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Development and survival of the spruce beetle, *Dendroctonus rufipennis*, in stumps and windthrow

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Canada

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Abstract

Data from a 7-year field study was analysed with respect to the effects of spruce windthrow, stumps, and other logging residue on variation in the following factors of spruce beetle populations: adult emergence, adult size and sex ratio, brood development, and brood survival. The mean date of emergence varied from the end of May to mid-June and the length of the emergence period varied from 26 to 57 days. Mean emergence date was not significantly affected by study site or host material. In combined samples for all years, there was no significant difference from a balanced sex ratio in 1-year-cycle adults by each combination of host type and study site, but there was significant female bias in 2-year-cycle adults. In both stumps and windthrow, the overall mean size (width of the pronotum) of beetles was significantly greater for 2-year-cycle beetles than for 1-year-cycle beetles, particularly in stumps (stumps: 2.20 vs. 2.65 mm; windfall: 2.45 vs. 2.59 mm), and was related to host quality. The first spring following attack, mean development index in stumps was significantly greater than in windthrow. In windthrow attacked during 1976, 5.4 and 0.7% of the broods developed on a 3-year cycle at the two study sites. At both study sites the percentage of 1-year-cycle beetles from stumps was significantly greater than from windthrow. Over the study period, 59% of all beetles emerged per year from stand edges plus logging residue, indicating the significance of harvesting operations in providing brood habitat for endemic populations. The large increases in population levels over the study period in stumps and windthrow at the two study sites did not result in increases in attacks on living trees. The results are discussed in relation to spruce beetle population dynamics.

Keywords: spruce beetle, *Dendroctonus rufipennis,* survival, windthrow, logging residue

Résumé

Les données d'une étude de terrain menée sur 7 ans ont été analysées afin de déterminer les effets de la présence de chablis ainsi que de souches et autres résidus de coupe d'épinettes sur les paramètres suivants des populations de dendroctone de l'épinette : émergence des adultes, taille des adultes, sex-ratio chez les adultes, développement larvaire et survie des larves. La date moyenne d'émergence des adultes se situait entre la fin mai et la mi juin, et la durée de la période d'émergence variait entre 26 et 57 jours. Il n'y avait aucun effet significatif du site ni du matériel hôte sur la date moyenne d'émergence des adultes. La sex-ratio, déterminée pour chaque combinaison site-matériel hôte et pour toutes les années de l'étude, ne présentait aucun écart significatif par rapport à une sex-ratio équilibrée chez les adultes ayant accompli leur cycle en 1 an, mais la proportion de femelles était significativement plus élevée chez ceux ayant accompli leur cycle en 2 ans. La largeur moyenne du pronotum des adultes était significativement plus grande chez les individus ayant accompli leur cycle en 2 ans que chez ceux l'ayant accompli en 1 an, en particulier chez ceux ayant accompli leur développement dans des souches (souches : 2,20 mm contre 2,65 mm; chablis : 2,45 mm contre 2,59 mm), et la taille des adultes était liée à la qualité du matériel hôte. Le premier printemps suivant l'attaque initiale, l'indice de développement moyen était significativement plus élevé pour les populations des souches que pour celles des chablis. Pour les chablis attaqués en 1976, le pourcentage de couvains ayant accompli leur cycle en 3 ans était de 5,4 % dans un des sites et de 0,7 % dans l'autre site. Dans les deux sites, le pourcentage d'individus ayant accompli leur cycle en 1 an était significativement plus élevé pour les souches que pour les chablis. Chaque année de l'étude, 59 % des individus se développaient à la lisière de peuplements ou dans des parterres de coupe, ce qui montre que l'exploitation crée pour les populations établies des sites de ponte favorables au développement des larves. Sur la durée de l'étude, le niveau d'infestation des souches comme des chablis a augmenté de façon importante aux deux sites, mais il ne s'est pas accompagné d'une augmentation des attaques sur des arbres vivants. Les résultats sont analysés par rapport à la dynamique des populations de dendroctone de l'épinette.

Mots clés : dendroctone de l'épinette, survie, chablis, résidus de coupe

1. Introduction

The spruce beetle, *Dendroctonus rufipennis* (Kirby) (Coleoptera: Curculionidae, Scolytinae), is native to the spruce (*Picea* spp.) forests of North America. Its distribution is transcontinental in Canada (Bright 1976). All native spruce species can be infested but the major hosts in western Canada are white spruce (*P. glauca* [Moench] Voss), Engelmann spruce (*P. engelmanni* Parry), and their hybrids. During epidemics some non-host trees, especially *Pinus* spp., may also be attacked and killed.

The spruce beetle normally has a 2-year life cycle (Wygant and LeJeune 1967). However, depending on temperature conditions, the duration of the life cycle can vary from 1 to 3 years. Regardless of the length of the life cycle, brood adults overwinter and emerge to attack host material during the following spring and early summer period. Endemic populations normally infest weakened or decadent trees, fresh windthrow, logs, and logging residue. Fresh logging residue such as stumps and cull logs (Dyer and Taylor 1971; Schmid 1977) and wind-felled trees (Wygant and LeJeune 1967) are colonized readily by spruce beetles. Under the right conditions for brood establishment and survival, spruce beetle adults emerging from these host materials may constitute a significant proportion of the resident beetle population in a timber harvesting area (Safranyik et al. 1983) to the extent that they may increase the risk of catastrophic outbreaks in apparently healthy trees. During such outbreaks, the large-diameter spruce component of stands characteristically suffers the greatest mortality.

In 1972 a field study of spruce beetle population dynamics was established in central British Columbia (BC) in two adjacent timber harvesting areas. The objectives of this study were to determine the effects of two distinct host materials, windthrow and stumps, on a) adult emergence, b) adult size and sex ratio, c) brood development and survival, and d) changes in population levels.

2. Materials and Methods

This study was carried out between 1972 and 1979 in two adjacent timber supply harvesting licenses of 940 ha (study site WF) and 1680 ha (study site D) in the Naver Forest (53º 24' N, 122º 20'W), located 50 km southeast of Prince George, BC. The area was classified as having good to medium growing sites at an elevation range of 900–1400 m. The mean elevation of study site WF was approximately 200 m lower than that of study site D. Stands in the study sites were comprised of mature (> 150 years old) spruce hybrid population (*P. glauca* × *P. engelmanni*) and subalpine fir (*Abies lasiocarpa* [Hook] Nutt.), with spruce dominating the overstorey. A few mature Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco), lodgepole pine (*Pinus contorta* var. latifolia Engelm.), white birch (*Betula papyrifera* Marsh.), and aspen (*Populus tremuloides* Michx.) were also present. At site WF, the average diameter at 1.3 m (breast height) of the spruce trees greater than 20 cm in diameter was 49.5 cm, and average density was 139.5 trees per ha. The corresponding figures for site D were average diameter of 52.4 cm and average density of 97.9 trees per ha. Both areas were clearcut during late fall and winter.

2.1 Surveys of Logging Residue, Windthrow, and Trees

The size distribution and infestation status of logging residue, i.e., spruce stumps, cull logs, and tops, was measured by surveying randomly located, 120.7 m (6 chain) line transects after the flight period of the spruce beetle each year from 1972 to 1979 (Safranyik and Linton 1987). The following information was recorded for each intersected stump of at least 20 cm (8 inch) diameter at the mid-point between the top and the mineral soil: height from mineral soil, mid-height diameter, infestation status (presence or absence), and percent bark remaining. Intersected cull logs were recorded only if the diameter at the larger end was greater than 15.2 cm (6 inches) and its length from the larger end to 15 cm diameter was greater than 91 cm (3 ft). The following measurements of cull logs were made: both end diameters, bole length, infestation status, and percent bark remaining. Measurement of diameter, stump height, and piece length was made to the nearest 2.5 mm (0.1 inch), nearest 2.5 cm (1 inch) and nearest 30.4 cm (1 ft) respectively. The exclusion of stumps and cull logs with dimensions smaller than those stated above was based on observations that such host materials were rarely attacked by spruce beetle.

The characteristics of windthrow were assessed annually using permanent line transects inside the stands and along stand edges. The number of spruce stems that had fallen was determined each year with one exception: stand-edge transects were not measured in area D during 1976. Both experimental areas were stratified in order to distribute the sampling effort and to reduce sampling time. Where possible, stratum sizes were multiples of 48.5 ha (or 402 × 1207 m; 120 acres; 1320 × 3960 ft), the size of the primary sampling unit. In these strata, a number of primary units were selected at random, and with equal probability and replacement. Each selected primary unit was subdivided into four 100.5 × 1207 m (12.1 ha) strip plots (the second-stage units). Two strip plots were selected at random and without replacement from each selected primary unit. The line transects ran lengthwise through the centre of the strip plots.

