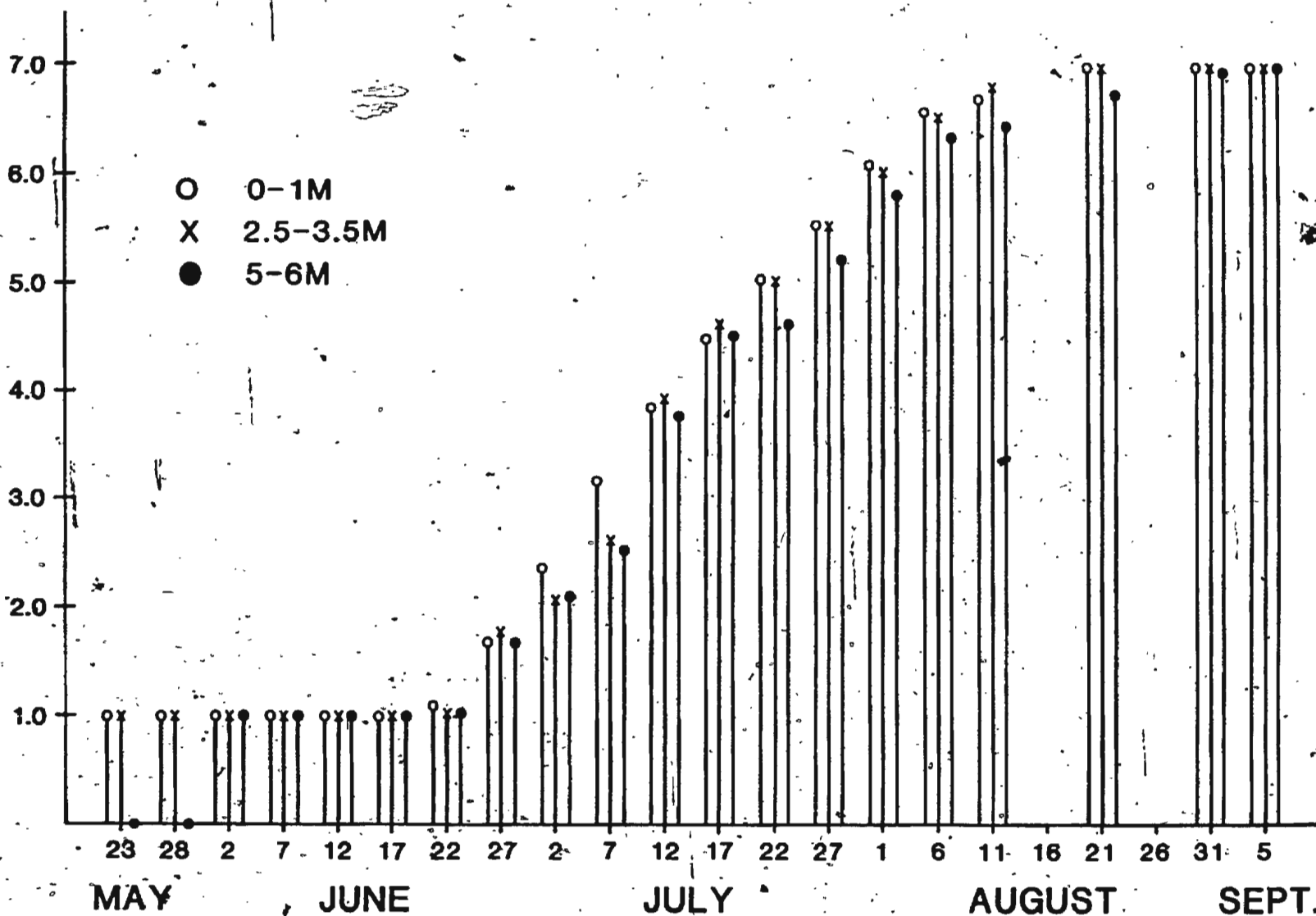
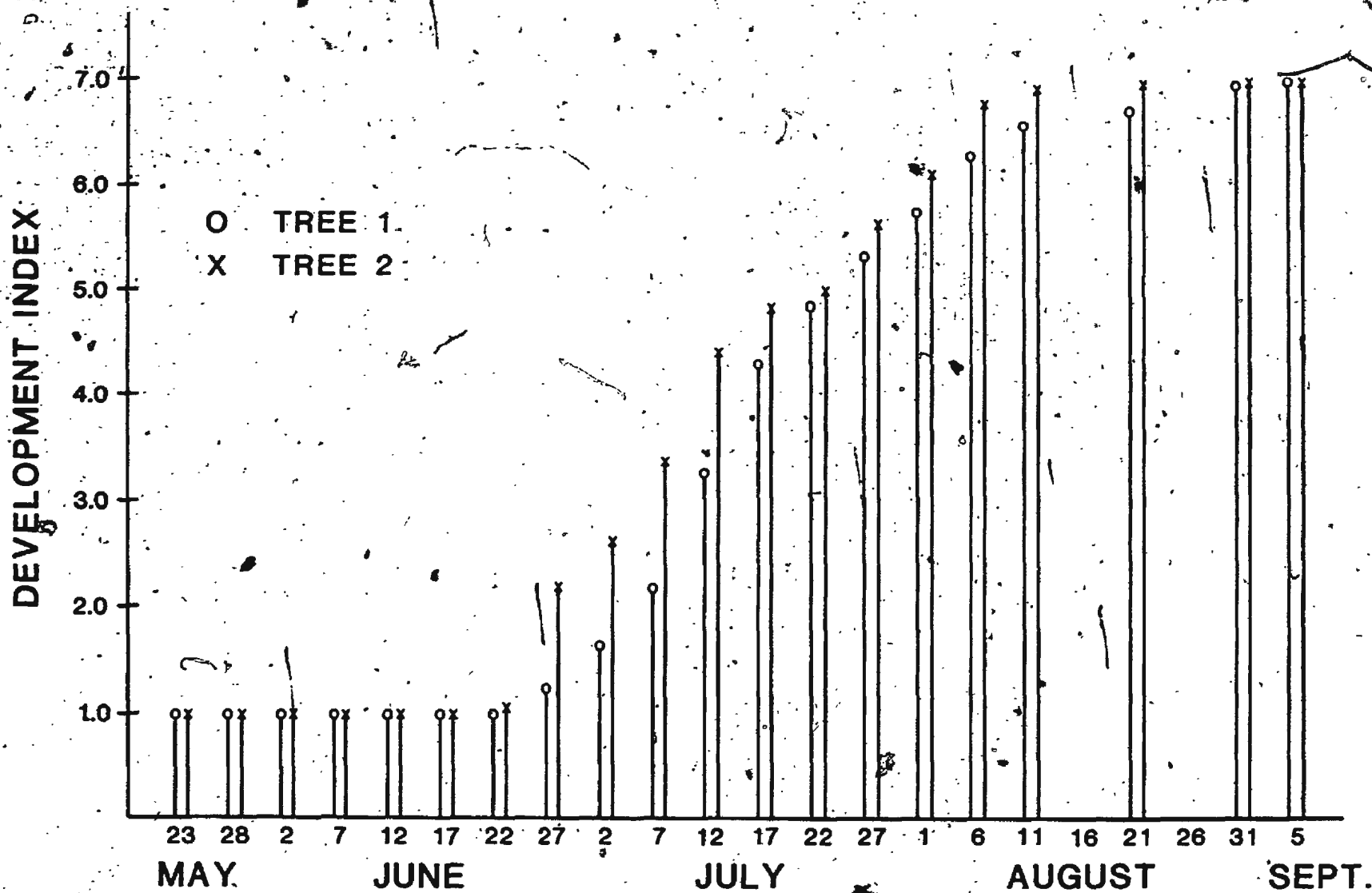


Figure 21. Development index of *Dendroctonus simplex* brood in two Brood I sample trees in Newfoundland field populations from 23 May to 5 September 1983 (n= six 100 cm² samples per tree per sample period for all trees combined).



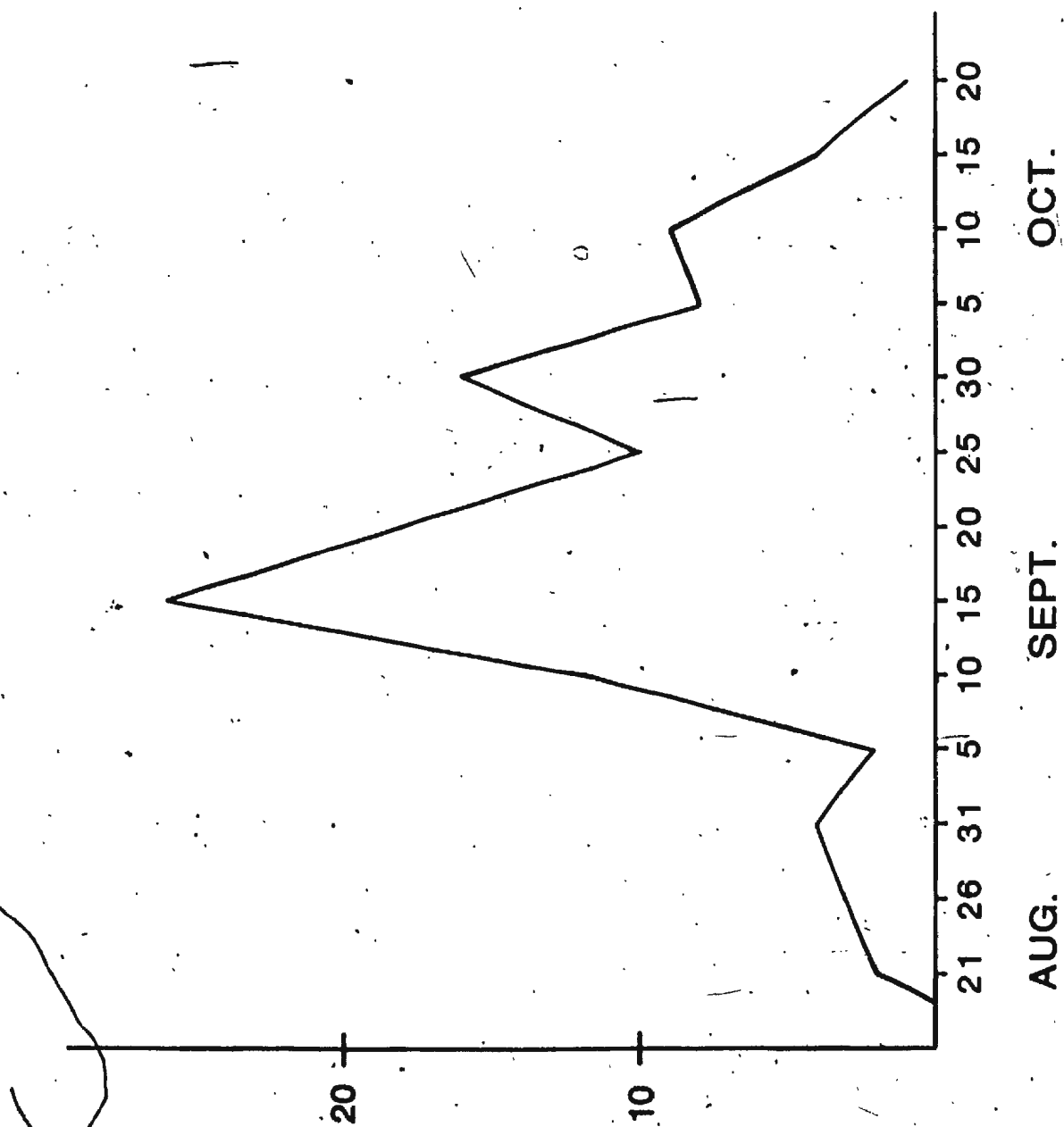
only in the brood trees.

In 1983 new Brood I adults emerged from brood trees between 20 August and 20 October with peak emergence from 10 to 20 September (Fig. 22). An average of 35% of live brood adults emerged from the two sample trees. Emergence was 47%, 33% and 24% representing 5.8, 6.3 and 2.4 beetles per 100 cm² at 0.5 m, 2.5 m and 5 m, respectively. The density of live beetles that did not emerge was 6.6, 12.9 and 7.4 per 100 cm² for the three respective sample heights. No Brood II adults emerged. Emerged beetles possessed poorly developed flight muscles and were judged incapable of flight. Some emerged beetles walked along the bark surface in a general downward direction and others fell to the ground at the base of the trees. No beetles were observed to enter galleries at the bases of trees. Beetles were absent in duff samples collected on 3 December near the bases of the two sample trees.

Galleries in the lower 25 to 30 cm of the boles and in large roots were examined on 3 December and many held large aggregations of brood adults (Fig. 23). Adult density at three sample heights within 1 m of the ground decreased with increased height and was almost three times higher at 0 to 20 cm than at 80 to 100 cm (Table 13). Beetle density was significantly different between the three sample heights. It is not known if Brood I adults emerged from all infested trees at the study site to congregate in galleries at the

Figure 22. Total number of new brood adults emerged from two Brood I trees in Newfoundland field populations of *Dendroctonus simplex* from 20 August to 20 October 1983.

