PATTERNS OF LANDING OF SPRUCE BEETLES, *DENDROCTONUS RUFIPENNIS* (COLEOPTERA: SCOLYTIDAE), ON BAITED LETHAL TRAP TREES

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Abstract

The distribution of spruce beetles (*Dendroctonus rufipennis* [Kirby]) landing on lethal trap trees was studied in each of 2 years. A wire basket and sticky boards on each tree were used to trap beetles. Significantly more beetles landed on the north side of the boles than on the other three aspects. The density of beetles that landed increased sharply to about 1.6-2.4 m above ground and then decreased. A three- parameter empirical model was used to describe the relationship. On average, about ¾ of all the beetles that landed did so below the maximum height of insecticide treatment (4 m). The proportion of beetles from the lower 4 m of the bole that were trapped in the wire baskets ranged from 11% to 57% and averaged 33%. High correlations between numbers of beetles trapped in wire baskets at the paired trap trees each year, and between beetles trapped in wire baskets and on corresponding sticky boards showed that catches in the baskets were good indicators of the total numbers of beetles that landed on trap trees.

Relative heat accumulation in the stand in degree-hours above a base temperature of 13.3°C during the day was a good indicator of the relative numbers of beetles that landed on the sticky boards. On typical days, beetles began to land on trap trees in mid-morning; landings peaked between 1500 hours and 1600 hours and ceased by 2000 hours.

Résumé

La répartition des dendroctones de l'épinette (*Dendroctonus rufipennis* [Kirby]) se posant sur des arbres pièges létaux a été étudiée au cours de deux années. Sur chaque arbre, les dendroctones ont été capturés au moyen d'un panier métallique et de pièges collants. On a constaté qu'ils se posaient en nombres significativement plus éléves sur le côté nord des troncs que sur les trois autres côtés. La densité des dendroctones augmentait de façon marquée jusqu'à environ 1,6-2,4 m de hauteur puis diminuait. Un modèle empirique comportant trois paramètres a permis de décrire la fonction. En moyenne, les trois quarts environ de tous les dendroctones qui se sont posés l'ont fait au-dessous de la hauteur maximale d'application d'insecticide (4 m). La proportion des dendroctones qui ont été capturés dans les paniers métalliques à 4 m ou moins de hauteur variait de 11 à 57%, la moyenne étant de 33%. Les corrélations élevées observées entre, d'une part, les nombres de dendroctones capturés dans les paniers métalliques sur les paires d'arbres pièges chaque année et, d'autre part, les dendroctones capturés dans les paniers métalliques et sur les panneaux collants correspondants ont montré que les captures dans les paniers étaient de bons indices des nombres totaux de dendroctones se posant sur les arbres pièges.

La chaleur accumulée relative dans le peuplement au cours de la journée en degrés-heures au-dessus d'une température de base de 13,3°C s'est révélée un bon indicateur des nombres relatifs de dendroctones se posant sur les panneaux collants. Ordinairement, les arrivées des dendroctones sur les arbres pièges commençaient au milieu de la matinée, atteignaient un maximum entre 15 et 16 h et cessaient vers 20 h.

Introduction

The spruce beetle (*Dendroctonus rufipennis* [Kirby]), an indigenous species throughout the natural range of spruce (*Picea* sp.) in Canada and the United States, is a highly destructive pest of mature spruce forests, killing millions of trees during outbreak periods (Dyer 1973). Beetles of both sexes aggregate at host trees in response to pheromones released by females following the start of egg gallery excavation. A synthetic pheromone, frontalin, was found to be effective in inducing attacks on living spruce trees (Dyer and Chapman 1971) and has good potential for monitoring and manipulating beetle populations. Under endemic conditions pheromone-baited living trees are usually successfully attacked and treatment with insecticide is necessary to save them and to kill the attacking beetles (Dyer 1973, 1975). For monitoring beetle flight activity and population trends, these lethal trap trees are fitted with wire baskets at the bases to catch the killed beetles (Dyer 1973). It is assumed that the numbers of beetles in the baskets are closely related to the numbers that landed.

Spruce beetle broods must overwinter as adults prior to emergence in the late spring or early summer when they fly and attack new host material (Schmid and Frye 1977). Flight and attack generally begin when maximum shade temperatures have exceeded the approximate flight threshold of 14.5°C (Werner and Holsten 1985) to 16°C (Dyer 1973) for several days. The diurnal flight pattern and flight activity in relation to heat accumulation above the flight threshold have not previously been investigated.