In each selected strip plot, two sets of systematically arranged, permanent prism plots were established along the line transect in three groups of five plots per set for estimating live and infested spruce tree density. Each set of plots was selected with a random starting location. In each group, the centre of one prism plot was located on the line transect and the other prism plots were located 40.1 m (122 ft) from the centre of this plot, one in each of the cardinal directions. Infested spruce trees were tallied on all prism plots, but live spruce trees at the beginning of the study were tallied only on the centre plot of each group of prism plots.

When a stratum was irregular in shape and not a multiple of the primary unit, it was divided into primary units of various sizes that were selected with probability proportional to primary unit size and with replacement. Prism plots were located at random in each selected primary unit, and lines connecting the centres of the prism plots were designated as line transects. A total of 13 and 15 line transects were established in study sites WF and D respectively.

Stand-edge strata consisted of 40.2 m (2.0 chains) wide strips along roads and cutting boundaries created by the logging operations. A total of nine and eight stand edge strata were selected at random in areas WF and D respectively. The line transects in the stand edge strata ran through the strip centres and were parallel to the stand edges. Depending on their exposure to storm-force winds, spruce trees along stand edges can be highly susceptible to windthrow for a number of years following clearcutting.

For each windfall intersected the following information was recorded: bole length from the butt to the point where diameter was 15.2 cm (6 inches), both end diameters, direction (azimuth) of fall, and infestation status (presence or absence). Bole length and diameter were recorded to the nearest 30.4 cm (1 ft) and 2.5 mm (0.1 inch) respectively. Approximately 28 km of line transect were assessed in the stand interiors each year.

2.2 Surveys for Brood Establishment and Survival

In infested stumps and windfall, spruce beetle attacks and resulting brood were sampled three to five times during the beetles' life cycle as follows: early summer following establishment of egg galleries; late summer–early fall; May of the 2nd year; late summer–early fall of the 2nd year; May of the 3rd year.

2.2.1 Stumps

All clearcuts were sampled at both study sites. Five to 20 infested stumps, the primary sampling units, were sampled per clearcut. Stumps were selected at random, with equal probability and without replacement. The same stumps were used for all sampling stages to ensure that specific broods were followed throughout their life cycle. The bark area of each stump was divided into four sections representing the north–top, north–bottom, south–top, and south–bottom quarters. For each of the first four sampling stages, two randomly located, 10.2 cm (4 inches) diameter discs of bark plus about 5 mm wood were removed from each of the four bark sections of a stump using a hole saw and chisel. The discs were placed in plastic bags, labelled, and brought to the laboratory for dissection. The following information was recorded for each disc: a) numbers of eggs, larvae, pupae, and adults; b) total length of egg galleries; c) number of attacks; d) number of separate egg galleries; e) length of unsuccessful egg galleries; and f) phloem thickness. Due to the low density of the slash, brood survival was not recorded from this material. No samples were taken at the first sampling stage (early summer) in 1973.

2.2.2 Windthrow

Newly infested windthrow was sampled each year at both study sites. The infested bark area of spruce windthrow was the primary sampling unit. Windthrown trees were selected for sampling at random, with equal probability and without replacement. The frequency and time schedule of brood sampling in windthrow was the same as described in Section 2.2. The same primary units were retained for all sampling stages. For each of the first four sampling stages, four to 12 shallow discs of bark and wood 10.2 cm (4 inches) in diameter (the secondary units) were removed using a hole saw. The discs were located in pairs on opposite sides of the bole at approximately equidistant points along the length of the infested length of the windthrow. The discs were placed in plastic bags, labelled, and taken to the laboratory where the same information was recorded as for the bark samples from stumps (described in Section 2.2.1).

For the last sample stage (May of the 3rd year following attack), emergence traps made from 10.2 cm (4 inches) diameter cans were fitted into shallow kerfs through the bark and outer sapwood at randomly selected locations within the four bark sections of stumps and along the boles of windthrow. Beetles that emerged into the traps were captured in glass vials fitted onto the bottom of the trap. Beetles were removed at 2–4 day intervals; were labelled by date of emergence, host material, and location; and were stored in clean vials in a refrigerator at about 3–5°C until processed as described in Section 2.3 below.

During early June 1973, 30.5 cm (1 ft) square glass barrier traps were placed on tops of stumps in new clearcuts to trap dispersing and attacking spruce beetles. The glass barriers were affixed above metal troughs containing an antifreeze solution to trap beetles. In early June 1980, a close-mesh, hardwire basket was attached near the base of a spruce tree baited with frontalin and the lower 6 m of its bole sprayed with lindane (insecticide) for capturing spruce beetles that were attracted by the bait and knocked down by the insecticide. Beetles from barrier traps and the wire basket were handled and stored as described above.

2.2.3 Trees

The density of live spruce at the beginning of the study and the density and bark area per year of infested spruce ≥ 20.3 cm (8 inches) in diameter at 1.3 m (breast height; DBH) were determined using permanent, variable radius plots (BAF = 4.59) established along the windfall survey transects at the beginning of the study period as described above in Section 2.2.2. In study sites WF and D, 390 and 450 variable radius plots were established, respectively, for estimating annual densities and bark areas of infested spruce ≥ 20.3 cm DBH. Estimation of the density of live spruce ≥ 20.3 cm DBH at the beginning of the study was based on one-fifth of the total number of permanent prism plots established in each of the two study sites (see Section 2.2.2).

2.3 Determination of Adult Size and Sex

The width of the pronotum of adult spruce beetles was measured at its widest point using calibrated ocular micrometers with accuracies of 0.05 and 0.033 mm. Sex was determined using the characteristic shape of the seventh abdominal tergite (Lyon 1958).

2.4 Development Index

The following index values were assigned to the brood stages of the spruce beetle: 1 = egg; 2–5 = instars one to four; 6 = pupa; 7 = adult. Larval instars were determined based on the width of the head capsule (Hall and Dyer 1974).

2.5 Data Analysis

2.5.1 Density and Bark Area of Infested Hosts

The density, Nl, in number per ha, and bark area, Sl, in m^2 per ha, of cull logs and windthrown trees were calculated (after DeVries 1973) as in equations [1a] and [1b] respectively:

[1a] $$Nl = (10000\ /IL)\sum_{i=1}^{n} (1/li)$$

[1b] $$Sl = (5000\pi\ /IL)\sum_{i=1}^{n} (d1_i + d2_i)$$

where li is the piece length (m) of windthrow $I; d1_i$ and $d2^i$ (m) are the end diameters of the windthrow; L is the length of the line transect (m); n is the number of intersected windthrown trees; and I is the average intersection angle in radians between the windthrow and line transect. It was necessary to use equation 3, where I replaces the expected mean interception angle ($2/\pi$) in the standard formula, to eliminate the potential for bias resulting from the non-random distribution of the angles of interception between the line transect and cull logs or windthrown trees.

I was calculated as in equations [2a] and [2b] (Batschelet 1981):

[2a] $$I = arctan\{[(1/n)\ \sum^n sin(i)]/[(1/n)\ \sum^n cos(i)]\},\ if\ (1/n)\ \sum^n cos(i) > 0.$$

[2b] $$I = 180^o + arctan\{[(1/n)\ \sum^n sin(i)]/[(1/n)\ \sum^n cos(i)]\},\ if\ (1/n)\ \sum^n cos(i) \leq 0.$$

where i is the intersection angle of a windthrow with the line transect, calculated from the azimuth of the intersected windthrow and the azimuth of the line transect. (The other symbols are the same as defined earlier.)

The numbers (Ns) and bark area (Ss) per ha of stumps was calculated as in equations [3a] and [3b] respectively:

[3a] $$Ns = (10000\pi\ /L)\sum^{i=1} (1/dm_i)$$

[3b] $$Ss = (10000\pi\ /L)\sum^{i=1} (h_i)$$

where dm_i and h_i are stump mid-diameter (m) and stump height respectively.

2.5.2 Emergence, Adult Size, and Sex Ratio

Dates of emergence of spruce beetles from stumps and windfall and dates of capture of flying beetles were expressed as Julian date. Variation among years and host materials in spruce beetles captured in emergence traps were analysed by one-way analysis of variance (ANOVA), and means were compared by Tukey's test. Flying beetles were caught in barrier traps in 1973 and landing beetles were captured in a wire basket near the base of a baited spruce tree that was sprayed with insecticide in 1980. Results from beetles caught in 1973 and 1980 were not included in the ANOVA because in both of these years flying or landing beetles were trapped (as opposed to the emerging beetles that were captured in emergence traps in other years). Dispersing or attacking beetles include re-emerged adults as well as brood adults from distant sources and different thermal environments that have affected the onset and duration of emergence.