NO. OF EMERGED BEETLES



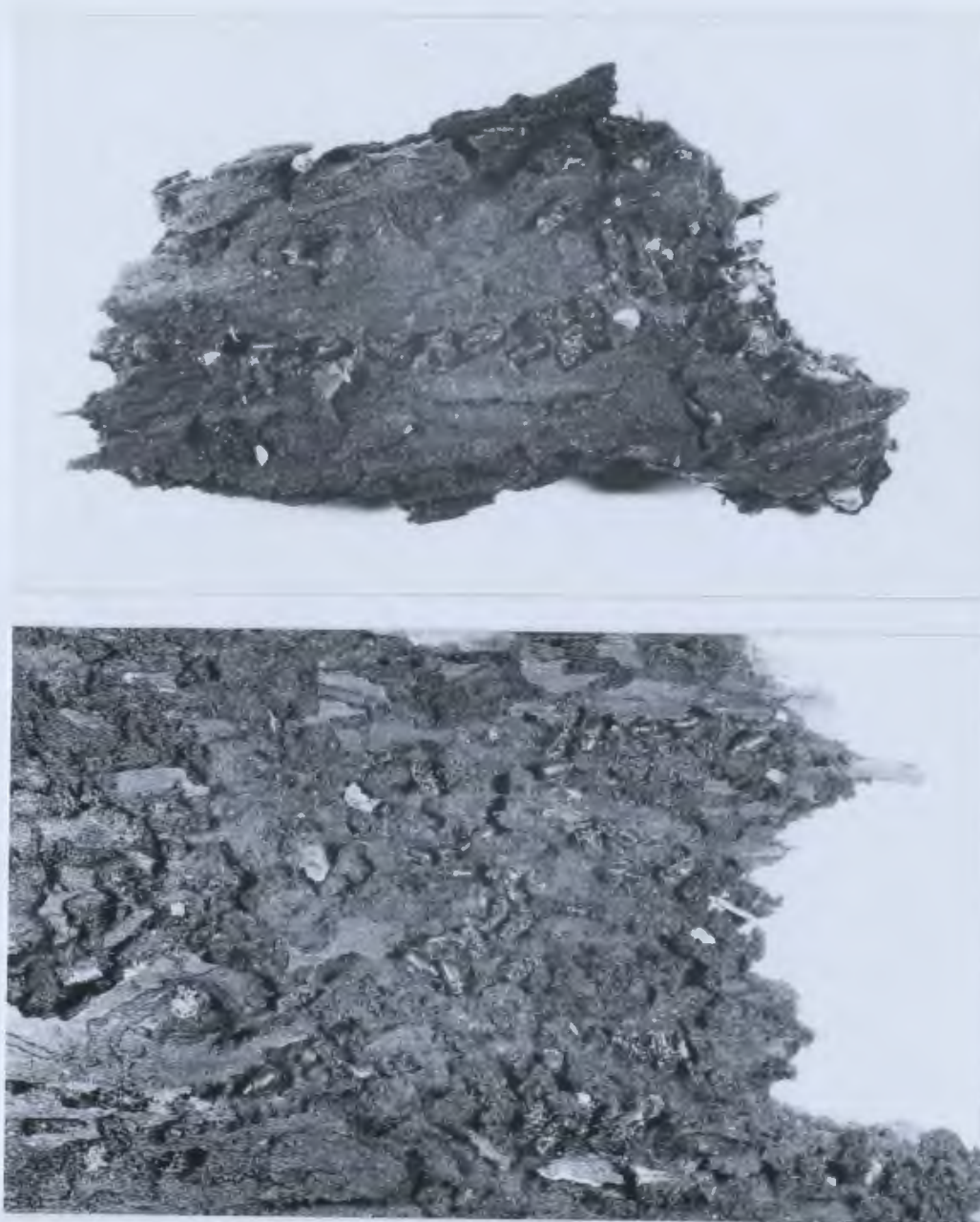


Figure 23. Aggregations of hibernating *Dendroctonus simplex* adults in phloem samples taken from the base of a larch in December 1982 in Newfoundland (magnification= .7X).

Table 13. Mean (\pm standard deviation) density of overwintering Dendroctonus simplex adults at three sample heights of five larch trees in Newfoundland field populations on 3 December 1983 (n= 2 samples per height per tree).

SAMPLE HEIGHT (cm)	MEAN BEETLE DENSITY PER 100 cm (\pm SD)					
	TREE 1	TREE 2	TREE 3	TREE 4	TREE 5	AVERAGE
0 - 20	34.5 \pm 14.8	23.0 \pm 4.2	26.0 \pm 7.1	32.5 \pm 5.0	28.0 \pm 2.8	28.8 \pm 7.4
40 - 60	20.5 \pm 9.2	19.5 \pm 2.1	23.5 \pm 5.0	15.5 \pm 2.1	15.0 \pm 0.0	18.8 \pm 4.9
80 - 100	10.0 \pm 2.8	15.5 \pm 5.0	11.5 \pm 6.4	10.0 \pm 1.4	8.5 \pm 2.1	11.1 \pm 3.9

base.

3.2 MORTALITY

3.2.1 Brood mortality

There was high mortality among *D. simplex* brood in Newfoundland field populations in 1983 caused by several agents. Instar specific mortality and the proportion of mortality due to each causal agent generally varied between instars, between heights of trees, between trees and between first and second broods.

Egg, larval and pupal mortality

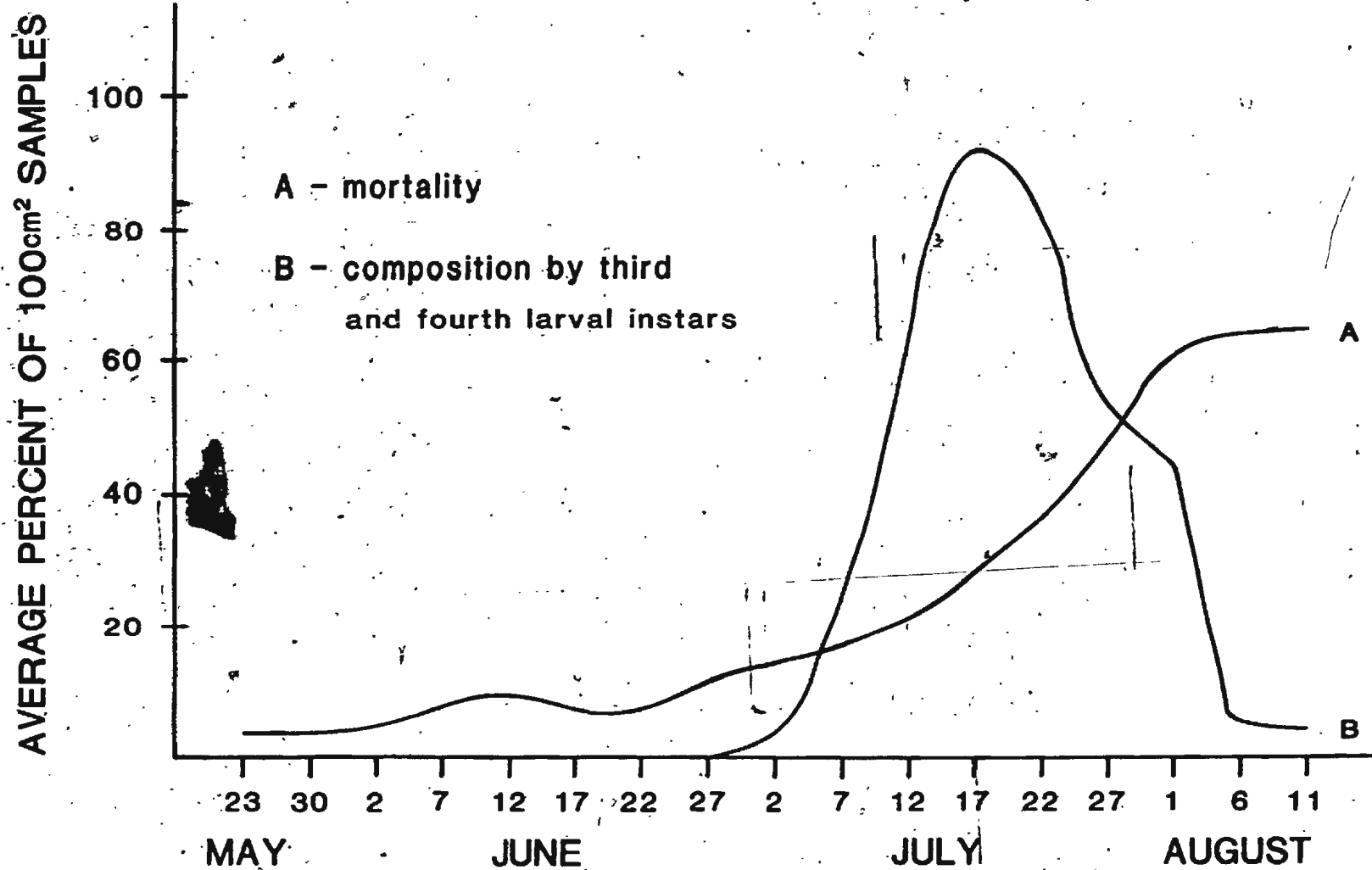
In field populations third and fourth larval instars had the highest mortality and the pupal instar the lowest (Table 14). Average mortality of Brood I larvae increased sharply as percent composition of brood in samples by third and fourth larval instars increased (Fig. 24).

There were significant differences in mortality between sample heights of Brood I trees for third and fourth larval instars (Appendix G) with mortality at 0 to 1 m significantly lower than at the other heights (Table 14). Mortality of the other instars did not differ significantly between sample heights. Mortality of third and fourth larval instars and pupae in field populations differed significantly between the two Brood I sample trees (Appendix H) with highest mortality occurring in Tree 2. There were no

Table 14. Estimated instar specific mortality for each sample height of Brood I and Brood II trees in Newfoundland field populations of Dendroctonus simplex in 1983 and for broods in caged larch bolts.

BROOD	SAMPLE HEIGHT (m)	PERCENT MORTALITY (NUMBER OF 100 cm ² SAMPLES)					
		EGG	LARVA I	LARVA II	LARVA III	LARVA IV	PUPA
I	0 - 1	8.8 (33)	9.4 (29)	8.2 (24)	9.6 (18)	19.6 (12)	6.5 (12)
"	2.5 - 3.5	8.8 (31)	9.4 (27)	8.5 (24)	17.3 (21)	33.0 (12)	7.6 (12)
"	5 - 6	8.5 (32)	9.0 (27)	8.8 (24)	19.7 (15)	37.5 (12)	9.5 (12)
"	Average	8.7 (96)	9.3 (83)	8.5 (72)	14.8 (54)	29.2 (36)	7.6 (36)
II	0 - 2	14.9 (35)	9.3 (16)	7.9 (15)	10.2 (11)	33.3 (9)	6.4 (10)
Bolts	—	5.0 (21)	1.8 (21)	0.9 (21)	0.7 (21)	0.5 (21)	0.1 (21)

Figure 24. Average mortality of *Dendroctonus simplex* brood in 100 cm³ phloem samples and average percent composition of brood by third and fourth instar larvae in Brood I sample trees in Newfoundland field populations from 23 May to 11 August 1983.



significant differences for the other instars. Only egg mortality differed significantly between Brood I and Brood II (Appendix I) with egg mortality in Brood I, at 8.7%, lower than that in Brood II, at 14.9% (Table 14). Broods reared in caged larch bolts had significantly lower mortality for all instars than did Brood I in field populations (Table 14).

(Estimates of total mortality from egg to adult, calculated by dividing average density of brood adults in trees before emergence for hibernation in the fall by average density of eggs laid by parents, were consistently higher than estimates calculated by multiplying percent mortality in each instar (Table 14) by proportion of original number of adults that lived to reach that instar and summing for all instars (Table 15). Total brood mortality at 0 to 1 m was lower by about 15 to 20 percent units than at 2.5 to 3.5 m and 5 to 6 m. Total mortality for Brood I and Brood II field populations was similar, however, mortality was much lower for broods produced in caged larch bolts.

Causal agents

Mortality due to pathogens, predators, hymenopterous parasitoids, resinosis and low temperatures were recognizable in field populations. Pathogens caused the largest recognizable proportion of mortality among eggs, the second larval instar and pupae of both broods (Table 16).

Table 15. Total mortality from egg to adult for each sample height of Brood I and Brood II sample trees in Newfoundland field populations of Dendroctonus simplex and for broods in caged larch bolts.

BROOD	SAMPLE HEIGHT (m)	PERCENT MORTALITY							AVERAGE NUMBER / 100 cm ² (NUMBER OF SAMPLES)		TOTAL** MORTALITY (%)
		EGG	LARVA I	LARVA II	LARVA III	LARVA IV	PUPA	TOTAL*	EGGS	BROOD ADULTS	
I	0 - 1	8.8	8.6	6.8	7.3	13.4	3.6	48.5	57 (36)	20 (9)	65
"	2.5 - 3.5	8.8	8.6	7.0	13.1	20.6	3.2	61.3	58 (36)	11 (10)	81
"	5 - 6	8.5	8.2	7.3	15.0	22.9	3.6	65.5	56 (36)	8 (13)	86
"	Average	8.7	8.5	7.0	11.2	18.9	2.9	57.2	57 (108)	12 (32)	79
II	0 - 2	14.9	7.9	6.1	7.3	21.2	2.7	60.1	22 (50)	4 (4)	82
Bolts	—	5.0	1.7	0.8	0.7	0.5	0.1	8.8	—	—	—

* Estimated by multiplying instar specific mortality (Table 14) by the proportion of the original number of individuals that lived to reach that instar and summing for all instars

** Estimated by dividing average brood adult density in brood trees before winter emergence by average density of eggs laid by parents

Table 16. Percent of total mortality within each instar attributable to each causal agent, for Brood I and Brood II in Newfoundland field populations of Dendroctonus simplex in 1983.

INSTAR	BROOD I								BROOD II							
	NUMBER DEAD	PERCENT OF TOTAL MORTALITY						PERCENT SURVIVORS	NUMBER DEAD	PERCENT OF TOTAL MORTALITY						PERCENT SURVIVORS
		PT	PR	H	R	T	U			PT	PR	H	R	T	U	
Egg	421	22.3	*	—	*	—	77.7	91.3	70	15.7	—	—	*	—	84.3	75.1
Larva I	241	22.0	3.3	7.1	28.6	—	39.0	90.7	47	21.3	—	—	40.4	—	38.3	90.7
Larva II	149	18.8	4.0	20.1	10.1	—	46.9	91.5	32	31.3	—	—	18.8	12.5	37.4	92.1
Larva III	379	13.5	1.6	67.8	—	—	17.7	85.2	19	25.0	—	40.0	—	15.0	20.0	89.8
Larva IV	503	9.7	0.8	72.4	—	—	17.1	80.8	52	5.8	—	7.7	—	59.6	26.9	66.7
Pupa	67	49.3	3.0	—	—	—	47.7	92.4	3	67.7	—	—	—	—	33.3	93.6
Weighted Average	1754	18.0	1.3	38.0	4.9	—	37.8	42.8	223	18.3	—	5.4	11.2	17.0	48.1	39.9

PT - pathogens; PR - predators; H - hymenopterous parasitoids; R - resinosis; T - low temperatures;
 U - unknown causes; * - could not be recognized and included in unknown causes.