The objectives of this study were to describe (a) the distribution over time and height of spruce beetles arriving at lethal trap trees, (b) the relationship between catches in screen baskets and the numbers of beetles landing on the treated portion of the tree bole, and (c) the diurnal and directional patterns and the intensity of landing in relation to temperature.

Materials and Methods

Field Procedures. The experiments were carried out in 1979 and 1980 in a stand of mature spruce (*P. glauca* (Moench) Voss x *P. engelmannii* Parry hybrid population), in the Naver Forest about 65 km southeast of Prince George, British Columbia. Two spruce trees were prepared as lethal trap trees each year: on 22 May 1979 and on 6 May in 1980. The trap trees, 41.9 cm to 64.3 cm in dbh, were typical of mature trees in the area and located about 2 km apart, 10-25 m inside the stand. Nearby clearcuts were harvested during the winter of 1974-75 and the slash was no longer suitable for breeding by spruce beetles. One of the trap trees (EA) was used in both years; the other (EI in 1979) was successfully attacked by spruce beetles above the treatment height later in the season and was replaced in 1980 with another tree (EH).

The trees were sprayed to run-off with 1% lindane in water to a height of 4 m. Tree diameter was measured at the maximum spray height in order to estimate the treated bark area. A basket made from aluminum fly screen was placed around the stem of each tree at a height of 30 cm to catch insects killed by the insecticide. The rim of the basket projected about 60 cm above ground and 35 cm from the bole of the trees. A 5-ml polyethelene Boston Bottle (from Bel-Art Products, Pequannock, N.J.) containing 1 ml of a mixture of ⅓ frontalin and ⅔ alpha-pinene (Dyer and Safranyik 1977) was attached to each tree at 1.35 m. Hardboard panels (20 cm wide, factory-painted a light tan colour on one side, and uniformly coated with Stikem Special (from Michel and Pelton Co., Emeryville, CA.) were nailed to the north side of each trap tree. In 1979, the sticky boards extended from 0.6 m (rim of the basket) to the height of insecticide treatment on tree EI and to 6.0 m on tree EA. In 1980, the sticky boards were extended from 0.6 m to 6.0 m on both trap trees. The boards were marked at 30-cm intervals to facilitate tallying of trapped beetles by height level. In 1980, 30 cm x 20 cm sticky boards, treated as described earlier, were also affixed at the three other cardinal directions at 1.5 m to study the distribution of spruce beetles around the tree bole.

All baskets were checked and cleared of dead beetles thrice weekly. Insects were collected and preserved in vials containing 70% alcohol for later identification and counting. Sticky boards were cleaned and spruce beetles were tallied by 30-cm height intervals each time the baskets were cleared. In addition, on days when maximum temperatures were expected to exceed the flight threshold, spruce beetles landing on the sticky boards were tallied hourly throughout the daily flight period. A few Douglas-fir beetles *(D. pseudotsugae* Hopk.) may have been included in the tallies as cross attraction is possible (Dyer and Lawko 1978), but the absence of any Douglas-fir trees within a kilometre should have made the numbers inconsequential. In 1979, hourly records were made on 19 days between 3 June and 6 July and in 1980 on 15 days between 30 May and 15 July.

Temperature was measured with two thermographs inside standard Stevenson screens. One was set up in a clearcut area, about 50 m from a stand edge and 1 km distant from the farthest trap tree (EA). The second was located 30 m inside the stand, 80 m from the other screen.

Analysis. The variation in the numbers of spruce beetles trapped at 1.5 m in the 4 cardinal directions in the two trap trees was studied by analysis of variance in a randomized block split-plot design with the daily catches being the replicates. Mean catches per cardinal direction were compared by Duncan's Multiple Range Test. The data were converted to $\sqrt{x+1}$ prior to analysis.

Based on visual inspection of graphs showing numbers of trapped spruce beetles (Y) on the mid-points of height intervals (X = 0.75 m, 1.05 m etc.) on the bole, the following empirical model was selected to describe the relationship:

$$Y = CX^{B}\exp[-AX] \qquad (1)$$

Where Y is the total number of spruce beetles trapped per 30 cm x 20 cm area; X is the height in m of mid-points of height intervals on the bole; A,B and C are regression constants to be estimated. Eq. 1 was fitted by the method of least squares in the following linearized form:

$$\ln Y = C' + B' \ln X - A'X \qquad (2)$$

Maximum height of landing by spruce beetles was assumed to be at the greater of the two points (X_{max}) corresponding to an estimated 0.1 trapped beetles per 30 cm x 20 cm area from Eq. 1. Calculation of X_{max} was required to predict total numbers of landings, and the proportion of landings below the maximum height of treatment. The total numbers of beetles landing on a trap tree (T_{all}) during the trapping period was estimated in two ways: (Method 1) by assuming that the density of beetles trapped at a given height level on the north side is the same as that on the other three aspects; and (Method 2) by assuming that the densities of beetles trapped per aspect at 1.5 m relative to the density trapped at the same height on the north aspect held for all heights up to X_{max}. In 1979, estimates were made using method 1; the 1980 estimates were made using both methods. Estimates of T_{all} were calculated by multiplying the density of trapped beetles on the north aspect in each 30-cm height interval i($\hat{Y}i$, Eq. 1, first method) or the weighted density of trapped beetles ($\bar{Y}wi$, second method) by the estimated bark area corresponding to that height interval and summing these products over all height intervals to X_{max}. $\bar{Y}wi$ is computed as in Eq. 3.

$$\bar{Y}wi = \hat{Y}i(\bar{Y}_{all}/Yn) \qquad (3)$$

where $\bar{Y}_{all}$ is the mean density of trapped beetles on the four aspects at 1.5 m, Yn is the density of trapped beetles on the north aspect at 1.5 m, and $\hat{Y}i$ and $\bar{Y}wi$ are as defined earlier.

The total numbers of spruce beetles that landed below the maximum height of insecticide treatment (Tp) was computed in a similar manner to that described for T_{all}. The proportion of the beetles that landed below the maximum height of insecticide treatment (Ps) was estimated by the ratio Tp/T_{all} and the proportion of beetles trapped in the wire screen basket (Pb) was estimated as the ratio of the total catch in the basket (Nb) to Tp. The relationship between the numbers of beetles trapped in the basket and the numbers of beetles trapped on the sticky boards below the maximum height of insecticide treatment was analyzed by correlation analysis.

In selecting the flight threshold temperatures, based on temperature records in the clearcut area and inside the stand, we compared hourly temperature records with corresponding beetle activity as reflected by the beetles trapped on the sticky boards. The highest temperatures at which no beetles were trapped in the clearcut (tc) and in the stand (ts) on days following the first recorded flight were designated as the flight thresholds in open areas and in the stand, respectively. The relationships between the numbers of beetles trapped on sticky boards (Ns) and (1) heat accumulation in degree hours (Dh) above the flight threshold temperature, and (2) successive trapping periods during the day, were examined using regression analysis. Prior to analysis, both Dh and Ns were expressed as proportions of the corresponding daily totals in order to compensate for large daily variation in numbers of trapped beetles due to temperature differences among the overwintering sites.

Results

Analysis of variance indicated significant differences among blocks (days) ($p < 0.01$) and aspects ($p < 0.01$) in the mean numbers of spruce beetles trapped/day on 20 cm x 30 cm sticky boards at 1.5 m on the bole (Table 1). The catch ranged between 0 and 140.0 and averaged 78.9 beetles. The catch on the north aspect was significantly larger ($p < 0.01$) than those on the other aspects and there were no differences among the east, south and west aspects (Table 2). There were no significant differences ($p > 0.05$) in the daily catches of beetles between trees or in the interaction between trees and aspects.

The numbers of spruce beetles trapped on the north sticky boards increased from a height of 0.75 m to near 2.0 m and then declined (Table 4). However, the height at which the largest numbers of beetles were trapped varied among trees and ranged between 1.35 m and 2.25 m. The empirical model (Eq. 1) gave excellent fit to the relationship between numbers of spruce beetles trapped per 20 cm x 30 cm area of sticky board and the corresponding mid-point of 30-cm height intervals on the bole (Table 4, Fig. 1). For tree EA, parameters A and B (parameters that control the shape of the function) were nearly the same in both years. The height level of estimated maximum catches (Y_{max}, Table 3) for both trees in 1979 agreed closely with the data (Table 4), but in 1980 Y_{max} for both trees was about one height class greater than in the field. The estimated maximum height on the bole for landing by spruce beetles ranged between 8.0 and 13.7 m; for tree EA, the maximum was about the same each year.

Table 1. Analysis of variance of the numbers of spruce beetles trapped per day on 30 cm x 20 cm sticky boards attached to the four aspects at 1.5 m of two spruce trees baited with pheromone and treated with insecticide to 4 m on the bole in 1980. Data were transformed to $\sqrt{x+1}$ prior to analysis.