Deviation from a balanced sex ratio of adult spruce beetles was analysed separately by chi-square for combinations of study area, year of emergence, and host material. The overall numbers of male and female adults by life cycle duration were also compared separately by chi-square in the two host materials.

The mean size of each sex within years and from different host materials were compared between study sites by paired t-tests. The t-probabilities (p_i) from all of the data sets (k) were combined separately for each host material in a chi-square statistic to test the difference between the sexes as follows: χ^2 =2k (-2logp_i) with 2k degrees of freedom where logarithms are to the base e (Steel and Torrie 1980).

Because the emergence traps were small, most traps had no beetles in them at the time of collection. Therefore, in order to compare the size of 1- and 2-year-cycle spruce beetles, the data were pooled for each host type prior to analysis and mean sizes were compared by t-tests. For analysis of the effect of position on the stump (bottom half vs. top half) on adult size, data from each position were pooled over stumps and mean sizes were compared by t-test. Variation among windthrow in the size of emerged spruce beetles was analysed by ANOVA in a completely randomized design.

2.5.3 Brood Development and Survival

Mean development index (DI) between types of host material within years and study sites were compared by t-test. The relation between mean development index per sample stage and the proportion of larvae in samples that contained only larvae, pupae, and adults was analysed by linear regression.

Analysis of within-generation survival of the spruce beetle was done using the combined data set from each year and study site, and was done separately for each type of host material. The mean density of beetles surviving to each sampling stage, and the corresponding mean DI in a specific year, was determined from pooled data over all sampled pieces (windthrow or stumps). The relationship between log (mean brood density) and mean DI was analysed by polynomial regression. The survivorship curves for stumps and windfall (Figures 1 and 2) were developed as follows: First, the data consisting of mean DI and corresponding mean brood density for each combination of year and sampling stage was pooled by study site. Second, mean DI values were grouped on the nearest DI class midpoints, from 1 to 7, corresponding to the seven brood stages. Third, overall mean brood density and standard error were calculated for each DI class and plotted on the corresponding DI class midpoint.

Yearly mean densities per m^2 of spruce beetle attacks, and emerged spruce beetles by host material and study site, were calculated by converting the respective samples to numbers per m^2, summing the results, and dividing by sample size. Mean attack density was based on all attacks (successful and unsuccessful) in the late summer samples taken during the 1st year because later samples were deemed less reliable due to deterioration of the habitat. Mean density of 1-year-cycle and 2-year-cycle spruce beetles was determined separately based on the appropriate sample series, and total yearly emergence was calculated as the sum of these two values.

Yearly totals of spruce beetle attacks and emerged adults by host material and study site were calculated as products of yearly estimates of the sample area (in ha), infested bark area (in m^2), and the respective density per m^2. Estimates of the densities of infested host material and infested bark area were determined from equations [1a–1b] and [3a–3b].

3. Results

3.1 Adult Emergence

The mean Julian day of emergence from emergence traps over the 6-year period between 1974 and 1979 varied by only 13 days, from the end of May to mid-June, and did not vary significantly between study sites or host material (Table 1). In 1974 the mean Julian dates of emergence from windthrow at both study sites were significantly later than seven of nine other year–host combinations (Table 1). The length of the emergence period in windfall ranged from 26 days in 1974 to 57 days in 1976. The mean Julian date of capture of dispersing beetles in barrier traps (1973) and that of landing beetles captured at a baited spruce tree (1980) were later than the mean Julian dates for beetles captured in emergence traps (Table 1).

Table 1. Julian dates of trap placements and mean (SE = standard error) Julian dates by year and sample size (N) of emergence or flight of the spruce beetle from windthrow and stumps in the two study sites.

Year	Traps Placed[1]	Mean Date	SE	N	Notes
1973	152	173.36[2]	0.936	176	Barrier trap catches in clearcut in study site WF and D.
1974	148	163.03 c[3]	0.550	91	Emergence trap catches in windthrow. Study site WF.
1974	148	163.03 c	1.165	29	Emergence trap catches in windthrow. Study site D.
1975	128	151.74 ab	0.752	127	Emergence trap catches in windthrow. Study site WF.
1975	134	150.29 a	2.226	155	Emergence trap catches in windthrow. Study site D.
1976	134	155.25 ab	1.774	56	Emergence trap catches in windthrow. Study site WF.
1976	134	156.28 abc	2.409	56	Emergence trap catches in windthrow. Study site D.
1977	124	150.99 a	1.093	95	Emergence trap catches in windthrow. Study site WF & D.
1977	124	158.91 bc	1.304	58	Emergence trap catches in stumps. Study site WF.
1977	126	152.50 ab	0.531	94	Emergence trap catches in stumps. Study site D.
1978	129	153.86 ab	1.068	67	Emergence trap catches in windthrow. Study site WF.
1979	130	150.09 a	0.773	62	Emergence trap catches in windthrow. Study site WF.
1980	154	178.62[2]	0.088	1876	Trap catches at a baited tree. Study site WF.

[1]Julian date of trap placement
[2]Mean emergence dates in 1973 and 1980 were not compared with mean emergence dates for the other year–host type combinations because during these 2 years dispersing and landing beetles were captured, as opposed to emerging beetles, due to different trapping methods used.
[3]Means followed by the same letters are not significantly different (Tukey's test, p=0.05)

3.2 Sex Ratio

Numbers of emerged male and female spruce beetles from stumps and windthrow by year and study site, and chi-square tests for deviation from a balanced sex ratio, are given in Table 2. Only one of 32 samples had a male bias. For 1-year-cycle spruce beetles from stumps, there was no significant deviation from a balanced sex ratio in any of the samples from the two study sites (Table 2). For 1-year-cycle beetles from windthrow, in one of six samples (1976) there was a significant female bias. However, this was a small collection of only 13 beetles. Based on combined samples for all years, there was no difference from a balanced sex ratio in 1-year-cycle beetles in either host type in the two study sites.

In one of 10 samples from stumps and four of 12 samples from windthrow, the proportion of 2-year-cycle females was significantly greater than expected based on a balanced sex ratio (Table 2). In combined samples for all years, the proportion of females in 2-year-cycle beetles was significantly greater than expected for each combination of host type and study site based on a balanced sex ratio.

The overall proportion of female beetles emerging from stumps, taken over all years and study sites, was 0.542 for 1-year-cycle beetles and 0.583 for 2-year-cycle beetles. The corresponding proportions for samples taken from windthrow were 0.549 and 0.614. For the combined data from the two study sites, there was no significant difference in the proportion of the sexes in either host type (for 1-year-cycle beetles: $\chi^2_{1df} = 0.189$, p = 0.844; for 2-year-cycle beetles: $\chi^2_{1df} = 1.114$, p = 0. 561).

Table 2. Numbers of male and female beetles and chi-square tests of deviation from a balanced sex ratio of 1-year- and 2-year-cycle spruce beetle adults emerged from stumps and windthrow in two study sites.

Year Attacked	Year Sampled	Sex	Site WF				Site D			
			Stumps		Windthrow		Stumps		Windthrow	
			N	Chi-sq.	N	Chi-sq.	N	Chi-sq.	N	Chi-sq.
1973	1974	Female	18	-	22	-	27	-	17	-
		Male	12	1.200 ns	12	2.941 ns	26	0.0188 ns	12	0.862 ns
		Female	-	-	49	-	-	-	-	-
		Male	-	-	42	0.538 ns	-	-	-	-
	1975	Female	53	-	-	-	13	-	10	-
		Male	42	1.344 ns	-	-	9	0.727 ns	7	0.529 ns
		Female	15	-	-	-	72	-	-	-
		Male	11	0.615 ns	-	-	49	4.372 ns	-	-
1974	1976	Female	-	-	34	-	39	-	26	-
		Male	-	-	18	4.923*	21	5.400 ns	22	0.333 ns
		Female	-	-	12	-	-	-	38	-
		Male	-	-	11	0.048 ns	-	-	14	11.076***
1975		Female	-	-	7	-	20	-	11	-
		Male	-	-	7	0.000 ns	20	0.000 ns	2	6.231*
		Female	-	-	-	-	13	-	-	-
		Male	-	-	-	-	8	1.076 ns	-	-
	1977	Female	4	-	27	-	-	-	20	-
		Male	2	0.667 ns	27	0.000 ns	-	-	14	1.059 ns
1976		Female	-	-	-	-	-	-	21	-
		Male	-	-	-	-	-	-	29	1.280 ns
	1978	Female	5	-	33	-	5	-	61	-
		Male	5	0.000 ns	22	2.200 ns	2	1.286 ns	44	2.752 ns
		Female	-	-	62	-	-	-	44	-
		Male	-	-	29	6.531*	-	-	21	8.138**
1977	1979	Female	82	-	-		-	-	-	-
		Male	68	1.307 ns	-	-	-	-	-	-
		Female	23	-	-	-	-	-	-	-
		Male	13	2.777 ns	-	-	-	-	-	-
Total 1-yr. cycle		Female	18	-	78	-	60	-	49	-
		Male	12	1.200 ns	61	2.079 ns	54	0.0571 ns	43	0.391 ns
Total 2-yr. cycle		Female	182	-	168	-	129	-	196	-
		Male	141	4.680*	107	13.531***	81	10.971***	122	17.220***