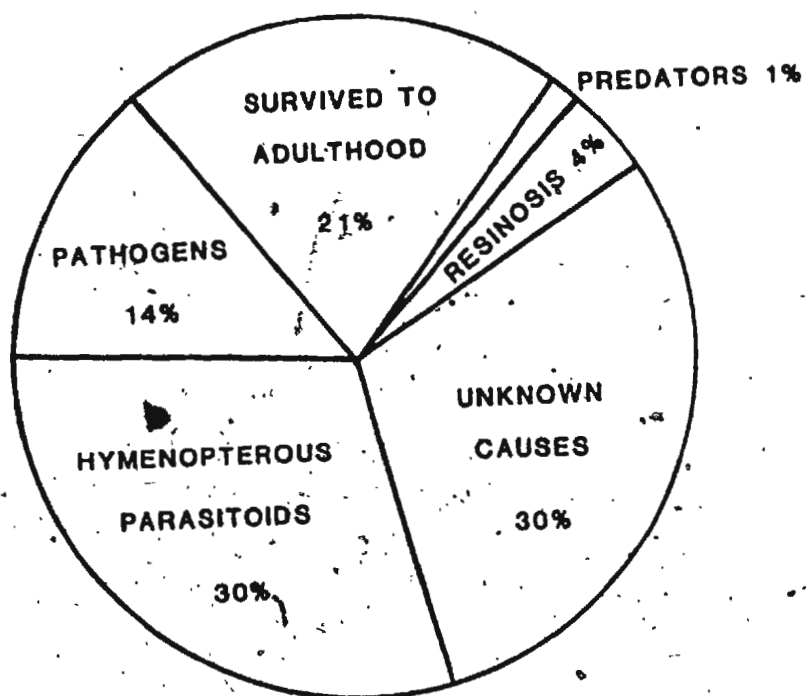
Hymenopterous parasitoids generally caused the largest proportion of mortality among third and fourth larval instars and resinosis among first instar larvae. Mortality of eggs due to resinosis was not recognizable but was likely significant. Low temperatures caused the most mortality among fourth instar larvae of Brood II. (Table 16).

Parasitoids and pathogens caused the largest recognizable proportion of mortality in Brood I and Brood II, respectively (Fig. 25). Mortality due to resinosis in Brood II was twice that for Brood I and mortality due to parasitoids in Brood II was only one-sixth of that for Brood I. Low temperatures caused 14% mortality in Brood II but none in Brood I. Parasitoids caused the largest recognizable proportion of mortality at each sample height of Brood I trees but their effect was twice as high at 2.5 to 3.5 m and 5 to 6 m than at 0 to 1 m (Fig. 26). Mortality caused by the other agents was similar for all sample heights. Parasitoids also caused the largest recognizable proportion of mortality in each of the two Brood I sample trees (all sample heights combined) but was higher in Tree 2 than in Tree 1 (Fig. 27). Mortality caused by the other agents was similar between sample trees.

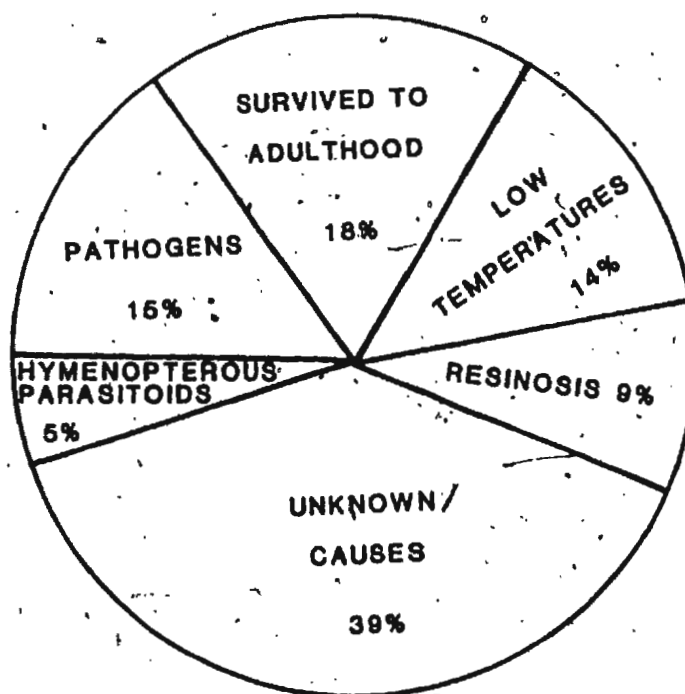
Brood adult mortality

Mortality among teneral brood adults in Brood I trees before winter was 6.1% (N= 51 dead beetles) and 8.7% (N= 2 dead beetles) in Brood II trees. Most of this mortality

Figure 25. Percent mortality attributable to each causal agent for Brood I and Brood II in Newfoundland field populations of *Dendroctonus simplex* in 1983.

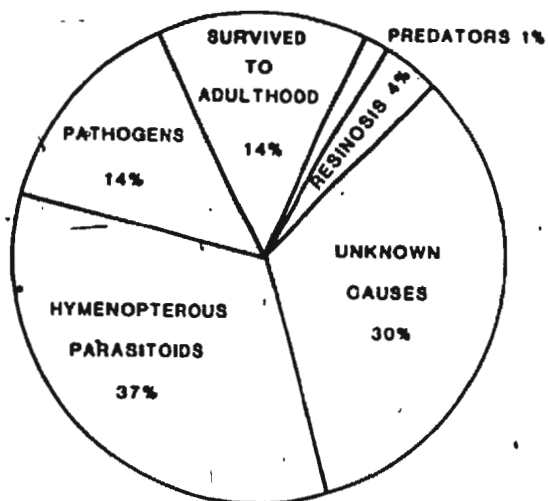


BROOD I

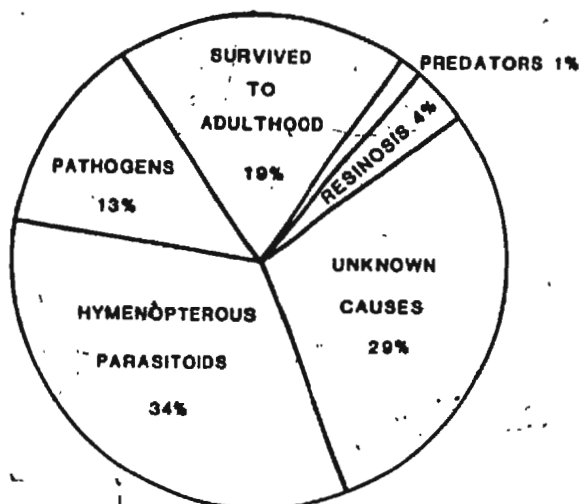


BROOD II

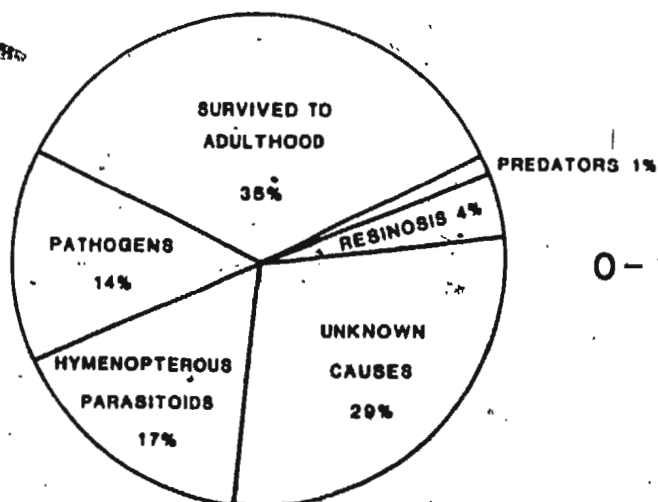
Figure 26. Percent mortality attributable to each causal agent at three heights of Brood I sample trees for Newfoundland field populations of *Dendroctonus simplex* in 1983.



5-6M

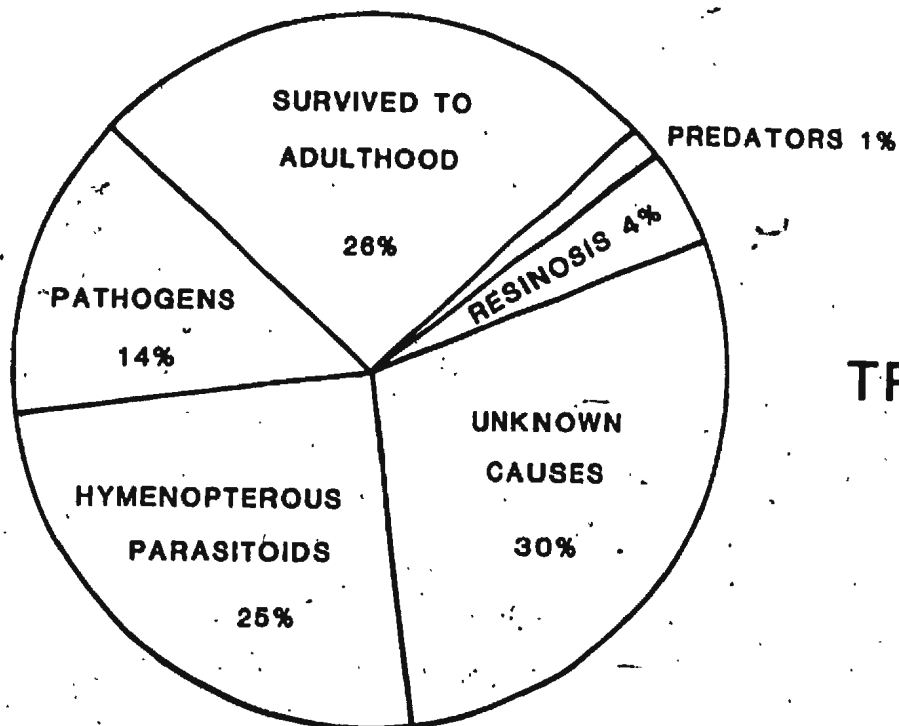


2.5-3.5M

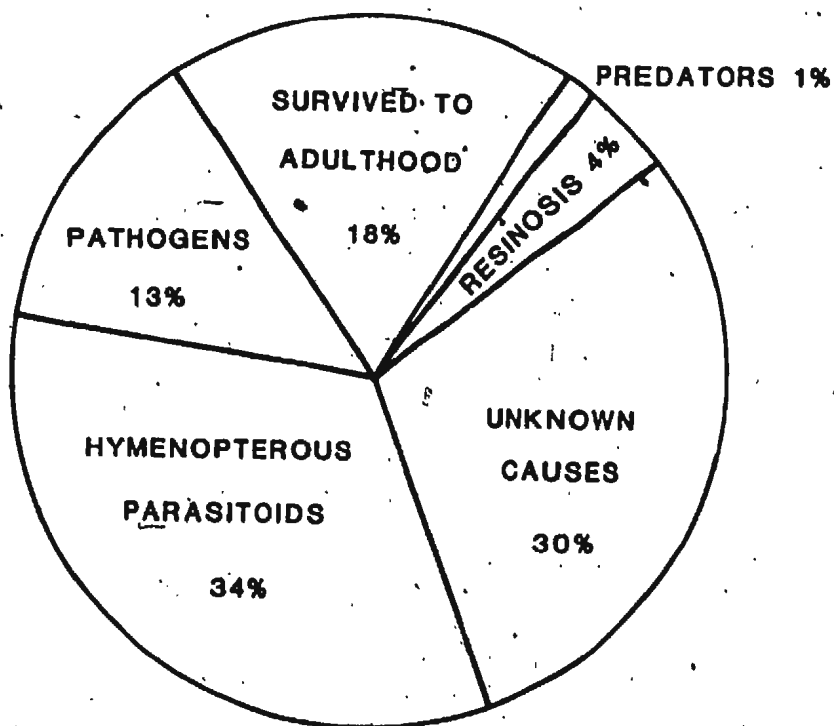


0-1M

Figure 27. Percent mortality attributable to each causal agent in two Brood I sample trees for Newfoundland field populations of *Dendroctonus simplex* in 1983.



TREE 1



TREE 2

appeared to be caused by pathogens. There was no significant difference in brood adult mortality between Brood I and Brood II, between sample heights of Brood I trees or between the two Brood I sample trees. No teneral adult mortality was observed among broods produced in caged larch bolts.

Brood adult mortality caused by woodpecker predation varied between years and trees. During the winter of 1982/83 there was very little woodpecker predation at the study site. However, during the 1983/84 winter woodpecker predation was higher and all 13 trees containing brood adults at the study site were foraged upon by woodpeckers, from 1 m above ground level to the top of the infested bole. From less than 1% to approximately 10%, with an estimated average of 3%, of the bark surface of infested bole of each tree was removed by woodpecker foraging. As much as 60% to 80% of the bark on some trees can be removed by woodpeckers (Raske 1984 - personal communication).

Mortality caused by low temperature is discussed in a separate section.

3.2.2 Overwintering mortality and cold tolerance

Overwintering mortality

Increase in mortality of overwintering adults between the two sampling dates, 19 November 1982 and 21 April 1983, was assumed to be overwintering mortality. There was an overall increase in mortality between the two sampling

dates, however, only two of four sample trees showed a significant increase (Table 17). Overwintering mortality averaged 7.8% for all sample trees. Adult mortality at 0.5 m and 2.5 m increased significantly between sampling dates but did not at 5 m (Table 17). There was a significant increase in mortality among beetles that overwintered at the northern aspect of trees as opposed to the southern aspect where there was no significant increase (Table 17).

Snow level was never higher than 30 cm around the bases of sample trees during the winters of 1982/83 and 1983/84, respectively.

Cold tolerance

Adult *D. simplex* collected from field populations on 6 October 1983, 11 November 1983 and 2 January 1984 and stored at selected temperatures for various lengths of time generally showed an increase in mortality at each temperature as treatment duration increased (Table 18). Mortality among beetles collected from field populations on 6 October and 11 November generally showed the greatest increase during the first two days of treatment at each temperature. As treatment duration increased beyond two days mortality rate gradually decreased. Mortality was lowest at 0 °C and was increasingly higher at 5 °C, -5 °C, -10 °C, -15 °C and -20 °C, respectively. Mortality among beetles collected from field populations on 11 November was generally lower at each temperature and treatment duration

Table 17. Mortality among overwintering Dendroctonus simplex adults in Newfoundland field populations in fall 1982 and spring 1983 by sample tree, height and tree aspect.

SAMPLE TREE	SAMPLE HEIGHT (m)	TREE ASPECT	19 NOVEMBER 1982		21 APRIL 1983		OVERWINTERING MORTALITY** (%)	F-RATIO
			NO. 100 cm ² SAMPLES	PERCENT MORTALITY	NO. 100 cm ² SAMPLES	PERCENT MORTALITY		
1	All	All	6	1.3	6	12.0	10.7	8.19*
2	"	"	6	11.7	6	14.3	2.6	0.02
3	"	"	6	2.8	6	13.2	10.4	11.75*
4	"	"	6	1.5	6	8.5	7.0	2.26
Average / Total			24	4.6	24	12.4	7.8	9.09*
All	0.5	All	8	4.6	8	14.2	9.6	7.17*
"	2.5	"	8	3.2	8	12.6	9.4	4.80*
"	5.0	"	8	6.2	8	8.8	2.6	0.12
"	All	North	12	4.3	12	15.0	10.7	7.32*
"	"	South	12	4.9	12	9.9	5.0	2.51

* significant at $p < 0.05$

** difference in mortality between the two sampling dates

Table 18. Percent mortality of Dendroctonus simplex adults
at various temperature and duration treatments (n= 50 beetles
per sample).

DATE BEETLES COLLECTED FROM FIELD	TREATMENT TEMPERATURE (°C)	PERCENT MORTALITY AT EACH TREATMENT DURATION (days)					
		2	4	8	16	32	64
6 October 1983	5	2	0	10	6	10	30
	0	0	0	6	6	22	18
	-5	32	36	44	26	52	50
	-10	58	30	46	48	72	100
	-15	100	100	100	100	--	--
	-20	100	100	100	--	--	--
11 November 1983	5	0	0	2	14	12	28
	0	0	0	0	6	10	4
	-5	22	30	28	30	32	22
	-10	30	34	50	48	40	68
	-15	62	68	70	100	--	--
	-20	84	100	100	--	--	--
2 January 1984	5	0	0	0	2	10	10
	0	0	0	2	2	2	6
	-5	0	2	2	0	4	6
	-10	0	0	0	2	4	6
	-15	0	0	0	2	12	10
	-20	0	2	0	4	8	10

than for beetles collected on 6 October and mortality among beetles collected on 2 January was even lower.

Percent mortality of *D. simplex* adults at -15°C and -20°C generally differed between acclimated and non-acclimated beetles for each treatment duration (Table 19). It took much longer for mortality to reach 100% among acclimated beetles than among non-acclimated ones.

Pronotal width was used as an index of beetle size. For each treatment duration at -5°C and -10°C average size of living beetles was larger than that of dead beetles. The difference was significant for only one treatment duration at -5°C but for four treatment durations at -10°C (Table 20). However, average size of living beetles for all treatment durations combined at each temperature and for the grand average of both temperature treatments combined, was significantly larger than that of beetles killed by the treatments (Table 20).

Percent mortality among males was higher than among females for most treatments (Table 20). Male mortality was only three percentage units higher than female mortality for all samples stored in -5°C combined, whereas, male mortality was 15 percentage units higher than female mortality in all samples stored at -10°C combined.

Sex and beetle size appear to be related to mortality. Females tend to be larger and more likely to survive.

Table 19. Percent mortality of acclimated and non-acclimated Dendroctonus simplex adults at two cold temperature treatments for various treatment durations (n= 50 beetles per sample). Beetles were collected from the field on 6 October 1983.

TREATMENT TEMPERATURE (°C)	TREATMENT DURATION (days)	PERCENT MORTALITY	
		ACCLIMATED* BEETLES	NON-ACCLIMATED BEETLES
-15	2	28	100
	4	76	100
	8	92	100
	16	100	100
-20	2	74	100
	4	98	100
	8	100	100

* Acclimation was accomplished by decreasing the storage temperature of the beetles from 5 °C to the desired treatment temperature by intervals of 5 °C every 2 days.

Table 20. Average pronotal width of live and dead adult

Dendroctonus simplex and percent mortality among males and females for each treatment duration at -5 °C and -10 °C (n= 50 beetles per sample). Beetles were collected on 11 November 1983.

TEMPERATURE TREATMENT (°C)	TREATMENT DURATION (days)	AVERAGE PRONOTAL WIDTH IN mm (NO. BEETLES)		PERCENT MORTALITY	
		LIVE	DEAD	MALES	FEMALES
-5	2	1.81 (39)	1.75 (11)	23.1	20.8
	4	1.79 (35)	1.76 (15)	28.6	36.4
	8	1.82 (36)	1.79 (14)	32.0	24.0
	16	1.82 *(35)	1.77 (15)	42.3	29.2
	32	1.80 (34)	1.76 (16)	36.4	28.6
	64	1.81 (39)	1.76 (11)	20.0	25.0
	Average	1.81*(218)	1.77 (82)	30.0	27.3
-10	2	1.88 (35)	1.84 (15)	39.3	18.2
	4	1.86 *(33)	1.78 (17)	33.3	30.4
	8	1.87 *(25)	1.80 (25)	43.5	48.1
	16	1.85 *(26)	1.78 (24)	55.0	40.0
	32	1.83 (30)	1.79 (20)	46.4	31.8
	64	1.87 *(16)	1.79 (34)	81.2	44.4
	Average	1.86*(165)	1.79 (135)	50.6	35.9
Grand Average		1.83*	1.78	40.3	31.6

* Pronotal widths of live individuals significantly ($p < 0.05$) larger than those of dead.

3.3 ASSOCIATED ORGANISMS

Fifty-two species of insects, spiders, mites and nematodes were associated with *D. simplex* in eastern Newfoundland in 1983, of which as many as nineteen may have been predators and as many as eight may have been parasitoids (Table 21). Most of the remainder were competitors, scavengers or fungus feeders.

3.3.1 Predators

The species observed to prey upon *D. simplex* were the beetle *Rhizophagus* sp., larvae of a fly species of *Medetera* and larvae of a stratiomyid fly species. The most common predator was *Medetera* sp. In 1982 *Medetera* larvae and pupae overwintered in the same trees as *D. simplex*, emerged as adults between 10 and 20 June 1983 and arrived at trees containing *D. simplex* brood by 12 June. Stratiomyid and *Medetera* larvae were observed to prey on *D. simplex* larvae from 27 June to 21 August and overwintered in trees with their hosts. No stratiomyid adults were observed. Stratiomyid and *Medetera* larvae were observed to feed upon dead *D. simplex* larvae and adults in the spring. Adult *Rhizophagus* were found in galleries preying on *D. simplex* larvae and pupae from 17 June to 11 August. Adults were also collected from *D. simplex* infested trees during the winter. No larvae were observed. Predators were not found in *D. simplex* galleries in Brood 11 trees.

Table 21. Associates of Dendroctonus simplex in eastern Newfoundland.

C - competitor; PR - predator; P - parasitoid; S - scavenger;

F - fungus feeder; A - adults; L - larvae; J - juveniles; E - eggs;

H - hyperparasitoid.

SPECIES	NUMBER COLLECTED	PROBABLE ROLE
COLEOPTERA		
Cerambycidae		
<u>Stictoleptura canadensis</u> (Oliv.)	25 L	C, PR*
Curculionidae		
<u>Hylobius pinicola</u> Coup.	2 A	C
Histeridae		
<u>Paromalus bistriatus</u> Er.	2 A	PR
Lathridiidae		
<u>Corticaria</u> sp.	4 A	F
Nitidulidae		
<u>Epuraea truncatella</u> Mann.	50+ A; 500+ L	F
Ptilidae sp.	12 A	F
Rhizophagidae		
<u>Rhizophagus</u> sp.	10 A	PR
Scolytidae		
<u>Crypturgus pusillus</u> (Gyll.)	1 A	C
<u>Dryocoetes autographus</u> (Ratz.)	1 A	C
<u>Polygraphus rufipennis</u> (Kby.)	2 A	C
Scymaenidae		
<u>Stenichnus</u> sp.	1 A	S
Staphylinidae		
Aleocharinae 3 spp.	500+ A	PR
<u>Atheta</u> sp.	19 A	PR
<u>Atrechus macrocephalus</u> (Nordm.)	5 A	PR
<u>Carphacis nepigonensis</u> (Bernh.)	3 A	PR
<u>Nudobius cephalus</u> (Say)	9 A	PR
<u>Phloeonomus pusillus</u> Grav.	50+ A	PR
<u>Placusa</u> sp.	42 A	PR

Table 21 cont'd

<u>Quedius laevigatus</u> Gyll.	4 A	PR
<u>Siagonium americanum</u> Melsh.	1 A	PR
<u>S. punctatum</u> Lec.	2 A	PR

DIPTERA

Cecidomyiidae		
<u>Aprionus asemus</u> Pritchard	2 A	F
Dolichopodidae		
<u>Medetera</u> sp.	4 A; 300+ L	PR/S
Lonchaeidae		
<u>Lonchaea maniola</u> McAlpine ?	1 A	PR
Scatopsidae		
<u>Rhexoza</u> sp.	1 A	F
Sciaridae		
<u>Chaetosciara</u> sp.	4 A	F
<u>Scatosciara</u> sp.	7 A	F
Stratiomyidae		
Pachygastrinae sp.	100+ L	PR
Xylophagidae		
<u>Xylophagus abdominalis</u> Lw.	1 A	PR

HEMIPTERA

Anthocoridae		
<u>Tetraphleps uniformis</u> Parshley	4 A	PR
<u>T. canadensis</u> Provancher	1 A	PR

HYMENOPTERA

Braconidae		
<u>Spathius canadensis</u> Ashmead	18 A; 100+ L	P
Diapriidae		
<u>Coptera atricornis</u> Ashmead	4 A	P
Ichneumonidae		
<u>Gelis</u> sp.	1 A	H

Table 21 cont'd

Pteromalidae

<u>Chlorocytus</u> sp.	1 A	P or H
<u>Dibrachys</u> sp.	1 A	P or H
<u>Lamprotatus</u> sp.	5 A	P or H
<u>Rhopalicus tutela</u> (Walker)	20 A; 100+ L	P
<u>Xiphydriophagus meyerinckii</u> (Ratz.)	8 A	P or H

Torymidae

<u>Liodontomerus</u> sp.	1 A	P or H
<u>Roptrocercus xylophagorum</u> (Ratz.)	7 A; 500+ L	P

ARANEAE

Clubionidae

<u>Clubiona canadensis</u> Emerton	4 J	
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Erigonidae

<u>Grammonota</u> sp.	23 J	
<u>Sisicottus montanus</u> (Emerton)	1 A	
<u>S. montigenus</u> Bishop and Crosby	2 A	
<u>Pocadicnemis pumila</u> (Blackwall)	1 A	

OPILIONES

<u>Odiellus pictus</u> (Wood)	14 J; 26 E	?
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ACARI

Uropodidae

<u>Oodinychus</u> sp. <u>soeiata</u> -group	5000+ A	?
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Parasitidae

<u>Paragamasus</u> sp.	5000+ A	?
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NEMATODES

<u>Cryptaphelenchus</u> sp.	many	F
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* accidental; ? role unknown

The three predator species appeared to be more abundant in the lower 2 m of tree boles, however, there was little quantitative data to confirm this.

Other species suspected but not observed to prey on *D. simplex* were larvae of the flies *Lonchaea maniola* and *Xylophagus abdominalis*, the Bugs *Tetraphleps uniformis* and *T. canadensis*, the hisster beetle *Paromalus bistriatus* and the staphylinid beetles. The staphylinids *Atheta* sp., *Carphacis nepigonensis* and the three unidentified aleocharine species were observed to eat dead insect material. All the suspected predators of *D. simplex* were collected from beetle galleries except for *L. maniola* and *X. abdominalis* adults which were collected from the bark surface of *D. simplex* infested trees. Of the staphylinid species - *Phleonomus pusillus*, *Atheta* sp., *Quedius laevigatus*, *Nudobius cephalus*, *Placusa* sp. and the three unidentified aleocharine species overwintered in the same trees as *D. simplex* where they were most abundant in the lower 2 m of infested bole at densities of up to forty to fifty per 100 cm², mainly aleocharines, in some trees. Many staphylinid larvae were found in *D. simplex* galleries but were not identified.

3.3.2 Parasitoids

Of the ten species of Hymenoptera only the larvae of *Roptrocerus xylophagorum*, *Rhopalicus tutela* and *Spathius*

canadensis were observed to feed on *D. simplex* larvae, *R. xylophagorum* being the more abundant. The other Hymenoptera are believed to be either parasitoids of *D. simplex* or of other insects associated with *D. simplex* or hyperparasitoids.

Larvae and pupae of the three species observed to parasitize *D. simplex* overwintered in the same trees as their hosts in 1982, resumed development in the spring of 1983 and emerged between 19 June and 8 July. Eggs and larvae were observed in *D. simplex* larval mines by 21 June and 27 June, respectively. Adult *R. xylophagorum* were observed to mate on the external surface of trees containing *D. simplex* brood. Mating of the other Hymenoptera species was not observed. Some *R. xylophagorum* females entered larch beetle egg galleries via ventilation or entrance holes, presumably to oviposit, while others oviposited through the bark. Only one egg was laid on or near each host (Fig. 28). Adult *R. tutela* and *S. canadensis* were not observed in egg galleries but oviposited through the bark. All observed *D. simplex* larvae with parasitoid eggs laid on or near them were immobile, apparently dead or paralyzed. Larvae of the three known *D. simplex* parasitoids were ectoparasitic (Fig. 28) on all *D. simplex* larval instars but were much more abundant on third and fourth instars. Parasitoid larvae were found in all regions of the infested boles of Brood I trees but were most abundant in the middle and upper regions. The average number of parasitoid larvae per 100 cm² of phloem was four,

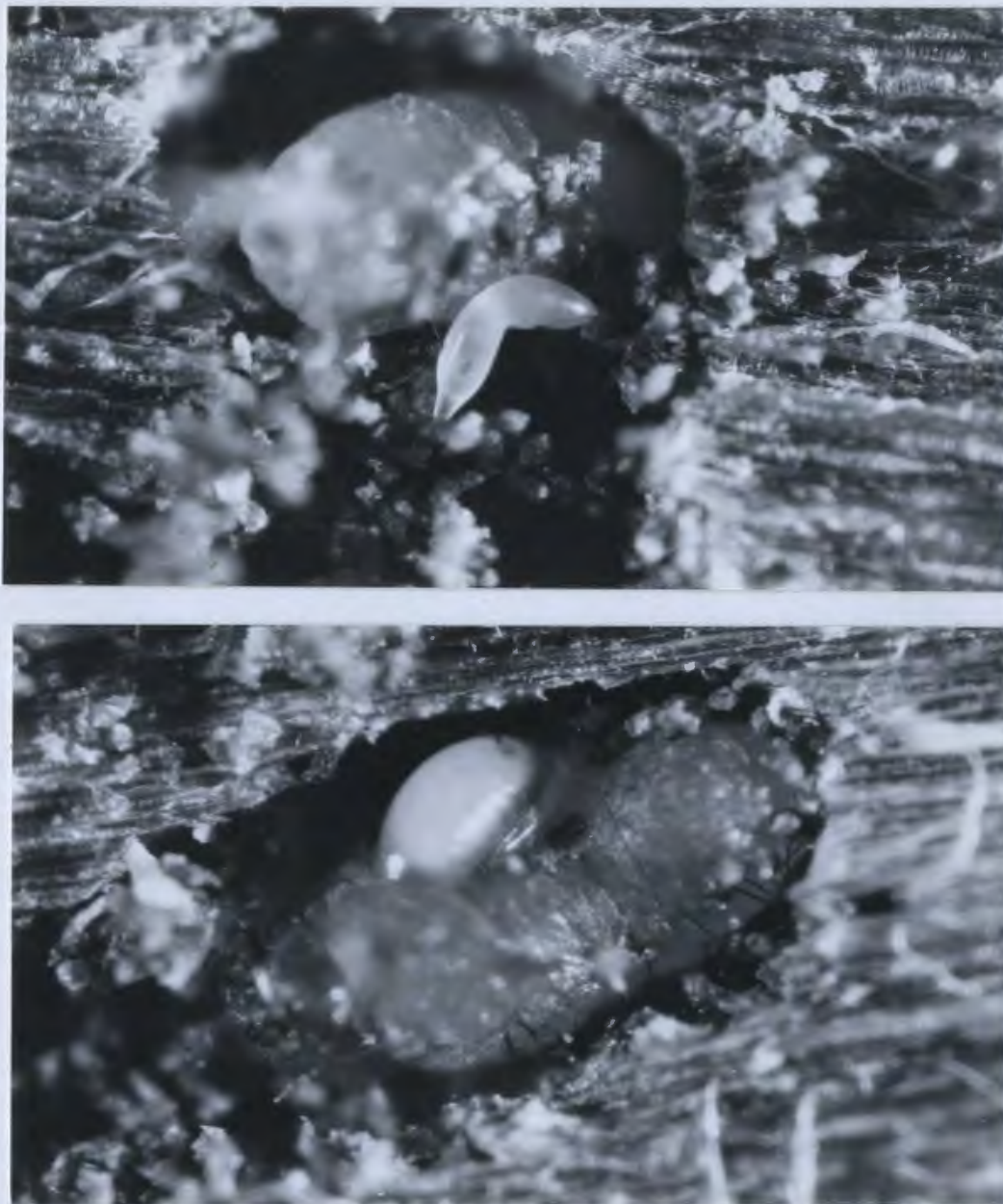


Figure 28. Egg and larva of *Roptrocerus xylophagorum* (Ratz.), a common hymenopterous parasitoid of *Dendroctonus simplex* in Newfoundland. Top. egg (magnification= 28X), Bottom. larva feeding on a *D. simplex* larva (magnification= 20X).

eight and eight at 0.5 m, 2.5 m and 5 m, respectively. Densities of up to 28 larvae per 100 cm³ were observed. Very few parasitoids were found in Brood II trees.