Notes: ns not significant; * significant at p=0.05; ** significant at p=0.01; *** significant at p=0.001

3.3 Adult Size

There was a significant difference in the mean widths of the pronotum between the sexes of emerged spruce beetles in only one of 31 samples (Appendix 1). Overall, there were no differences in the mean size of the sexes in stumps ($\chi^2_{(26)} = 16.79$, $p = 0.91$) or windthrow ($\chi^2_{(28)} = 39.10$, $p = 0.087$). In stumps, the mean width of the pronotum was 2.32 mm for females and 2.33 mm for males. The corresponding figures for windthrow were 2.31 mm and 2.32 mm.

Based on the preceding results of no difference in mean size between the sexes, variation in beetle size by life cycle duration within and among hosts was based on combined data from the two sexes.

In both stumps and windthrow, the mean sizes of 2-year-cycle adult spruce beetles of both sexes were larger than the corresponding means for 1-year-cycle beetles (Table 3). The overall combined mean width of the pronotum of the two sexes was significantly larger for 2-year-cycle beetles than the corresponding mean for 1-year-cycle beetles (stumps: $t_{14df} = 5.144$, $p \leq 0.01$; windthrow: $t_{93df} = 5.921$, $p \leq 0.001$).

The mean sizes in Table 3 are based on all samples taken from within several stumps and windthrow and mask the possible effects of location within or among individual hosts. The mean sizes by sex and position on stumps of 1- and

2-year-cycle spruce beetles are given in Table 4. For both the 1-year-cycle and 2-year-cycle beetles, the mean width of the pronotum of the sexes combined was significantly greater for samples from the bottom halves of the stumps compared with the top halves (1-year-cycle: $t_{28df} = 5.034$, $p \leq 0.01$; 2-year cycle: $t_{17df} = 3.341$, $p \leq 0.01$). The top halves of stumps were generally warmer, had thinner bark, and the inner bark had deteriorated faster due to weathering, compared with the lower halves.

An example of the effect of variation in beetle size among windthrow attacked the same year is given in Table 5. There was significant variation among windthrow in the size of the two sexes combined ($F_{8,141df} = 4.120$, $p \leq 0.001$). This variation in size may have been caused by differences in exposure or host quality, or a combination of these factors.

Table 3. Mean (SE = standard error) widths of the pronotum in mm and sample sizes (N) by year and sex and for both sexes combined for 1-and 2-year cycle spruce beetles from stumps and windthrow at two study sites.

	Year Emerged: 1977			Year Emerged: 1978		
Sex	**Mean**	**SE**	**N**	**Mean**	**SE**	**N**
Study site WF, stumps attacked in 1976						
Female (F)	2.248	0.0587	10	2.640	0.0380	5
Male (M)	2.132	0.0739	7	2.656	0.0720	5
F + M	2.200	0.0654	17	2.648	0.0575	10
Study site D, windthrow attacked in 1976						
Female	2.448	0.0130	21	2.589	0.0116	61
Male	2.444	0.0101	29	2.587	0.0296	44
F + M	2.446	0.0114	50	2.588	0.0211	105

Table 4. Mean (SE = standard error) width of the pronotum in mm by sex and position on stumps and sample size (N) for emerged spruce beetles in two study sites.

	Top of Stump			Bottom of Stump		
Statistics	**Mean**	**SE**	**N**	**Mean**	**SE**	**N**
Study site WF, attacked 1976, beetles emerged 1977						
Female (F)	2.343	0.025	22	2.482	0.024	20
Male (M)	2.275	0.017	9	2.400	0.043	7
F + M	2.323	0.0182	31	2.461	0.0205	27
Study site D, attacked 1975, beetles emerged 1977						
Female (F)	2.170	0.059	8	2.370	0.008	61
Male (M)	2.213	0.097	3	2.307	0.026	22
F + M	2.182	0.048	11	2.353	0.015	83

Table 5. Mean (SE = standard error) width of the pronotum in mm by sex and sample size (N) of spruce beetles in windthrow at study site WF. Windthrown trees were attacked in 1977 and adults were sampled May 11, 1979.

Windthrow	Females			Males			Females and Males		
	Mean	SE	N	Mean	SE	N	Mean	SE	N
1	2.396	0.0238	13	2.244	0.0741	8	2.338 abc	0.0351	21
2	2.144	0.0315	4	2.244	0.0649	6	2.204 a	0.0424	10
3	2.289	0.0345	18	2.271	0.0315	20	2.279 abc	0.0243	38
4	2.157	0.0644	5	2.323	0.0273	3	2.219 ab	0.0453	8
5	2.233	0.0589	6	2.412	0.0947	2	2.278 abc	0.0536	8
6	2.546	0.0417	15	2.395	0.0443	8	2.493 c	0.0358	23
7	2.278	0	2	2.362	0.0661	4	2.334 abc	0.0454	6
8	2.315	0.0473	2	2.613	0	1	2.414 bc	0.1068	3
9	2.294	0.0268	17	2.278	0.0260	16	2.286 abc	0.0194	33
Mean/Total	2.335	0.0191	82	2.298	0.0239	68	2.318	0.0153	150

Note: Means followed by the same letters are not significantly different (N-S-K test, p = 0.05)

3.4 Spruce Beetle Development in Stumps and Windthrow

Spruce beetle development, measured by the development index, in the two host types by year and study site are given in Table 6. When data were available from both stumps and windthrow, the development index for spruce beetle broods the first spring following attack was significantly greater in stumps compared to windthrow in all but one case. Up to the first spring following attack, development indices in both stumps and windthrow were greater for the WF study site than the corresponding values for the D site. Differences in mean development index were statistically significant for two of three cases in windthrow (1973: $t_{353df} = 6.622$, $p \leq 0.001$; 1974: $t_{197df} = 3.798$, $p \leq 0.001$) and both cases in stumps (1973: $t_{197df} = 6.251$, $p \leq 0.001$; 1976: $t_{389df} = 1.960$, $p \leq 0.05$).

Spruce beetle broods developed to the adult stage within 2 years in all cases except in windthrow attacked during 1976. Of the spruce beetle broods from the 1976 attack in windthrow, 5.2 and 0.7% were still mature larvae or pupae in study sites WF and D respectively in the third spring following attack. So these beetles apparently developed on a 3-year cycle.

In the combined data from stumps and windthrow in those samples where larvae and more advanced life stages were present, mean development index (DI) was linearly related to the proportion of larvae (P) (equation [4]):

$$[4] \quad DI = 7.09 - 2.64\,P,\ r = 0.943,\ N = 23,\ p \leq 0.001$$

Based on this equation, when a sample contained only larvae, the predicted mean development index was 4.45 (about halfway between the third and fourth larval instars).

Table 6. Mean development index (DI), standard error (SE), and sample size (N) by year of attack and sample date for spruce beetles in stumps and windthrow at the two study sites.

Year Attacked	Date Sampled	Study Site WF			Study Site D			Host Material
		DI	SE	N	DI	SE	N	
1973	Oct. 2, 1973	6.477 a[1]	0.109	116	5.446 a	0.111	83	Stumps
1973	Oct. 2, 1973	4.950 b	0.025	146	4.550 b	0.045	209	Windthrow
1974	May 20, 1975	-	-	-	3.780 a	0.086	63	Windthrow
1974	May 21–22, 1975	4.680	0.145	72	4.170 a	0.059	127	Windthrow
1974	May 30, 1975	-	-	-	4.570 b	0.091	145	Stumps
1974	May 10, 1976	-	-	-	7.000	0	29	Windthrow
1975	May 28, 1975	2.900	0.780	20	-	-	-	Windthrow
1975	May 10–11, 1976	-	-	-	5.195 a	0.113	113	Windthrow
1975	May 10–11, 1976	-	-	-	5.103 a	0.016	29	Stumps
1976	May 18–23, 1977	5.340 a	0.209	52	5.080 a	0.041	339	Stumps
1976	May 18–23, 1977	4.900 a	0.092	416	4.880 b	0.011	946	Windthrow
1976	May 18, 1978	6.916	0.047	154	6.991	0.013	138	Windthrow
1977	Aug. 23, 1977	4.713	0.050	136	-	-	-	Windthrow
1977	Sept. 12, 1978	6.571	0.163	21	-	-	-	Stumps
1977	May 10, 1978	4.829 a	0.039	333	-	-	-	Windthrow
1977	May 15, 1978	5.950 b	0.427	38	-	-	-	Stumps
1977	May 9–11, 1979	7.000	0	133	-	-	-	Windthrow
1978	Sept. 12, 1978	5.794 a	0.081	141	-	-	-	Windthrow
1978	Sept. 12, 1978	6.571 b	0.163	21	-	-	-	Stumps
1978	May 9, 1979	6.660 a	0.011	53	-	-	-	Stumps
1978	May 11, 1979	5.911 b	0.122	68	-	-	-	Windthrow

[1] Within study site and year of attack, mean development index between stumps and windthrow followed by the same letters are not significantly different (t-test, p = 0.01).