3.3.3 Competitors

The beetles - *Stictoleptura canadensis*, *Hylobius pinicola*, *Crypturgus pusillus*, *Dryocoetes autographus* and *Polygraphus rufipennis* are phloem feeders that may occur in larch trees and, therefore, possible competitors with *D. simplex*. However, all of these species, except *S. canadensis*, were rare in *D. simplex* infested trees. The scolytid species were all collected in emergence traps indicating that they emerged from beneath the bark, however no larvae were observed. Larvae of *S. canadensis* were found in three trees containing *D. simplex* brood. They were first observed on 6 July and remained in trees to overwinter in the phloem layer. This species was the most abundant competitor in 1983 and was likely also an accidental predator of *D. simplex*. The two *H. pinicola* weevils were collected from the bark surface of a tree, containing *D. simplex* brood, as they were commencing gallery construction.

3.3.4 Miscellaneous

Of the insects found in *D. simplex* egg galleries - the beetles *Corticaria* sp., *Epuraea truncatella*, the ptilid and the flies *Aprionus asemus*, *Rhexoza* sp., *Chaetosclara* sp. and

Scatosclara sp. were likely fungus feeders. Adults of these species began arriving at *D. simplex* infested trees in July. The scymaenid beetle *Stenichnus* sp. was likely a scavenger. The commonest of these species was *E. truncatella*. This species entered trees inhabited by *D. simplex* in late July and early August and spent the winter. Eggs were laid in the spring and parent adults emerged in May and June. It is not known if they flew to other trees. Larvae developed in trees after larch beetle emergence and emerged as adults in late July and early August to seek new trees in which to overwinter.

No spiders were found in *D. simplex* egg galleries although many juveniles and some egg sacs of *Clubiona canadensis* and *Grammonota* sp. and mature adults of *Sisicottus montanus*, *S. montigenus* and *Pocadicnemis pumila* were collected from the external bark surface. Eggs of the harvestman *Odiellus pictus* were found in trees with overwintering *D. simplex*. Eggs and juveniles were also found in egg galleries in Brood I trees in spring and early summer.

More than 95% of overwintered *D. simplex* that emerged in the spring of 1983 had phoretic mites attached to their ventral surface (Fig. 29). Mites were not attached to beetles in egg galleries but many were observed moving throughout the galleries and larval mines. Predation by mites on *D. simplex* was not observed. Reemerged beetles did

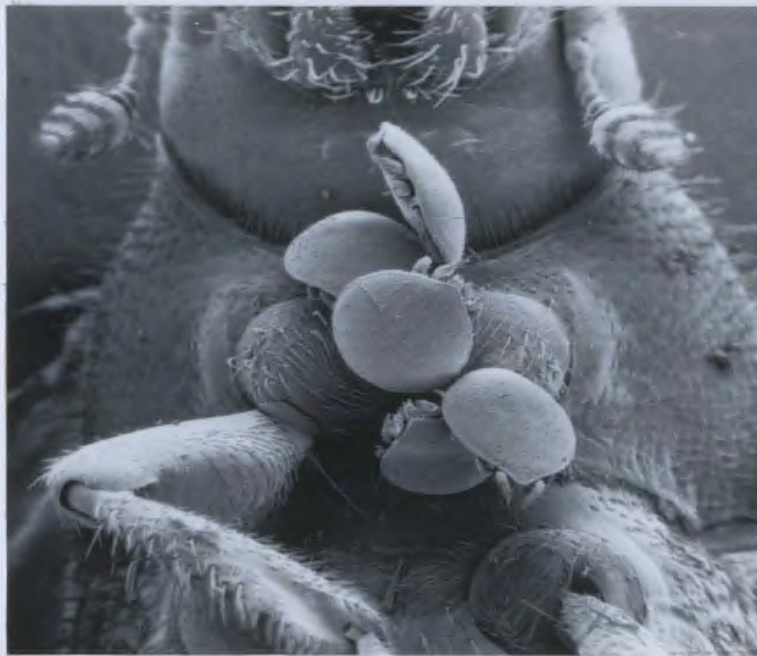


Figure 29. Phoretic mites attached to the ventral surface of the thorax of an emerged *Dendroctonus simplex* adult (magnification= 50X).

not have mites attached to them.

Phoretic nematodes of the genus *Cryptaphelenchus* were found in clusters beneath the elytra of overwintering and emerged *D. simplex* adults (Fig. 30) but none were found under the elytra of adults in egg galleries or reemerged, adults. Large numbers of these nematodes were observed moving throughout the phloem.

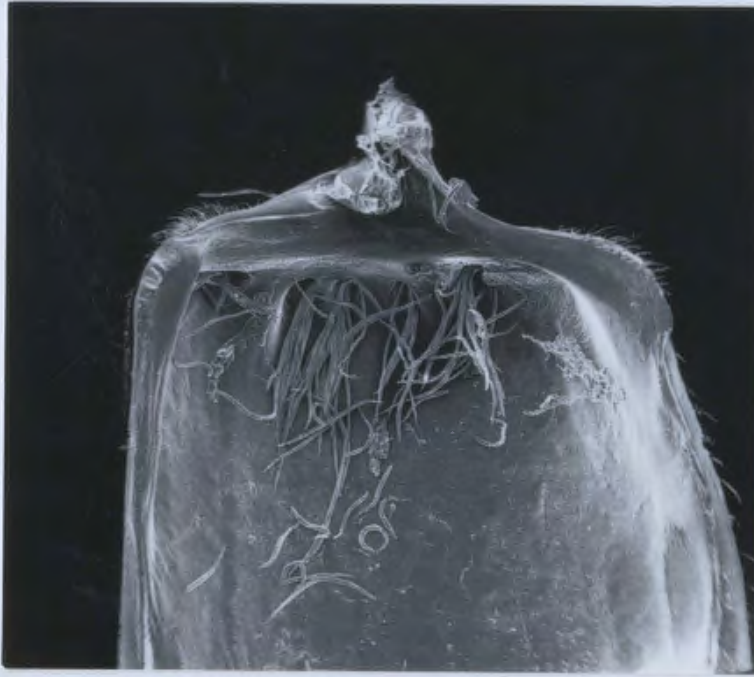


Figure 30 Aggregation of dauerlarvae of phoretic nematodes of the genus *Cryptaphelenchus* on the ventral surface of an elytrium of an emerged *Dendroctonus simplex* adult (magnification= 70X).

4. DISCUSSION

4.1 LIFE HISTORY

4.1.1 Environmental influences on activity and behaviour

Temperature is considered to be the most important abiotic factor influencing bark beetle activity and behaviour. It has been shown to influence the basic components of bark beetle life history - emergence (Borden and Fockler 1973; Gray *et al.* 1972), host attack (Lucht *et al.* 1974), reemergence (Gagne *et al.* 1982), oviposition (Haack *et al.* 1984; Wagner *et al.* 1981) and development (Annala 1969). All components of the life history of *D. simplex* in Newfoundland exhibit strong relationships with temperature.

Spring emergence, flight, host attack and reemergence

Coincidence of *D. simplex* spring emergence peaks with periods of high mean daily air temperature (Fig. 5) indicates a temperature influence on emergence. More beetles emerging from the sun-exposed south side of tree boles than from the shaded north side during the first part of the emergence period (Fig. 6) is evidence that temperature is important in governing start of emergence. Before overwintered beetles emerged their flight muscles increased in size to enable flight. Since fat body size did not decrease before emergence the energy for flight muscle

development was likely provided by feeding. Food in the guts of emerged beetles is evidence of feeding before emergence. The sun-exposed south sides of tree boles have the highest subcortical temperatures in winter and early spring (Powell 1967; Danks 1978). Therefore, larch beetles overwintering in the south side likely commenced feeding, flight muscle development and emergence earlier than beetles in the north side. Differential emergence with respect to tree aspect has been observed for other *Dendroctonus* species (Lucht et al. 1974; Safranyik and Jahren 1970) and for species of *Trypodendron* (Dyer 1962) and *Ips* (Gehrken and Zackariassen 1977).

Earlier emergence of females than males (Fig. 5) is likely not temperature related but conforms with the generalization that the sex which selects and attacks host trees emerges first (Stark 1982).

It is not known why emergence at 5 m started two to four days later than at the lower heights (Fig. 7).

Temperature influences on larch beetle flight, host attack and reemergence was also evident. Attack peaks, which reflect peaks of flight, coincided with peaks in mean daily air temperature (Fig. 9) and most reemergence peaks and declines coincided with temperature increases and decreases, respectively (Fig. 11).

Occurrence of emergence, attack (and hence flight) and reemergence between 10:30 and 17:00 hours each day suggests that these processes are also influenced by temperature on a diurnal basis since these hours are usually the warmest of the day. However, *D. simplex* emergence may also be influenced by circadian rhythms as has been reported for *Dendroctonus ponderosae* Hopkins (Gray et al. 1972; Watson 1970). Circadian rhythms may also occur for larch beetle flight, host attack and reemergence.

A prerequisite for bark beetle activity is temperatures above the lower threshold for that activity. Threshold temperatures usually vary between activities, species and localities (Annala 1969; Rudinsky and Vite 1956). Lower threshold temperatures for larch beetle activities could not be precisely determined since only mean daily air temperatures were obtained for these studies. Therefore, although larch beetle emergence and host attack did not occur on days when mean air temperature was 4 °C or less (Figs. 5, 9) the threshold temperatures for these activities is likely slightly higher than 4 °C because air temperature during the part of the day when these activities occur is generally higher than the mean for the entire day. Emergence of most *Dendroctonus* species begins at 7 to 14 °C (Wood 1982). Emergence, host attack and reemergence involve the basic activities of walking and tunneling. Therefore, threshold temperatures for all three processes is likely about the same. Threshold temperature for flight is likely

slightly higher. Peaks of host attack, which reflected flight peaks, occurred on days when mean air temperature was 10 °C or higher (Fig. 9) suggesting that flight threshold temperature was close to 10 °C, likely slightly higher. However, most larch beetles may not fly until air temperature is much higher than the threshold. This has been reported for several species of *Dendroctonus* and other scolytid genera (Amman and Cole 1983; Annala 1969; Rudinsky and Vite 1956; Wood 1982). Attacks that occurred on days when air temperatures were higher than the threshold for attack but lower than the flight threshold could have been initiated by beetles that had flown to new hosts on previous days but had failed to initiate attack.

In marginal climates bark beetle activities may be greatly prolonged because temperature frequently drops below the threshold. Spring climate on the Avalon Peninsula is characterized by frequent periods of rain, fog and mean daily air temperatures below 10 °C. Warm periods tend to be of short duration and warm sunny periods even shorter (Banfield 1983). This marginal climate was reflected by the erratic spring emergence of *D. simplex* which lasted 44 days. This resulted in a long flight period and a long attack period of 42 days (Fig. 9). Similar results have been reported for *Trypodendron* and *Ips* emergence, flight and host attack in Finland (Annala 1969; Annala et al. 1972). The first *D. simplex* reemergence period, which occurred in early summer, was only 32 days long likely due to the higher and

less variable air temperatures (Fig. 11). The short duration of 25 days for each the second attack and second reemergence periods in mid-summer (Fig. 8) was likely a result of even higher air temperatures.

The interval between start of emergence or reemergence and start of the following attack period is likely related to temperature, although wind speed and the proximity of suitable hosts may also be important. The eight day interval from the start of spring emergence to the first attack may be due to the four days of cold weather just after emergence began (Fig. 5). However, the nine day interval from the start of the first reemergence period to the start of the second attack period cannot be explained by inclement weather since air temperatures were high at the time (Fig. 11). This interval is related to dispersal abilities of reemerged adults which is discussed in a separate section.

The length of time that beetles spend in hosts before reemergence is dependent upon egg gallery construction and oviposition rates and is, therefore, temperature related since egg gallery construction rate varies greatly with temperature (Table 5). Although not investigated, oviposition rate is likely also temperature related, as is the case for other scolytid species (Amman 1972b; Haack et al. 1984; Wagner et al. 1981). Although daily air temperature during first and second brood production in 1983 averaged 13 °C and 16 °C, respectively, this difference was

apparently not enough to cause a significant difference in average brood production rates between first and second broods which were 32 and 30 days, respectively.

Number of broods per year

Temperature appears to be not very important in influencing the number of *D. simplex* broods produced per year in Newfoundland. Larch beetle adults may be capable of producing more than one brood per year but most may be prevented from doing so by their inability to fly to new hosts following reemergence because flight muscles did not completely regenerate. A sample size of twelve beetles in 1983 was too small to judge the proportion of reemerged adults capable of flight. However, only 17% of 96 reemerged beetles collected in 1984 had fully developed flight muscles and were judged capable of flight. Therefore, most beetles would have to walk to new hosts to establish a second brood. This greatly limits dispersal of a population after initial establishment in a location. The dispersal range of walking beetles is apparently small since only the two girdled trees closest (2 to 3 m away) to Brood I trees were attacked by reemerged beetles in 1983 even though there were four other girdled and eight to ten non-girdled trees within a 20 m radius. Also, in 1984 reemerged parents lacking fully developed flight muscles attacked only the larch bolts placed 2 m from first brood trees but not material farther away which was only attacked by beetles with fully developed

flight muscles. Thus, most reemerged parents are effectively excluded from the second attacking population. The proportion of reemerged beetles capable of flight is probably too small to overcome the resistance of and, hence, successfully attack standing, uninjured larch and may be able to establish second broods only in standing weakened trees, fallen trees, stumps and logging slash. The observation that second broods were produced only in girdled trees and cut bolts in both 1983 and 1984 and that no standing, uninjured trees were attacked, lends support to this theory.

Lawko and Dyer (1974) reported that 82% of reemerged *Dendroctonus rufipennis* (Kirby) were unable to fly because their flight muscles were too small. They suggested that some beetles may have been forced out of their galleries by resin flow before they could regenerate new flight muscles. However, this does not explain lack of complete flight muscle regeneration in *D. simplex* since little resin flow from larch was observed during the study. Lack of fully developed flight muscles in reemerged *D. simplex* has not been reported previously.

Simpson (1929) reported one brood of *D. simplex* per year in 1925 and 1926, three in 1927 and two in 1928 in New Brunswick. However, his studies were done using caged larch bolts and beetles so that reemerged adults did not have to fly to reach new breeding material. Swaine (1911) reported

two broods of *D. simplex* in one year (locality unknown) but the second brood was produced in felled larch lying close to stumps from which adults were reemerging. Other felled trees lying slightly farther away were not attacked. This may suggest that reemerged beetles did not fly.

Brood development

The effect of temperature on *D. simplex* brood development rates is evident from laboratory studies where instar developmental time decreased with increased rearing temperature (Table 11). However, instar developmental times were difficult to measure for field populations. Estimates of instar developmental times for field populations, calculated as the interval between dates of first appearance of succeeding instars in field samples (Table 12), are likely inaccurate because: (1) the interval between samples (five days) was long and (2) estimates were based on the small proportion of the total population that moulted to a new instar before the others and may not be representative of the entire population. However, there is evidence of a temperature influence on *D. simplex* development in field populations as developmental time of the pupal stage in Brood II was much longer than for the same instar in Brood I (Table 12). The developmental times of the third and fourth larval instars also may have been longer for Brood II but this was not evident from the field data for development (Table 12), probably due to the lack of precision of the

estimation method. However, the duration of these two instars, as well as pupae, in field populations in 1983 was much longer for Brood II than for Brood I (Fig. 19). This implies a slower development rate, likely due to low temperature which averaged 6 °C lower for the duration of these instars in Brood II than in Brood I (Table 12). The differences in brood development, as measured by a development index, between the two Brood I sample trees at each sample period (Fig. 21) may also be attributed to temperature. Tree 1 was constantly shaded and, therefore, subcortical temperatures were likely lower than those of the sun-exposed Tree 2 where *D. simplex* development was always slightly ahead of that in Tree 1 (Fig. 21). Similar results have been reported for *Ips typographus* L. (Annala 1969).

Estimates of instar developmental times for Brood I in 1983 were generally similar to those reported by Prebble (1933) for New Brunswick field populations (likely first brood) in 1929 (Table 12). However, developmental times for the egg and first and second larval instars were almost twice as long as those measured for New Brunswick populations possibly because of lower spring temperatures in Newfoundland.

By influencing brood development rate temperature influences the proportion of a brood that matures before winter. This proportion is important because only the adult stage is cold hardy. The number of brood that reaches

adulthood before start of winter thus directly affects the size of the attacking population the following spring. Some *D. simplex* larvae were reported to survive winter in caged larch bolts in New Brunswick in 1927 (Simpson 1929) but these bolts were likely at ground level and covered with an insulating layer of snow during most of the winter. However, snow levels around bases of trees on the Avalon Peninsula during most years are usually less than 50 cm and for most of the winter snow does not cover any of the tree base. There is generally much more snowfall in most other parts of the range of *D. simplex* which may insulate larvae in the lower bole of standing trees and in stumps and fallen material enabling them to better survive the winter. Nonetheless, several workers report young adults to be the principal overwintering stage in mainland Canada and the northeastern United States (Blackman and Stage 1918; Swaine 1911; Wood 1963).

Voltinism

One larch beetle generation was produced in each summer of 1983 and 1984. Other workers also report one generation per year in other parts of the species range (Blackman and Stage 1918; Hopkins 1909; Simpson 1929; Wood 1963). Swaine (1911) reported two generations in one year in Quebec but his "second generation" may have been a second brood. He observed some brood adults emerging in August and at the same time observed new attacks on nearby logs. He concluded

that the brood adults were starting a new generation. . . However, these new attacks may have been caused by reemerging parents. New brood adults also emerged in late summer and early fall in Newfoundland (Fig. 22) but lacked fully developed flight muscles and were judged incapable of flight to new hosts. They did not produce a second generation but entered galleries at the base of brood trees to hibernate.

Winter adaptations

Emergence of new brood adults before winter and re-entry for hibernation at the base of trees has been reported for only *D. rufipennis* within the genus *Dendroctonus*. This habit enhances survival because 1 to 2 m of tree base is usually covered by snow in winter keeping temperatures there near 0 °C (Schmid and Frye 1977). Snow cover also protects beetles from woodpecker predation (Schmid and Frye 1977). However, snow covered only 20 to 30 cm of tree bole for only two to three weeks during the winters of 1982/83 and 1983/84 at the study site and this gave beetles overwintering at the tree bases little protection from cold. As a result, overwintering mortality of *D. simplex* at 0.5 m was at least as high as at other heights during the 1982/83 winter (Table 17). However, there was no woodpecker predation below 1 m. Movement of *D. simplex* to lower parts of tree boles may have survival value in regions where snowfall is greater.

I do not know why only a portion of *D. simplex* brood adults emerged to hibernate in tree bases. Emergence of *D. rufipennis* for hibernation at tree bases was 3% to 88% for the years in which investigated (Knight 1961).

The decrease in mortality of *D. simplex* adults at various temperature treatments from early fall to winter (Table 18) indicates development of cold hardiness. Lower mortality among acclimated beetles than among non-acclimated ones (Table 19) also suggests an increase in cold tolerance. The method by which *D. simplex* increases cold hardiness is not known. Cold hardiness in some other scolytid species is increased by production or increased production of cryoprotectants such as glycerol and sorbitol (Amman and Cole 1983; Gehrken and Zackariassen 1977; Ring 1977). Larger size or higher concentrations of cryoprotectants may be involved in the higher survival of females than males. Such differential survival of cold has been reported for *D. ponderosae* (Safranyik 1976; Watson 1971) where higher levels of sorbitol in females may account for their higher survival (Ring 1984 - personal communication). The larger average size of larch beetles that survived cold temperatures (Table 20) may simply reflect the larger average size of females. Better survival of cold treatments by larger beetles than smaller ones has been reported for *D. ponderosae* (Safranyik 1976) but significant size differences between sexes was not demonstrated.

Conclusions

At most, only two broods and one generation⁷ of *D. simplex* per year occurs in Newfoundland. Climate is the most important factor influencing seasonal life history of *D. simplex*. The climate generally permits beetles to lay two complements of eggs per year. However, the number of parents able to establish a second brood is much smaller than for the first because most reemerged beetles cannot fly to new hosts. Such a small number of beetles may not be able to overcome the resistance of neighbouring, healthy trees and may be capable of producing second broods only in breeding material which has little or no resistance such as injured trees, stumps and fallen material (windthrows, logging slash). Also, a large proportion of the second brood will likely be killed by cold before reaching maturity. Hence, the second brood does not contribute significantly to the overall population the following spring. Since climate is not conducive to production of a second larch beetle brood, lack of complete flight muscle regeneration in most reemerged beetles may be a result of selection for a single brood per year in Newfoundland.

4.1.2 Host selection and colonization

Like most scolytids *D. simplex* is selective in its colonization of host plants with respect to both host species and physiological condition. Usually it attacks

larch trees weakened by factors such as defoliation flooding, fire and logging (Drouin and Turnock 1967; Grisdale and MacLeod 1962; Hopkins 1909; Wood 1963; 1982). Attack susceptible trees comprise a relatively scarce and temporary resource whose suitability does not extend beyond one beetle generation and whose distribution throughout the environment is scattered (Raffa and Berryman 1980). Therefore, larch beetles must detect and exploit resources which have an unpredictable spatial and temporal distribution.

The mechanism of host selection for many species of scolytids has been postulated to be initiated by host odors which beetles detect and follow to the source (Andersen 1977; Moeck *et al.* 1981; Heikkinen 1977). This is termed "primary attraction". An alternate hypothesis is random initial landing of beetles on various hosts and non-hosts. Beetles landing on suitable hosts, detected by gustatory cues (Raffa and Berryman 1980), initiate gallery formation and produce an aggregation pheromone, whereas, beetles landing on non-suitable hosts redisperse (Hynum and Berryman 1980; Moeck *et al.* 1981; Raffa and Berryman 1980; Wood 1972). Such a strategy ensures that a larger proportion of the host population will be investigated and that few susceptible hosts will escape detection. I observed larch beetles landing on tree species other than larch and on larch which, subsequently, were not attacked. This may support the hypothesis of random initial landing of beetles.

The defences of larch trees selected for attack by pioneer *D. simplex* must be overcome before colonization is successful. Like many other conifers species, healthy larch defend by extensive pitch production in response to bark beetle attack (Drouin and Turnock 1967). The toxic resin entraps and kills or expells beetles attempting to bore into the tree. There was very little pitch production by ungirdled larch attacked by *D. simplex* at the study site in 1983, perhaps indicating a highly weakened state. However, there was much pitch production by many naturally attacked trees across Newfoundland in 1979, 1981 (Raske 1983 - personal communication) and 1984, causing many unsuccessful colonization attempts.

Many scolytid species use mass attack to overcome tree defences (Wood 1982). Mass attack is facilitated by the production of aggregation pheromones by the pioneer beetles (females in the genus *Dendroctonus*). Aggregation pheromones are produced in the midgut and transported to the environment by frass passing through the gut (Wood 1982). These pheromones attract beetles of both sexes to the same tree where they also construct entrance holes. However, not all larch beetle females constructed their own entrance holes. Some used entrance holes constructed by other females which likely conserved energy by relieving the female of the task of boring through the outer bark and overcoming tree resistance. The near simultaneous attacks by beetles responding to aggregation pheromone overwhelms tree defences

enabling successful colonization (Wood 1982). The larch beetle also mass attacks trees and presumably produces an aggregation pheromone, although one was not demonstrated.

Larch beetles in Alaska were strongly attracted to a synthetic mixture of seudenol and alpha-pinene (Baker *et al.* 1977; Werner *et al.* 1981) suggesting that these compounds may be components of the natural aggregation pheromone of the species.

Colonization by larch beetles only in regions of larch boles with phloem thickness of 2 mm or more (Table 2) and observations of abandoned entrance holes in regions with very thin phloem suggests that females may also respond to physical factors such as phloem thickness when selecting a site to start gallery construction. It would be more beneficial for beetles to construct galleries in thicker phloem since tunneling in thin phloem would necessitate deep scoring of the wood surface which would utilize energy that could otherwise be put into reproduction. Also, brood produced in thin phloem may be more susceptible to dessication.

4.1.3 Mating and egg gallery construction

Males were generally not present when females initiated gallery construction. Female behaviour before male arrival differed from that after male arrival. Galleries were kept free by pushing frass out of the entrance holes. This

probably exposed the aggregation pheromone in the frass to the environment for dispersal as well as prevented galleries from becoming blocked with frass which would obstruct male entrance. Similar behaviour has been reported for *D. ponderosae* (Amman 1975; Rasmussen 1974). When males arrived they cleared the frass and constructed turning niches and ventilation holes which likely enabled females to put more energy into egg production (Amman 1975; Rasmussen 1974; Reid 1958a). Also, egg gallery construction rate doubled after males arrived.

Stridulation by males before entrance into galleries may serve to stop production of aggregation pheromone by females (Rudinsky 1968) or may be part of territorial behaviour discouraging other males from entering male occupied galleries thereby distributing the male population more efficiently (McGhehey 1968).

There are several possible factors that determine egg gallery length and shape. The vertical nature of *D. simplex* galleries may minimize severing of vertical resin ducts and, hence, resin flow (Stark 1982). The sinuous and branching gallery pattern may reflect a tendency for females to avoid other galleries by turning away from them. As more phloem is utilized avoidance of other galleries becomes difficult resulting in galleries intersecting and anastomosing. The great variation in egg gallery length (Table 4) may be related to available unused phloem. Females initiating

galleries toward the end of the attack period may find little unused phloem and be forced to construct shorter galleries (Wagner et al. 1982). Although larch beetle attack density was much lower for Brood II trees than for Brood I trees (Table 9), average egg gallery length was shorter in Brood II trees (Table 4). Possibly this was due to greater resistance of Brood II trees, colder temperatures or lower vigor of females.

4.1.4 Oviposition

For many species of *Dendroctonus* the number and density of eggs laid is a density dependent function of attacking adults (ie. crowding) with adults efficiently utilizing their resources by producing more eggs per pair (E/P) and more eggs per cm of gallery length (E/cm) in less crowded conditions (Amman and Pace 1976; Cole 1962, 1973; Coulson et al. 1978; McMullen and Atkins 1961). Proximity of other galleries may be detected by auditory signals (stridulation, boring noises) or qualitative changes in the phloem (dehydration, spread of microorganisms introduced by beetles, chemical changes etc.) (Wagner et al. 1982). The effects of crowding on oviposition may be offset by increased food supply (ie. thicker phloem). Thus oviposition may be a function of both phloem thickness and crowding (Amman 1972a). There is evidence to support and contradict that *D. simplex* exhibits similar response to crowding and food supply. Pairs of beetles introduced to larch bolts

produced significantly higher E/P (Table 8) and E/cm (Table 7) than those in Brood I trees suggesting that beetles were responding to the much more crowded conditions in the Brood I trees by producing fewer eggs and by spacing eggs farther apart. Additionally, the Brood I tree that exhibited the higher E/cm also possessed significantly thicker phloem and lower egg gallery length per 100 cm² (GL) (an index of crowding). However, regression of E/cm on phloem thickness and GL accounted for only 4% of total variation indicating that the two predictors had very little influence on E/cm. The considerable unexplained variance in E/cm may be attributed to unmeasured variables such as tree resistance (resin production), phloem quality (moisture content, microorganisms) and air temperature (exposure) (Amman 1972a, 1972b; Beanlands 1967; Wagner et al. 1981).