3.5 Brood Survival

Mean brood density as a function of development index for stumps and windthrow are shown in Figures 1 and 2, respectively. In both host types, brood survival was inversely related to development index and, on average, broods suffered greater than 50% mortality from egg stage to first instar larvae. In stumps, the survival curve declined steeply to the mean second instar stage and stayed relatively flat at the later brood stages. In windthrow, on average, little mortality occurred between the first and second instars and survival declined gradually at the later brood stages.

In stumps (Bs) and windthrow (Bw), change in brood density per m^2 with development index (DI) was described by equations [5] and [6] respectively:

[5] $$Ln(Bs) = 9.04 - 1.20DI + 0.07DI^2,\ N = 42,\ R = 0.824,\ p \leq 0.001$$

[6] $$Ln(Bw) = 8.40 - 0.48DI + 0.02\ DI^2\quad N = 37,\ R = 0.875,\ p \leq 0.001$$

where logarithms are base *e*.

Equations [5] and [6] provide estimates of expected brood survival as functions of brood development. Deviations from these estimates result from the variation in initial brood density, and the subsequent effects of main factors of mortality.

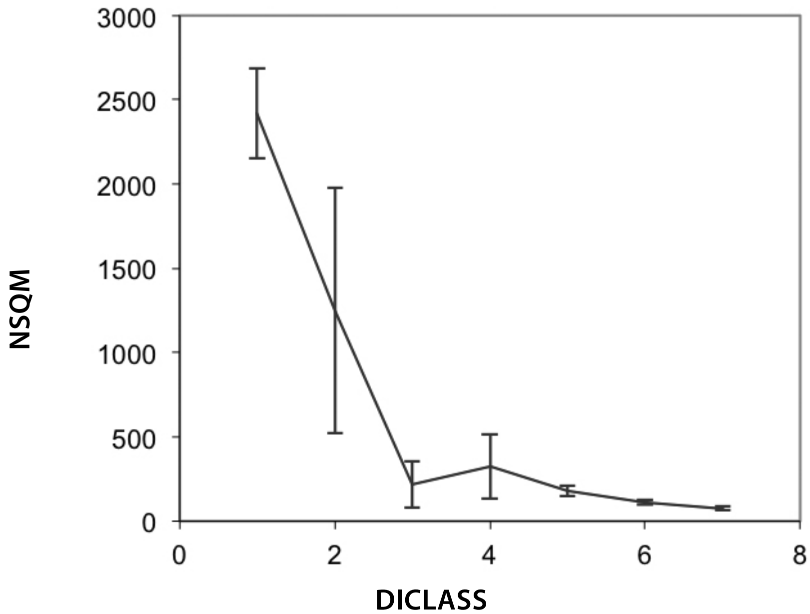

Figure 1. Mean density and standard error of spruce beetles per square meter (NSQM) in stumps by development index class (DICLASS). The class midpoints, 1 to 7, correspond to the DI index values for the seven brood stages.

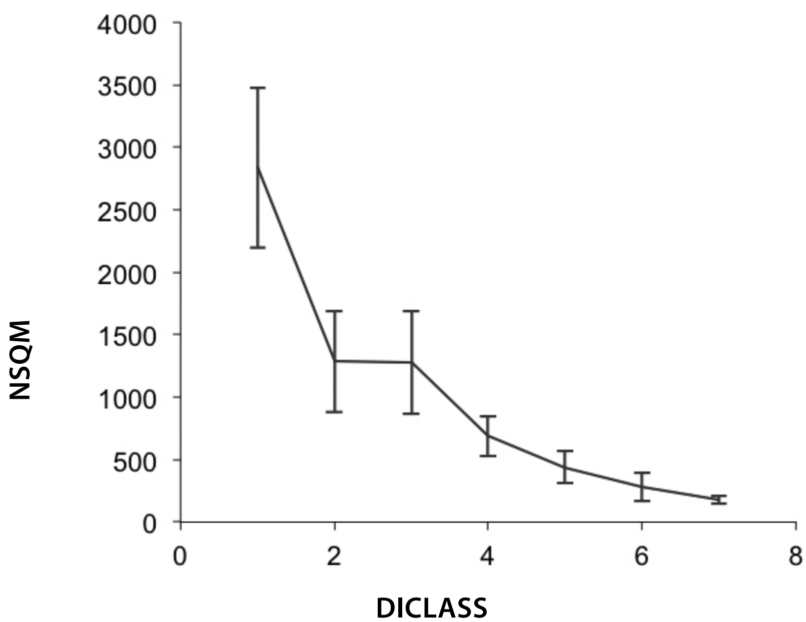

Figure 2. Mean density and standard error of spruce beetles per square meter (NSQM) in windthrow by development index class (DICLASS). The class midpoints, 1 to 7, correspond to the DI index values for the seven brood stages.

3.6 Population Size by Year, Host Type, and Study Site

Annual totals of emerged spruce beetles within study sites by host material (Table 8) were determined as products of land area (ha), density (m^2/ha) of infested bark (Table 7), and attack or adult density (No./m^2) (Appendix 2) in each study site.

During the 1973–1976 period, study site D had nearly four times the mean size of harvested area and longer stand edges than study site WF (Table 7).

In study site WF, the mean percentage (SE) of 1-year-cycle spruce beetles that emerged from windthrow was 31.5% (11.1) and the corresponding value for beetles that emerged from stumps was 72.5% (10.9.9) (Table 8). In study site D, the mean percentage (SE) of 1-year-cycle spruce beetles that emerged from windthrow was 31.8% (12.8) and the corresponding value for beetles that emerged from stumps was 79.3% (8.1). These mean percentages are different from the means calculated from data in Appendix 2 because the former are based on products of infested bark areas and corresponding densities of 1- and 2-year-cycle adults whereas the latter is based only on densities of 1- and 2-year-cycle adults. The difference between host types in the mean percentage of emerged 1-year-cycle spruce beetles was statistically significant for both study sites (study site WF: $t_8 = 2.63$, $p \le 0.03$; study site D: $t_5 = 2.99$, $p \le 0.04$). Densities per generation of 1- and 2-year-cycle adults (Appendix 2) were not correlated in either host type (windthrow: $r_5 = 0.01$; stumps: $r_7 = 0.03$).

At study site WF, there was nearly a 60-fold increase in the size of the emerged spruce beetle population between 1976 and 1979, whereas at study site D there was a less dramatic but nonetheless persistent increase in population size throughout the study period (Table 8). For study site WF, the mean proportion (SE) of the spruce beetle adults that emerged from windthrow at stand edges plus those that emerged from logging residuals was 0.31 (0.04). The mean proportion (SE) of spruce beetles that emerged from stumps was 0.09 (0.04). For study site D the corresponding figures were 0.76 (0.07) and 0.42 (0.14) (Table 8).

The general trend of annual increases in beetle population size at the two study sites, especially during the last 3 years of the study, did not result in a parallel increase in the density of infested trees (Table 9). Most of the infested trees resulted from light attacks on the lower bole, usually within about 2 m of the ground. The attacked trees were of the larger diameter classes and were frequently located adjacent to recent windthrow, or were scarred on the lower bole or showed signs of root and butt rot.

Table 7. Area (ha) and infested bark (m^2) per ha by year of fresh logging residue (stumps and cull logs) in clearcuts and fresh windthrow in stand interiors and stand edges in the two study sites.