Although Brood II trees were less densely attacked than Brood I trees there was no significant difference in E/cm between the two (Appendix D). It is not known why fewer eggs were produced per pair of beetles in Brood II trees than in Brood I trees (Table 8). It may be due to resin production which was observed to be much higher for Brood II trees than for Brood I trees.

Brood density has also been related to phloem thickness with higher densities occurring in thicker phloem (Amman 1972a; Amman and Pace 1976). This relationship was not observed for *D. simplex* as regression of brood density on

phloem thickness resulted in a low r^2 value of 0.02. Lower brood density in Brood II trees (Table 9) was simply a reflection of low attack densities.

The maximum of four eggs per niche is due to there being four ovarioles per female. Hence, only four eggs can mature at a time. This agrees with data presented by Swaine (1911) for *D. simplex*. However, Hopkins (1909) reports as many as six eggs per niche.

Flight muscle histolysis, fat body degeneration, and gonad enlargement during egg gallery construction and oviposition is common among scolytids (Atkins and Farris 1962; Gray and Dyer 1972; McCambridge and Mata 1969; Reid 1958b, 1962). It has been hypothesized that flight muscle and fat body degeneration during the reproductive phase provides energy and materials for reproductive processes (Atkins and Farris 1962; Hocking 1954). While feeding by *D. simplex* adults during gallery construction likely provides some energy and materials for reproduction, flight muscle and fat body degeneration likely provides it much faster enabling oviposition to begin and reach a maximum sooner. Flight muscle degeneration may also function to provide more room for developing gonads, especially ovaries, which extend into the metathorax as flight muscles decrease in size (Reid 1958b).

The time required for gonad development in *D. simplex* females at the start of gallery construction accounts for

the initial egg free portion of galleries. The egg free terminal portion of galleries may be due to cessation of oviposition to prepare for flight muscle regeneration and other internal changes before reemergence. This has also been hypothesized for *Dendroctonus frontalis* Zimmerman (Wagner et al. 1981).

4.1.5 Brood development and behaviour

The observation of four larval instars for *D. simplex* in Newfoundland (Fig. 18) agrees with that of Prebble (1933) for New Brunswick populations. However, average head capsule widths of larval instars were larger than those recorded by Prebble (Table 10). It is not known why. Lindroth (1963) observed that some ground beetle species were larger in Newfoundland than in some other parts of their range and Genge (1985) noticed the same for caddisfly larvae. Lekander (1968) reported that the average ratio between average head capsule widths of two consecutive instars of larval scolytids was 1.32 (range= 1.17 to 1.48), not much different than the growth factor of 1.33 reported here for *D. simplex*.

Developing *D. simplex* brood likely obtain most of their nutrients from host phloem. Although I observed a few newly hatched larvae ingesting egg chorion and exuvia and many larvae and adults ingesting fungus and dead nematodes, the nutritional value of these materials is not known. Most of the larvae observed exhibited coprophagy suggesting that

chemical changes in the excrement, brought about by action of microorganisms, or the microorganisms themselves might be of nutritional value.

Cannibalism or entomocide (killing without ingesting) is known to occur among scolytid progeny at high densities (Berryman and Pienaar 1973; Cole 1973; Schmitz 1972; Schmitz and Rudinsky 1968). However, I did not observe this for *D. simplex* progeny in rearing chambers possibly because there were few encounters between progeny. I also did not observe evidence of cannibalism or entomocide in field populations where brood densities were much higher. It is likely that cannibalism and entomocide among progeny is normally incidental but may be an important natural control when populations are high (Berryman and Pienaar 1973; Schmitz 1972).

4.2 MORTALITY

Instar specific mortality estimates for most larval instars and pupae are thought to be accurate because dead individuals of these instars were easily detected. However, some dead eggs and first instar larvae were probably overlooked and some may have been entirely ingested by predators. Hence, mortality for these instars, especially the egg, is likely underestimated. If so, then total mortality from egg to adult, calculated by multiplying percent mortality in each instar by the proportion of the

original number of individuals that lived to reach that instar and summing for all instars, is also underestimated. Total mortality estimates calculated this way were consistently lower than those based on the difference between the average density of eggs and the average density of adults after brood maturation (Table 15). The second method is considered better for estimating total mortality.

Like most scolytids *D. simplex* has a high reproductive rate which, if left unchecked, would lead to overpopulation. Many mortality factors, along with food supply, are responsible for reducing *D. simplex* numbers. These mortality factors are basically the same as for other scolytid species and can be grouped into three categories: host resistance, abiotic factors and biotic factors. The mortality factors do not exert their effects equally among all *D. simplex* stages but, depending on instar susceptibility or abundance, are more effective against some instars than others.

4.2.1 Host resistance

Host resistance (resin production) to larch beetle attack and gallery construction was greatest during the early stages of host colonization. Only attacking adults, eggs and early larval instars sustained mortality by resinosis. Although I observed only four attacking adults pitched out and killed by resin flow at the study site in 1983, resinosis is probably an important mortality factor

among attacking adults most years. It was common throughout Newfoundland in 1979, 1981 (Raske 1983 - personal communication) and 1984. Death of eggs by resinosis could not be identified but was likely significant. Many larch beetle eggs were covered with resin but I could not determine if this caused mortality. Resinosis is an important mortality factor among eggs of many other scolytid species (Berryman 1968; 1973; Cole 1975; Reid 1963). The much higher resinosis-caused mortality among first and second larval instars in Brood II trees as compared to Brood I trees (Table 16) is understandable considering the apparent higher levels of resin production by Brood II trees. This may also explain the higher total egg mortality in Brood II trees (Table 14) even though egg mortality by resinosis could not be determined. It is likely that the much lower percent reemergence of *D. simplex* adults from Brood II trees, at 61%, as compared to Brood I trees, at 90%, may also have been influenced by higher resin production in Brood II trees.

4.2.2 Abiotic factors

The most important abiotic factor observed to cause mortality among *D. simplex* in Newfoundland was low temperature which killed 17% of the second brood in 1983 (Table 16). Temperatures low enough to kill *D. simplex* usually do not occur until mid to late October and, hence, cause no mortality among immature instars of the first brood

which reach maturity by August. If a second brood is produced it is generally small. Therefore, low temperature is not an important mortality factor among immature *D. simplex* even if the entire second brood is killed. Low temperature may be a very important mortality factor for overwintering adults although it was not during the winter of 1982/83. Winter mortality among adults is likely influenced by winter temperatures, snowfall and the proportion of the beetle population that migrates to tree bases before winter.

Mortality of *D. simplex* due to dehydration could not be determined in this study. However, I believe that dehydration may be an important mortality factor among eggs and larvae in trees and portion of trees with thin phloem. This has been reported for *D. ponderosae* in the northwestern United States (Amman and Cole 1983).

4.2.3 Biotic factors

Parasitoids were the most important biotic factor affecting *D. simplex* populations in this study. All four larval instars were parasitized in 1983 but the third and fourth were most severely parasitized (Table 16) because these were the instars most abundant when adult parasitoids were searching for hosts. No pupal parasitism was observed during the study (Table 16) although many species that parasitize scolytid larvae can also parasitize pupae

(Bushing 1965). The apparent absence of *D. simplex* egg parasitism is not surprising since bark beetle egg parasitoids are relatively rare (Dahlsten 1982). Egg parasitism may have been overlooked since egg parasitoids feed inside the chorion and are difficult to detect. Adult parasitism also may have been overlooked because parasitoids of adults feed internally and are not readily detectable unless hosts are dissected.

The higher total *D. simplex* brood mortality in the upper and middle regions of infested bole as compared to lower regions (Table 15) may be attributed mainly to parasitism which was approximately twice as high in those bole regions (Fig. 26). The difference in *D. simplex* parasitism along tree boles may be related to phloem thickness which decreases with height (Table 2). Adult parasitoids can oviposit on or near a *D. simplex* host only if it can successfully penetrate the bark and phloem layers with its ovipositor. Therefore, the short length of the ovipositors of *D. simplex* parasitoids likely enables more successful oviposition in regions of the bole with thin phloem (ie. middle and upper regions). Similar results have been reported for several other scolytid species (Dahlsten 1982).

Since mortality due to parasitism was calculated using only *D. simplex* individuals that had parasitoids feeding on them or that were paralyzed and had parasitoid eggs laid

near them, it is likely that percent parasitism is underestimated. Total parasitoid impact should be viewed as all host deaths resulting from the presence of parasitoids, not just those hosts utilized for reproduction (Van Driesche 1983). Parasitoid induced mortality must also include paralyzed hosts on which no oviposition occurred.

Mortality of *D. simplex* due to arthropod predators may also have been underestimated since an individual was counted as prey only if a predator was observed feeding upon it. All *D. simplex* instars were preyed upon but first and second larval instars and pupae received slightly more predation pressure than other instars (Table 16). Early larval instars may have more predators feeding on them or may be easier prey and pupae may be preyed upon more often because they are immobile. Egg predation was not observed but undoubtedly occurs.

The similarity in predator caused mortality between sample heights of Brood I trees (Fig. 26) indicates that phloem thickness had no effect on predator success. That is not surprising since beetles enter *D. simplex* galleries to oviposit or feed.

Although pathogens caused mortality among all *D. simplex* instars they were more effective against pupae (Table 16) suggesting that this stage was more susceptible. Pathogens were not identified but may have been bacterial, fungal or protozoan as all three groups cause mortality in

other scolytid species (Dahlsten 1982).

Intra- and interspecific competition for food are potentially important mortality factors among *D. simplex* populations. However, neither type of competition appeared to cause significant mortality among *D. simplex* in 1983. The possibility that the number of eggs laid per cm of gallery by *D. simplex* females was influenced by crowding and phloem thickness may have reduced intraspecific competition. Such density dependent oviposition behaviour has been suggested to reduce intraspecific competition in other *Dendroctonus* species (Dahlsten 1982). The low incidence of other phloem feeding species in trees inhabited by *D. simplex* (Table 21) implies that interspecific competition was also low.

4.3 ASSOCIATED ORGANISMS

After colonization by *D. simplex*, a larch tree soon becomes inhabited by other species of organisms which are attracted to the tree for one or more of the following reasons: (1) to prey upon or parasitize *D. simplex* or other organisms associated with it, (2) to feed on phloem, (3) to feed on fungi, (4) to use *D. simplex* galleries or bark crevices for shelter or reproduction, or (5) to scavenge. Because an infested tree provides so many attractions for other organisms it is not surprising that such a large number of species (52) were associated with *D. simplex* field populations in 1983. Many other scolytid species also have

large numbers of other species of associated organisms (Dahlsten 1982).

4.3.1 Predators and parasitoids

The major predator (*Medetera* sp.) and parasitoids (*Roptrocerus xylophagorum*, *Rhopalicus tutela* and *Spathius canadensis*) of *D. simplex* all have a common life history pattern, with adults arriving at beetle infested trees one to two weeks after the *D. simplex* host attack period. This suggests that predators and parasitoids are not attracted by larch beetle pheromones since pheromone production likely stops when females obtain mates, as with other scolytid species (Borden 1982). The interval between start of host attack by *D. simplex* and arrival of parasitoids may have an advantage for the parasitoids. Larvae of most parasitoid species generally remain on one host until development is complete (Dahlsten 1982). Hence, larvae feeding on larger hosts would have a larger food supply and possibly a better chance of completing development than those on smaller hosts. By the time parasitoids arrived at *D. simplex* infested trees in 1983 a large proportion of the beetle brood consisted of large third and fourth instar larvae, and these were the stages that were most often parasitized (Table 16). This would not be of advantage to predators which are capable of consuming more than one host.

V

Predators

The apparently higher density of predators in the lower 2 m of tree boles than in the higher regions may serve to reduce competition with parasitoids which were twice as abundant in the middle and upper regions than in lower regions. Therefore, more predation of *D. simplex* would be expected in the lower bole where predator density was highest, but this was not observed (Fig. 26).

Species of Stratiomyidae, *Medetera* and *Rhizophagus* are known to prey on scolytids (Chamberlin 1939) but *Medetera* is also known to prey on other insects beneath the bark and may be an important mortality factor of other predators and parasitoids (Beaver 1966). Although there were numerous other predator species collected from *D. simplex* galleries in this study it is not known if they preyed on larch beetles. Of these species the staphylinid beetles were the most abundant and potentially the most important group. Most of the staphylinid species associated with *D. simplex* are known to prey on other scolytid species (Chamberlin 1939; Hatch 1957). The high abundance of staphylinids, mainly aleocharines, in the lower parts of larch boles during winter suggests that they might be using galleries for shelter and hibernation. Fly larvae of the genus *Lonchaea* and *Xylophagus abdominalis* larvae are also well known predators of scolytids (Chamberlin 1939) but were not important in this study since only one adult and no larvae

of each was observed. Species of *Tetrableps* are known as aphid predators (Kelton 1966), however, some were found in *D. simplex* galleries and may be egg predators.

Parasitoids

All three Hymenoptera species observed to parasitize *D. simplex* during this study are also known to parasitize many other scolytid species (Bushing 1965; Chamberlin 1939). Although these parasitoids were very numerous no multiple parasitism or superparasitism were observed. Samson (1984) reported that each *R. xylophagorum* female oviposits on up to 23 *Ips grandicollis* (Eich.) larvae in the southern United States.

Of the other Hymenoptera associated with the larch beetle in this study - *Chlorocytus* sp., *Microbrachys* sp., *Lamprotatus* sp. and *Liodontomerus* sp. may be parasitoids of *D. simplex* or other associates or may be hyperparasitoids. No hyperparasitism was observed. Graham (1969) reported *Xiphydriophagus meyerinckii* to be a parasitoid of woodwasps. *Coptera atricornis* is a known parasitoid of *Lonchaea* spp. (Muesebeck 1980) and some *Gelis* spp. are known hyperparasitoids of braconid and ichneumonid wasps (Carlson 1979).

4.3.2 Competitors

The impact of other phloem feeding species on *D. simplex* could not be determined but was likely not

significant because of the small number of other phloem feeders present (Table 21). Only one to two adults each of *Erypturgus pusillus*, *Dryocoetes autographus*, *Polygraphus rufipennis* and *Hylobius pinicola* were captured during the study and no galleries or larvae were observed indicating that these captures may have been incidental. However, *P. rufipennis* can be abundant on larch (Raske 1984 - personal communication). Larvae of *Stictoleptura canadensis* may have competed with *D. simplex* larvae for food but were likely more important as accidental predators. Destruction of scolytid brood by cerambycid larvae has been reported (Coulson et al. 1979).