Year	Stand Interior Area	Edge Area[a]	Clearcut Area	Stand Interior Bark Area	Edge Bark Area	Clearcut Bark Area
Study site WF						
1973	789.9	37.4	58.0	22.40	74.63	65.43
1974	774.7	40.9	11.8	0.97	72.72	65.43
1975	742.4	44.2	40.3	9.88	68.23	96.32
1976	700.5	102.5	45.5	66.72	153.64	214.21
1977	648.7	107.2	51.8	79.92	224.32	137.13
1978	621.4	96.9	27.4	227.00	251.88	223.15
Study site D						
1973	1199.4	61.7	270.8	9.24	28.47	111.30
1974	1132.6	75.6	56.9	1.57	58.56	187.72
1975	784.3	145.2	226.0	0.99	55.00	112.70
1976	969.0	180.6	60.4	27.92	150.95	109.86

[a] Stand edge area was defined as the total area of 20 m strips of forest along the edges of clearcuts and logging roads.

Table 8. Totals of emerged spruce beetles per study site by year and host type, percent of 1-year-cycle beetles, and proportions of beetles emerged from clearcuts plus windthrow at stand edges[a].

Year	Stumps (1)	% 1-year Cycle	Stand Interior (2)	Stand Edge (3)	Stand + Edge (2+3)	%1-year Cycle	(1+3)/ (1+2+3)[a]
Study Site WF							
1975	48 842	42.9	1 653 236	311 638	1 964 874	12.9	0.18
1976	53 942	95.4	400 928	159 678	560 606	15.4	0.35
1977	759 841	89.3	1 767 999	646 294	2 404 293	52.4	0.44
1978	1 146 938	49.2	7 935 992	2 710 427	10 646 419	12.4	0.33
1979	824 237	85.7	28 110 777	7 779 940	35 890 717	64.3	0.23
Study Site D							
1975	1 089 000	80.0	343 249	117 800	461 119	20.7	0.78
1976	861 695	93.1	367 808	1 130 919	1 498 727	24.4	0.84
1977	1 202 442	64.9	1 776 316	2 747 174	4 523 490	69.7	0.87
1978	0	-	5 190 188	5 996 091	11 186 279	12.5	0.54

[a] Stand edge area was defined as the total area of 20-m strips of forest along the edges of clearcuts and logging roads.

Table 9. Mean tree diameter at 1.3m (DBH), densities of infested spruce trees and infested bark areas, and densities of spruce beetle attacks by year and study site.

Year	N	Mean DBH (cm)	Trees/ha	Bark Area (m^2/ha)	Attacks/ ha[a]
Study Site WF					
1974	5	60.45	0.217	0.057	1.03
1975	16	65.10	0.667	0.190	3.43
1976	6	54.18	0.445	0.071	1.28
1977	19	56.54	1.112	0.222	4.01
1978	10	66.04	0.395	0.117	2.12
Study Site D					
1974	4	71.12	0.123	0.041	0.74
1975	4	72.39	0.123	0.044	0.80
1976	1	48.26	0.049	0.011	0.20
1977	3	70.28	0.099	0.039	0.71
1978	10	70.89	0.741	0.190	3.44

[a] Based on average attack density of 1.68/ft^2 (Dyer et al 1974).

4. Discussion

Except for 1974, there was surprisingly small variation among years, hosts, and study sites in the mean Julian dates of emergence. The estimated later mean emergence date in 1974, compared to seven of the nine other year–host combinations (Table 1), combined with the relatively short emergence period, strongly indicates that in 1974 significant emergence occurred prior to the placement of the emergence traps. This resulted in truncation of the emergence curve at lower values (earlier emergence dates) and consequently a later estimate of mean emergence date. In 1973 and 1980 flying beetles were trapped, and traps were placed 10–15 days later compared to placement of the emergence traps in other years. Also, as some beetles re-emerge following initial attack (Lawko and Dyer 1974) and emergence can vary among sites, the apparent later emergence times reflected in mean catches of beetles in these 2 years were affected not only by late placement of traps but also by the dynamics of spruce beetle emergence and dispersal.

Spruce beetles begin to fly when shade temperatures exceed the flight threshold temperature of about 16°C (Dyer 1973). During the peak emergence period in central BC, landing on trap trees by spruce beetles began when shade temperatures were > 13.3°C. Relative hourly flight activity was directly related to heat accumulation above this temperature (Safranyik and Linton 1987). Therefore, variation in late spring temperature conditions among and within years and variation in the degree of shading of infested host materials are the main determinants of the onset and duration of post-hibernation emergence and flight of spruce beetles.

Beckwith (1972) reported that spruce beetles in Alaska emerged in May and June, with peak flight in late May, and Dyer (1973) reported that flight of beetles in southern BC began in late May. The results reported here for central BC suggest that the flight period of spruce beetles in western North America is similar over broad geographic latitudes.

Female bias in adult spruce beetles has been reported previously, both from natural populations (Massey and Wygant 1954; Dyer 1973) and from the progeny of spruce beetles placed in bolts (Safranyik and Linton 1983; Holsten and Werner 1990). Safranyik and Linton (1985) reported that under laboratory conditions the female ratio in spruce beetle broods was inversely related to spacing between egg galleries. Safranyik (1976) reported that the female ratio in mountain pine beetles increased following laboratory storage due to increased mortality of males, and Amman and Pace (1976) observed that environmental stress resulted in an increased female ratio. This study showed no such evidence of biased sex ratios. However, yearly total counts of adult spruce beetles for estimating sex ratio per host type and study site were generally small (less than 50 in over half of the samples [Table 2]) in this study due to the small size of the sampling units. Consequently, only relatively large observed differences in sex ratio would have been detected.

Based on the combined counts over all years, the balanced sex ratio in 1-year-cycle beetles observed from both host materials and in both study sites, and the significantly greater female ratio in 2-year-cycle beetles in both host types and study sites, suggest that either (1) males developed faster and were therefore disproportionately represented in the 1-year-cycle population; or (2) males suffered proportionately greater mortality compared to females, especially during the 2nd year of development. These aspects require further study.

There was no difference found in the mean widths of the pronotum of male and female spruce beetles. This study confirms previous reports based on field and laboratory experiments (Safranyik and Linton 1983; Sahota et al. 1987; Holsten and Werner 1990) and from sampling natural populations (Safranyik et al. 2010).

In this study, the main factors that affected adult size were temperature during development and host quality. Safranyik and Linton (1985) reported that the sizes of both sexes of adult spruce beetle were directly affected by the spacing of egg galleries. Therefore, competition for food and space may also significantly affect adult size. Hansen and Bentz (2003) reported that during the main emergence period (June) 1-year-cycle adults from trees had lower dry weight and total lipid content and less total egg production compared to 2-year-cycle beetles (Hansen and Bentz 2003). Because adult size is likely correlated with dry weight and lipid content, our results from stumps and windthrow are consistent with those of Hansen and Bentz (2003). In addition to egg production, adult size may also imply important effects on host location and reproduction via the effects on flight capacity and dispersal (Atkins 1961). This would significantly affect population dynamics.

Compared to windthrow in stand interiors, stumps generally represent a warmer sub-cortical habitat. This is the main reason for faster brood development in stumps compared with windthrow. Spruce beetle has a low emergence and flight threshold (Safranyik and Linton 1987; Holsten and Hard 2002). Consequently, attacks on host materials in clearcuts and in stand interiors tend to occur simultaneously. Even though the two study sites were adjacent to each other, the mean elevation of study site D was approximately 200 m higher than study site WF. Cooler temperature conditions due to higher elevation is the most likely reason for the generally slower brood development at study site D compared to study site WF (Table 6).

The spruce beetle has a 1-, 2-, or 3-year life cycle (Wygant and LeJeune 1967). The 3-year life cycle is relatively rare and occurs mainly in colder regions including high elevations. Development of a small percentage of the brood on a 3-year cycle in windthrow in only 1 of the 7 years of this study (1976) indicates that extended brood development was uncommon in the study areas, but that it can occur in central in BC.

Predictions of mean development index based on proportions of larvae in samples that contain larvae, pupae, and brood adults (equation [4]) can be used for quick field-assessment of brood development. Equation [4] was fitted to combined data from all years for both hosts and study sites. Because there can be considerable variation in temperature conditions among years, hosts, and study sites during beetle development, and because the DI reflects this variation, equation [4] provides only a guide to brood development in specific years and habitats.

The shape of the survivorship curve for spruce beetle in both host types (Figures 1 and 2) is intermediate between types II and III (Deevey 1947), typical of organisms that suffer high levels of mortality during early life stages. In stumps, weathering and large diurnal variation in temperatures during development of eggs and first instar larvae were the most likely causes of large initial mortality. This reduction in host quality would have been most pronounced in more exposed locations on stumps. In windthrow, most attacks occur on the sides and bottoms of the bole (Safranyik 2009). Although these areas offer the best protection from winter mortality and predation by woodpeckers, they tend to be the coolest and most moist places during egg development. During early phases of brood establishment, there is often still some snow in stands and night temperatures fall below freezing. These factors may contribute directly and indirectly to high egg mortality through affects on mating, gallery construction, and egg deposition.

The stand openings created by the harvesting operations increased the length of stand edges and windthrow. The infested bark area per hectare along stand edges can be several times that of stand interiors (Table 7). Because creation of stand edges in timber harvesting areas is a consequence of clearcutting operations, beetle populations in logging residue and stand edge windthrow are measures of the impact of clearcutting on spruce beetle population trend.

During the 1973–1976 period, study site D had nearly four times the mean harvested area and twice the mean stand edge area compared to study site WF (Table 7). These are the main reasons for the much lager proportions of beetles that emerged from clearcuts and stand edges in study site D compared to study site WF. These results indicate that clearcutting operations can contribute significantly to the size of spruce beetle populations. Although not all windthrow along stand edges is directly attributable to stand openings, in the sites we studied the average density of windthrow was 3–5 times greater at the stand edge than in the stand interiors (Safranyik et al. 1983).

At study site WF, the nearly 60-fold increase in the size of the emerged spruce beetle population between 1976 and 1979 (Table 8) was mainly caused by large annual densities of windthrow (Table 7) combined with large annual densities of emerging spruce beetles (Appendix 2, Tables A2-a and A2-b). In 1977 and 1979, 1-year-cycle beetles emerging from very large areas of infested bark that were attacked during 1976 and 1978 contributed 52.4 and 64.3% respectively to the total population. At study site D, the persistent increase in the size of the beetle population (Table 8) was mainly caused by annual availability of fresh windthrow, especially at stand edges (Table 7), combined with high annual densities of emerged spruce beetles (Appendix 2, Tables A2-d). For the same reasons described for study site WF, 1-year-cycle beetles comprised nearly 70% of the total population in site D in 1977, illustrating that development on a 1-year cycle can significantly increase the size of the attacking spruce beetle population.

The lack of correlation between densities of 1- and 2-year-cycle beetles was surprising and implies that total adult progeny per attack was not affected by life cycle duration. Duration of development to a specific stage is mainly a function of temperature-dependent development rates and temporal distribution of attacks, whereas brood survival is affected by a number of biotic and abiotic factors such as food and space, associated organisms, and lethal low temperatures. Consequently, even predominantly 1-year-cycle development may not always significantly affect generation survival.

Even though the attacks on trees located by the annual surveys at the two study sites were mainly unsuccessful, spruce beetle outbreaks did develop in the Bowron Lakes areas to the east and north of the study sites beginning in 1979 and were sustained until 1986 (CFS 1994; Turnquist 1987). Many of these areas sustained significant windthrow events during the late 1970s and early 1980s. This study demonstrates that sustained increases in spruce beetle populations can develop in windthrow and logging residue and increase the risk of damaging outbreaks at the landscape level, as had been suggested by earlier observations (Swaine 1924; Wygant and LeJeune 1967; Furniss and Carolin 1977; Safranyik et al. 1983). Not all such events, however, necessarily result in outbreaks in living, apparently healthy trees. While windthrow and logging residue create suitable habitat for brood production, these materials also represent a preferred breeding site for the insect that may provide a measure of protection for associated live trees, which are less preferred. In the area where study site WF was located, for example, 76 to 100% of windthrow in stand interiors, 37 to 99% of windthrow at stand edges, and 58 to 100% of stumps were infested annually over the study period (Safranyik et al. 1983), yet we did not detect mass attacks on living trees. An alternative explanation for our result, supported by the observation that not all large-scale windthrow or logging events are followed by outbreaks, is the coincidence of large-scale host susceptibility due to factors such as dry, cold soils (Holsten 1984), defoliation (Balch 1934; Ostaff and Newell 1981), competition (Hard 1987), or impairment of the root system of many trees from extensive wind sway. For example, the latter situation could arise under certain conditions of soil saturation and wind force that not only uproots trees, but also causes extensive damage to the root systems, trunks (splitting), or crowns of other trees that remain standing. The ability of such trees to take up nutrients and water in the short term would likely be severely impaired. This explanation of cryptic loss of defense is consistent with the observations that outbreaks in BC are of relatively short duration, lasting only 4–5 years or two to three spruce beetle generations (Dyer and Taylor 1971; Cottrell 1978).

In a detailed study of endemic and eruptive spruce beetle populations, Wallin and Raffa (2004) examined the role of population density in host selection behaviour and found that host acceptance changed with population phase. Beetles from both endemic and eruptive population phases colonized felled trees and were repelled by high concentrations of alpha-pinene, the predominant monoterpene produced by spruce. However, heritability assays suggested high genetic variance in host selection behaviour within populations. In media amended with phytochemicals, avoidance of high concentrations of alpha-pinene decreased with addition of other beetles, and this affect was more pronounced among beetles from eruptive than from endemic populations. The authors suggest that this density-dependent behaviour broadens the host range of eruptive beetles and can maintain heterogeneity among population phases. However, just what factors may underlie these population-dependent responses has not been established.

An interesting finding by Wallin and Raffa (2004) was that the total lipid content of eruptive beetles was significantly lower than that of endemic beetles. In the studies reported here, 1-year-cycle beetles were significantly smaller than 2-year-cycle beetles from both host types. Hansen and Bentz (2003) reported that 1-year-cycle adults from trees had lower dry weight and total lipid content compared to 2-year-cycle beetles during the main emergence period (June). Beetle size, as measured by the width of the pronotum, and lipid content are likely correlated. Since it is not clear whether Wallin and Raffa (2004) worked with 1-year- or 2-year-cycle beetles or mixtures of both types, it is possible that their collections of adult beetles from the eruptive population sites may have contained higher proportions of 1-year-cycle beetles than collections from the endemic population sites.

Overall, the results presented here indicate a) little variation in spruce beetle emergence among years and host types, b) consistently faster development in stumps compared with windfall, and c) large variation among years in the proportion of broods developing on a 1-year life cycle in both host types. Life cycle duration had significant effect on adult size and sex ratio; the former was also affected by host quality. Because fitness is likely correlated with adult size, in terms of dispersal and reproductive potential, we strongly suggest that variation in the duration of development among years and host materials is a key aspect of population dynamics. Combined with the distribution and abundance among years of large-diameter logging residue and windthrow, variation in the duration of life cycle can result in the development of epidemic populations that may attack living trees at the landscape level.

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Appendix 1. Mean Size of Spruce Beetles Collected from Two Sites in Central BC.

Table A-1. Mean (SE = standard error) widths of the pronotum in mm and sample size (N) by sex, year of attack, and emergence for spruce beetles from stumps and windthrow in two study areas. The mean widths of the pronotum for the sexes within year and study site were compared by t-test.

Year Attacked	Year Emerged	Statistics	Study Site WF				Study Site D			
			Female	Male			Female	Male		
1971–72[a]	1973	Mean	2.285	2.282			2.308	2.298		
		SE	0.022	0.017			0.027	0.028		
		N	43	27			60	47		
		t	-	0.107			-	0.257		
			Stumps		**Windthrow**		**Stumps**		**Windthrow**	
			Female	Male	Female	Male	Female	Male	Female	Male
1973	1974	Mean	2.170	2.203	2.315	2.223	2.264	2.283	-	-
		SE	0.029	0.041	0.029	0.034	0.039	0.025	-	-
		N	18	12	22	12	27	26	-	-
		t	-	0.838	-	1.971	-	0.407	-	-
	1975	Mean	2.253	2.209	-	-	2.256	2.306	-	-
		SE	0.041	0.051	-	-	0.021	0.021	-	-
		N	15	11	-	-	72	49	-	-
		t	-	0.068	-	-	-	1.623	-	-
1974	1976	Mean	-	-	2.398	2.382	2.107	2.122	2.374	2.378
		SE	-	-	0.017	0.026	0.026	0.027	0.017	0.035
		N	-	-	34	18	39	21	28	19
		t	-	-	-	0.016	-	0.371	-	0.114
		Mean	-	-	2.172	2.222	-	-	2.182	2.154
		SE	-	-	0.039	0.015	-	-	0.021	0.018
		N	-	-	12	11	-	-	38	14
		t	-	-	-	0.972	-	-	-	0.700
1975		Mean	-	-	2.171	2.136	2.078	2.087	2.189	2.237
		SE	-	-	0.047	0.035	0.034	0.061	0.039	0.015
		N	-	-	7	7	13	8	11	2
		t	-	-	-	1.629	-	0.133	-	2.196
	1977	Mean	2.210	2.220	2.449	2.354	2.346	2.296	2.350	2.400
		SE	0.0943	0.126	0.030	0.029	0.014	0.022	0.0262	0.018
		N	4	2	27	27	69	25	20	14
		t	-	0.070	-	2.287*	-	1.917	-	1.586

Table A-1 (continued). Mean (SE = standard error) widths of the pronotum in mm and sample size (N) by sex, year of attack, and emergence for spruce beetles from stumps and windthrow in two study areas. The mean widths of the pronotum for the sexes within year and study site were compared by t-test.