4.3.3 Miscellaneous

Species of Ptilidae, *Corticaria* and *Epuraea* are fungus feeders (Arnett 1968) as are species of *Rhexoza* (Cook 1981), *Aprionis* (Gagne 1981), *Chaetosclara* and *Scatosclara* (Steffan 1981). The interval of approximately two months between *D. simplex* arrival at host trees and arrival of fungus feeders likely provides time for fungus to grow in beetle galleries.

Spiders probably did not adversely affect *D. simplex* populations since none were observed in galleries or preying on beetles on the tree surface. *Clubiona canadensis* and *Grammonota* sp. were just using crevices and scales on larch boles to deposit eggs while the other species were likely incidental captures. Although eggs and juveniles of the

harvestman *Odielus pictus* were common in larch beetle galleries no predation on beetle brood was observed.

The phoretic mites may have been phloeophagous, mycetophagous or predators of other associated organisms but were not observed to prey on *D. simplex*. The phoretic nematodes were likely mycetophagous (Finney 1970).

5. SUMMARY

1. The bionomics of *D. simplex* was studied near St. John's, Newfoundland in 1982 and 1983 and in western Newfoundland in 1984.
2. Emergence occurred from 7 May to 19 June in 1983 and was temperature influenced since emergence peaks coincided with periods of high mean daily air temperature.
3. At first more beetles emerged from the sun-exposed south side of tree boles than from the shaded north side and more females than males. Emergence at 5 m started two to four days later than at lower heights. The highest density of beetles emerged at 2.5 m.
4. Dispersing larch beetles were observed to land on tree species other than larch and on larch which, subsequently, were not attacked. This appears to support the theory of random initial landing of beetles rather than "primary" attraction.
5. In 1983 the first host attack period occurred between 15 May and 25 June. Host attack was initiated by females and males arrived up to two days later. Up to four pairs of beetles used each entrance hole but each pair constructed its own egg gallery.
6. The middle of the bole was generally attacked first. No attacks occurred in areas where phloem was thinner than 2 mm.
7. Production of an aggregation pheromone by *D. simplex* was not demonstrated but likely does occur.

8. In 1983 the first reemergence period occurred between 25 June and 27 July. ~~Twenty~~ percent of all parent beetles reemerged but none were observed to fly.
9. Some reemerged beetles attacked new trees between 4 and 29 July, produced a second brood and reemerged between 5 and 30 August. Parents spent an average of 30 and 32 days in Brood I and Brood II trees, respectively.
10. Attack peaks, which reflect peaks of flight, coincided with peaks in mean daily air temperature and most reemergence peaks and declines coincided with temperature increases and decreases, respectively, indicating a temperature influence on flight, attack and reemergence.
11. No reemergence or attacks occurred on days when mean air temperature was 4 °C or less and peaks of host attack, which reflect flight peaks, occurred on days when mean air temperature was 10 °C or higher.
12. The long duration and erratic pattern of spring emergence and first attack period is a reflection of the cool, wet and variable spring climate on the Avalon Peninsula.
13. Occurrence of emergence, attack (and hence flight) and reemergence between 10:30 and 17:00 hours, i.e. the warmest part of the day, suggests that these processes are temperature related, at least partially, on a diurnal basis.
14. There were no flight muscles in twelve reemerged

D. simplex examined in 1983 and only 17% of 96 reemerged beetles examined in 1984 at Pynn's Brook had fully developed flight muscles and were capable of flight. Reemerged beetles lacking fully developed flight muscles did not attack larch bolts placed farther than 2 m away. Thus, most reemerged beetles were not capable of flight to new hosts and effectively excluded from the second attacking population.

15. During the second attack periods in 1983 and 1984 only two and three girdled trees, respectively, were attacked. No standing, ungirdled trees were attacked. The proportion of reemerged beetles capable of flight is probably too small to enable successful attack of standing, uninjured trees. Reemerged beetles may be able to establish second broods only in standing weakened trees, stumps or fallen material.
16. One generation and two broods of *D. simplex* can be produced per year in Newfoundland. However, the second brood is usually small and sustains high mortality due to cold temperatures and, therefore, does not contribute significantly to the overall population emerging the following spring.
17. Lack of complete flight muscle regeneration in most reemerged beetles may be a result of selection for a single brood per year in Newfoundland where climate is not conducive to production of a second brood.
18. *D. simplex* is monogamous. Only the female elongates egg

galleries. Males construct ventilation holes and turning niches and clear frass.

19. Egg galleries were vertical, slightly-sinuuous and often intersected each other. They averaged 41 cm and 26 cm in length in Brood I and Brood II trees, respectively.
20. Egg gallery elongation rates by females increased with increasing temperature in the laboratory. Elongation rates by females before male introduction was only half that when males were present.
21. Females laid zero to four eggs per niche with an average of 1.4. The number of eggs per cm of gallery length (E/cm) averaged 1.0 in the field and 2.0 in caged larch bolts. Only 4% of the variation in E/cm between samples could be accounted for by total-egg gallery length per sample (index of crowding) and phloem thickness.
22. Regression of number of eggs per 100 cm³ sample (E) on gallery length per sample (GL) yielded the equation: $E = 5.09 + 0.833 GL$, where $N=236$ and $r=0.91$. The length of egg galleries measured in the field was substituted into the equation to give estimates of the number of eggs per gallery which averaged 39 and 27 for Brood I and Brood II trees, respectively. The average number of eggs per gallery in caged larch bolts was 70. Mean brood density was 49 and 23 individuals per 100 cm³ for Brood I and Brood II trees, respectively.
23. During egg gallery construction and oviposition *D. simplex* flight muscles completely degenerated and fat

body decreased in size, presumably to provide energy and materials for the reproductive processes and room for developing gonads.

24. Four larval instars occurred. Mean head capsule widths of successive larval instars increased geometrically with an average growth factor of 1.33. Adult males were significantly smaller than females.
25. Instar developmental times for *D. simplex* decreased with increased temperature in the laboratory. Regression of developmental times of each instar on rearing temperature yielded r^2 values of not less than 0.48. Hence, the regression equations were considered satisfactory for estimating instar developmental time from rearing temperature. Cooler temperatures in the fall likely accounts for the longer duration of the third and fourth larval instars and pupae of Brood II than for Brood I.
26. Only adult *D. simplex* overwintered. Immature stages were not cold hardy. Low temperatures caused high mortality among the immature stages of the second brood.
27. Thirty-five percent of new brood adults emerged in the fall and reentered galleries at the base of trees for hibernation. This is presumably an adaptation to increase survival since snow cover may provide protection from cold temperatures and from woodpecker predation. However, on the Avalon Peninsula snowfall during the winter is usually too little to provide

significant protection to brood overwintering at the tree base.

28. Mortality of *D. simplex* collected from field populations on 6 October 1983, 11 November 1983 and 2 January 1984 and subjected to various cold temperature treatments and durations in the laboratory, decreased from early fall to winter indicating that beetles became more cold hardy. The method by which cold hardiness is obtained is unknown. Larger size or higher concentrations of cryoprotectants may be responsible for the better survival of cold treatments by females than by males.

29. Third and fourth larval instars had the highest mortality and pupae the lowest in field populations. Total mortality was 79% and 82% for Brood I and Brood II, respectively, and was much lower near the base of Brood I trees than at middle and upper regions.

30. Pathogens generally caused the largest recognizable proportion of mortality among eggs, second instar larvae and pupae, resinosis among first instar larvae and parasitoids among third and fourth instar larvae. Parasitoids and pathogens caused the highest recognizable proportion of mortality in Brood I and Brood II, respectively. Mortality due to parasitoids was twice as high at the middle and upper regions of tree boles than near the base possibly due to thinner phloem which may have allowed more successful oviposition by parasitoids through the bark.

31. Mortality among teneral brood adults before winter was 6.1% and 8.7% in Brood I and Brood II trees, respectively. Overwintering mortality was 7.8% during the winter of 1982/83. Mortality during winter was significantly higher among beetles at the north aspect of trees than at the sun exposed south aspect.
32. A total of 52 species of insects, spiders, mites and nematodes were associated with *D. simplex* in 1983. The most abundant predator was a species of *Medetera*. Three Hymenoptera species - *Roptrocercus xylophagorum* (Ratz.), *Rhopalicus tutela* (Walker) and *Spathius canadensis* Ashmead were observed to parasitize *D. simplex*. General life histories of these four species are briefly described.

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Appendix A. One way analyses of variance comparing length of Dendroctonus simplex egg galleries in Brood I trees, Brood II trees, and caged larch bolts.

TEST	SOURCE OF VARIABILITY	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
1	Brood I trees and Brood II trees	1	1157	1157	7.11*
	Error	29	4721	163	
2	Brood I trees and bolts	1	409	409	1.99
	Error	43	8827	205	
3	Brood II trees and bolts	1	386	386	2.09
	Error	26	4794	184	

* Significant at $p < .05$

Appendix B. One way analyses of variance comparing number of eggs per niche in Dendroctonus simplex egg galleries between Brood I sample trees (test 1), between sample heights of Brood I trees (test 2) and between Brood I and Brood II trees (test 3).

TEST	SOURCE OF VARIABILITY	DEGRESS OF FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
1	Brood I trees Error	1 1169	0.68 1209.33	0.68 1.03	0.66
2	Sample heights Error	2 1168	0.30 1209.72	0.15 1.04	0.14
3	Brood I and Brood II trees Error	1 1271	0.11 1298.53	0.11 1.02	0.11

* Significant at $p < .05$

Appendix C. One way analyses of variance comparing number of egg niches per cm of length of Dendroctonus simplex egg galleries between Brood I sample trees (test 1), between sample heights of Brood I trees (test 2) and between Brood I and Brood II trees (test 3).

TEST	SOURCE OF VARIABILITY	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
1	Brood I trees Error	1 66	0.1658 5.1845	0.1658 0.0786	2.11
2	Sample heights Error	2 65	0.2693 5.0811	0.1374 0.0782	1.72
3	Brood I and Brood II trees Error	1 74	0.3396 6.9665	0.3396 0.0941	3.61

* Significant at $p < .05$

Appendix D. One way analyses of variance comparing number of eggs per cm of length of Dendroctonus simplex egg galleries between Brood I sample trees (test 1), between sample heights of Brood I trees (test 2), between Brood I and Brood II trees (test 3) and between galleries in Brood I trees and those in caged larch bolts (test 4).

TEST	SOURCE OF VARIABILITY	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
1	Brood I trees Error	1 184	1.3636 14.7536	1.3636 0.0802	17.01*
2	Sample heights Error	2 183	0.3341 15.7831	0.1670 0.0862	1.94
3	Brood I and Brood II trees Error	1 234	0.2580 18.1181	0.2580 0.0774	3.33
4	Brood I trees and bolts Error	1 205	19.0673 19.2344	19.0673 0.0938	203.22*

* Significant at $p < .05$

Appendix E. One way analyses of variance comparing number of eggs laid per pair of Dendroctonus simplex adults per gallery between Brood I and Brood II sample trees (test 1) and between Brood I sample trees and caged larch bolts (test 2).

TEST	SOURCE OF VARIABILITY	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
1	Brood I and Brood II trees Error	1 29	803 3276	803 113	7.11*
2	Brood I trees and bolts Error	1 43	10571 25185	10571 586	18.05*

* Significant at $p < .05$

Appendix F. One way analyses of variance comparing Dendroctonus simplex brood density between Brood I sample trees (test 1), between sample heights of Brood I trees (test 2), and between Brood I and Brood II trees (test 3).

TEST	SOURCE OF VARIATION	DEGREES FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
1	Brood I trees Error	1 166	1069 52837	1069 318	3.36
2	Sample heights Error	2 165	600 53306	300 323	0.93
3	Brood I and Brood II trees Error	1 214	26141 57270	26141 268	97.68*

* Significant at $p < .05$

Appendix G. One way analyses of variance comparing within instar mortality between three sample heights of Brood I trees for Newfoundland field populations of Dendroctonus simplex.

INSTAR	SOURCE OF VARIABILITY	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
Egg	Tree Height	2	0.000031	0.000016	0.02
	Error	93	0.066997	0.000720	
Larva I	Tree Height	2	0.00021	0.00010	0.05
	Error	80	0.15251	0.00191	
Larva II	Tree Height	2	0.00187	0.00093	0.56
	Error	69	0.11421	0.00166	
Larva III	Tree Height	2	0.1541	0.0771	5.48*
	Error	51	0.7167	0.0141	
Larva IV	Tree Height	2	0.3335	0.1668	5.05*
	Error	33	1.0894	0.0330	
Pupa	Tree Height	2	0.0380	0.0190	1.46
	Error	33	0.4300	0.0130	

* Significant at $p < .05$

Appendix H. One way analyses of variance comparing within instar mortality between the two Brood I sample trees for Newfoundland field populations of Dendroctonus simplex.

INSTAR	SOURCE OF VARIABILITY	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
Egg	Brood I trees	1	0.000244	0.000244	0.34
	Error	94	0.066784	0.000710	
Larva I	Brood I trees	1	0.00313	0.00313	1.69
	Error	81	0.14959	0.00185	
Larva II	Brood I trees	1	0.00521	0.00521	3.29
	Error	70	0.11086	0.00158	
Larva III	Brood I trees	1	0.1879	0.1879	14.30*
	Error	52	0.6830	0.0131	
Larva IV	Brood I trees	1	0.4018	0.4018	13.38*
	Error	34	1.0212	0.0300	
Pupa	Brood I trees	1	0.0956	0.0956	8.73*
	Error	34	0.3725	0.0110	

* Significant at $p < .05$

Appendix I. One way analyses of variance comparing within instar mortality between first and second broods in Newfoundland field populations of Dendroctonus simplex.

INSTAR	SOURCE OF VARIABILITY	DEGREES OF FREEDOM	SUM OF SQUARES	MEAN SQUARES	F-RATIO
Egg	First and second broods	1	0.1628	0.1628	15.22*
	Error	129	1.3800	0.0107	
Larva I	First and second broods	1	0.0092	0.0092	2.68
	Error	97	0.3341	0.0034	
Larva II	First and second broods	1	0.00003	0.00003	0.01
	Error	85	0.17790	0.00209	
Larva III	First and second broods	1	0.0214	0.0214	1.51
	Error	63	0.8926	0.1417	
Larva IV	First and second broods	1	0.0142	0.0142	0.31
	Error	43	1.9899	0.0463	
Pupa	First and second broods	1	0.0315	0.0315	2.63
	Error	44	0.5254	0.0119	

* Significant at $p < .05$