Year Attacked	Year Emerged	Statistics	Study Site WF				Study Site D			
			Stumps		Windthrow		Stumps		Windthrow	
			Female	Male	Female	Male	Female	Male	Female	Male
1976		Mean	2.248	2.132	-	-	-	-	2.448	2.444
		SE	0.0587	0.074	-	-	-	-	0.013	0.010
		N	10	7	-	-	-	-	29	21
		t	-	1.165	-	-	-	-	-	0.024
		Mean	2.409	2.329	-	-	-	-	-	-
		SE	0.0357	0.0305	-	-	-	-	-	-
		N	42	16	-	-	-	-	-	-
		t	-	1.704	-	-	-	-	-	-
	1978	Mean	2.640	2.656	2.514	2.527	-	-	2.589	2.587
		SE	0.038	0.072	0.029	0.016	-	-	0.012	0.0296
		N	5	5	63	49	-	-	61	44
		t	-	0.102	-	0.305	-	-	-	0.069
		Mean	-	-	2.358	2.449	-	-	2.297	2.398
		SE	-	-	0.046	0.037	-	-	0.0606	0.068
		N	-	-	52	29	-	-	44	21
		t	-	-	-	1.324	-	-	-	1.1014
1977		Mean	2.524	2.580	2.332	2.353	-	-	-	-
		SE	0.010	0.084	0.021	0.018	-	-	-	-
		N	10	6	132	140	-	-	-	-
		t	-	0.0226	-	0.779	-	-	-	-
		Mean	-	-	2.306 [b]	-	-	-	-	-
		SE	-	-	0.0167	-	-	-	-	-
		N	-	-	46	-	-	-	-	-
		t	-	-	n/a	-	-	-	-	-
	1979	Mean	-	-	2.335	2.298	-	-	-	-
		SE	-	-	0.0278	0.0228	-	-	-	-
		N	-	-	82	68	-	-	-	-
		t	-	-	-	1.029	-	-	-	-
1978		Mean	2.250	2.250	2.409 [b]	-	-	-	-	-
		SE	0.0260	0.0474	0.0187	-	-	-	-	-
		N	23	13	29	-	-	-	-	-
		t	-	0.000	n/a	-	-	-	-	-

[a] Beetles were captured in barrier traps placed on tops of stumps in clear-felled areas during June 6–July 31, 1973.
[b] Combined statistics for the sexes; n/a = not applicable; * = difference in mean size between the sexes is significant at p = 0.05)

Appendix 2. Attributes of Spruce Beetles Collected from Stumps and Windthrow at Study Sites WF and D.

Table A-2a. Attack density (Attack D.), total egg gallery length (Tot. Gal.), spruce beetle density by sampling stage, density of 1-year-cycle adults (1-yr cycle), and % 1-year-cycle adults (% 1-year) in stumps by year of attack at study site WF. (St. error = standard error of mean).

Stage	1973 Attack			1975 Attack			1976 Attack			1977 Attack			1978 Attack		
	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error
Attack D.	20.12	148	2.47	72.94	40	13.6	53.05	40	14.08	13.26	40	6.37	102.78	40	18.02
Tot. Gal.	2.69	148	0.3	11.53	40	1.77	3.21	40	0.79	2.71	40	0.83	8.85	40	1.66
Sample 1	259.12	148	75.87	4108.09	40	910.26	2204.91	40	650.39	507.29	40	282.07	3372.02	40	848.44
Sample 2	-	-	-	281.83	40	63.24	354.77	40	111.1	205.57	40	59.61	95.22	39	32.67
Sample 3	76.56	212	17.78	13.26	40	10.4	179.04	40	51.7	135.94	40	43.91	139.42	39	51.24
Sample 4	11.9	156	5.17	27.2	39	13.05	76.26	40	45.22	13.26	40	7.91	-	-	-
Sample 5	6.56	62	2.7	20.94	38	12.78	39.79	40	15.89	16.57	40	10.75	3.31	40	3.32
1-yr cycle	39.65	212	10.99	16.57	40	13.59	69.63	40	29.57	72.94	40	33.84	115.62	39	48.52
% 1-year	85.80			44.17			63.63			81.49			97.22		

Table A-2b. Attack density (Attack D.), total egg gallery length (Tot.Gal.), spruce beetle density by sampling stage, density of 1-year-cycle adults (1-yr cycle), and % 1-year-cycle adults (% 1-year) in windthrow at study site WF. (St. error = standard error of mean).

Stage	1974 Attack			1975 Attack			1976 Attack			1977 Attack			1978 Attack		
	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error
Attack D.	38.74	89	7.71	46.13	23	15.84	42.51	78	7.81	45.66	61	10.69	44.21	36	16
Tot Gal	7.66	89	0.75	7.93	23	1.84	4.83	78	0.72	7.59	61	0.97	7.78	36	0.91
Sample 1	4148.66	89	573.35	743.86	23	317.48	1465.69	78	280.69	1465.41	61	256.97	2637.78	36	634
Sample 2	534.92	90	72.71	675.66	42	148.75	1035.5	78	164.86	718.39	60	92.31	636.6	30	70.65
Sample 3	129.44	84	23.56	216.83	63	30.99	641.59	154	56	412.36	119	44.93	300.62	30	53.49
Sample 4	154.73	90	38.58	171.99	64	31.12	268.96	143	30.27	306.14	120	38.57	-	-	-
Sample 5	45.15	94	13.83	114.81	67	23.91	148.78	156	18.7	193.41	96	28.72	-	-	-
1-yr cycle	28.42	84	12.33	8.42	63	4.11	19.81	154	5.16	18.94	119	5.77	128.2	30	-
%1-year	38.63			6.83			11.75			8.92					

Table A-2c. Attack density (Attack D.), total egg gallery length (Tot. Gal.), spruce beetle survival by sampling stage, density of 1-year-cycle adults (1-yr cycle), and % 1-year-cycle spruce adults (%1-year) in stumps at study site D. (St. error = standard error of mean).

Stage	1973 Attack			1974 Attack			1975 Attack			1976 Attack		
	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error
Attack D.	12.7	120	1.96	22.62	129	5.29	31.49	80	7.55	46.62	40	15.42
Tot. Gal.	1.55	120	0.24	3.38	129	0.6	4.74	80	0.84	4.06	40	0.94
Sample 1	78.6	120	17.8	1739.56	129	366.79	2516.58	80	514.85	2264.59	40	677.52
Sample 2	-	-	-	669.76	80	123.09	278.51	80	87.88	1097.46	40	339.72
Sample 3	105.04	226	17.48	255.3	80	57.69	129.31	80	31.82	311.67	40	68.31
Sample 4	9.26	272	4.72	82.89	80	23.81	39.79	80	14.63	35.7	40	17.07
Sample 5	28.94	81	6.76	92.83	80	25.67	16.58	80	5.92	15.3[a]	-	-
1-yr cycle	22.88	226	7.72	34.81	80	9.63	31.5	80	11.62	116.05	40	45.59
%1-year	44.15			27.27			65.51			88.35		

[a] estimated based on samples 4 and 5 of the 1975 data

Table A-2d. Attack density (Attack D.), total egg gallery length (Tot.Gal.), spruce beetle survival by sampling stage, density of 1-year-cycle adults (1-yr cycle), and % 1-year-cycle adults (%1-year) of spruce beetles in windthrow at study site D. (St. error = standard error of mean).

Stage	1974 Attack			1975 Attack			1976 Attack		
	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error	No./ sq.m	N	St. Error
Attack D.	26.25	96	5.42	39.43	37	13.48	66.31	60	11.14
Tot. Gal.	6.26	96	0.86	12.33	37	1.64	7.82	60	1.09
Sample 1	2077.81	96	380.28	1383.61	37	231.97	4451.81	60	711.98
Sample 2	865.22	84	142.49	-	-	-	1688.77	60	262.97
Sample 3	198.24	95	39.19	287.36	36	54.78	1238.95	60	136.07
Sample 4	121.57	24	41.44	69.99	36	22.1	568.39	119	51.19
Sample 5	182.36	40	54.49	151.57	35	53.03	174.94	120	28.94
1-yr cycle	15.35	95	5.09	40.52	36	15.67	56.37	60	14.15
%1-year	7.76			21.09			24.46		

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