Source of variation	d.f.	Sum Squares	Mean Squares	F
Blocks (days)	9	169.032	18.781	8.691**
Trees (T)	1	6.527	6.527	3.020^{ns}
Error I	9	19.449	2.161	
Whole units	19	195.008		
Aspects (A)	3	29.941	9.980	5.812**
A x T	3	3.495	1.165	<1^{ns}
Error II	54	92.748	1.717	
Sub units	60	126.184		
Total	79	321.190		

** Significant at the 99% probability level; ns = not significant ($p > 0.05$)

Table 2. Mean numbers per day and tree ($\bar{x}$), sample size (n), and standard deviation (sd) of spruce beetles trapped in 10 days on 30 cm x 20 cm sticky boards attached to the four aspects of two spruce trees at 1.5 m on the bole in 1980.

Aspect	n	$\bar{x}$[1/]	sd
North	20	18.55[a]	34.18
East	20	4.20[b]	8.41
South	20	8.25[b]	17.79
West	20	8.55[b]	17.33
Grand mean	80	9.86	17.18

The estimated number of spruce beetles that landed on the trap trees in the two years, calculated using method 1, which assumes that there was no difference by aspect in the relative frequency of landing, ranged from 7,628 to 32,356 (column 9, Table 3). For tree EA in 1979, the estimated number of landed beetles was more than twice that in 1980. Using method 2, which assumes that beetles landed on the four aspects with the relative frequencies observed at 1.5 m, in 1980 the estimated total landings were reduced by as much as 65% (column 10, Table 3) compared to the estimates made using method 1.

Assuming that equation 1 is a reliable descriptor of the density gradient of landing beetles up the bole, and that beetles land with equal frequency on all aspects, an estimated average of 77% (range 73% - 86%) landed below the maximum height of insecticide treatment (4 m). Based on the same assumption, an estimated average of 33% (range 11% - 55%) of the beetles that landed below the maximum height of insecticide treatment (4 m) were caught in the screen baskets (column 2 as a percentage of column 3, Table 5). On the other hand, based on the assumption of unequal frequencies of landings on the four aspects, the estimated number of beetles that landed below 4 m on the bole in 1980 (column 4, Table 5) was less (by 37%) than the number of beetles caught in the screen basket for tree EA and for tree EH the estimate was only 14% higher than the numbers caught in the screen basket.

Catches of spruce beetles in screen baskets and on the sticky boards at the two trap trees were significantly correlated ($p < 0.01$) in both years with the exception of tree EH in 1980 (Table 6). For this tree, the correlation between trapped beetles in the screen basket and on the sticky board was not significant ($p > 0.05$).

The highest temperatures at which no spruce beetles landed on the sticky boards in the two seasons were 14.4°C in the slash and 13.3°C in the stand. The regressions of relative numbers of beetles trapped on sticky boards during 1 to 2 hr collecting periods (Y) on the relative numbers of heat units for the collecting period (X) are given by Eq. 4 (Fig. 2) for stand temperatures and Eq. 5 for slash temperatures.

Table 3. Statistics for fitting eq. 1 to the total numbers of spruce beetles trapped on 30 cm x 20 cm sticky boards (Y) and height on the tree bole (X).

Tree and Year	Sample size	Equation parameters[1/] A	B	C	R^2	Ymax[2/]	Max. ht. landing[3/] (X_{max})	No. landed beetles (T_{all}) Est. 1[4/]	Est. 2[5/]
EA-1979	18	-1.132	2.581	473.800	0.724	2.28	13.4	32 347	-
EI-1979	13	-2.290	4.000	2227.300	0.998	1.75	8.0	32 356	-
EA-1980	18	-1.066	2.555	217.699	0.901	2.39	13.7	13 333	4702
EH-1980	18	-1.788	3.372	333.276	0.861	1.88	8.8	7 628	4127

1/ $Y = CX^B \exp[-AX]$ (Eq. 1).

2/ Ymax = -(B/A) from Eq. 1, the height (m) at which the estimated maximum catch occurred.

3/ The greater of two heights (m) on bole corresponding to an estimated 0.1 beetles trapped per 30 cm x 20 cm sticky board surface during the trapping period (Eq. 1)

4/ Estimated numbers of spruce beetles that landed on the trap trees, assuming the same relative frequency of landings on all aspects as on the north aspect.

5/ Estimated numbers of spruce beetles that landed on trap trees assuming that the relative frequencies of landings on the four aspects at all heights were the same as those observed at 1.5 m.

Table 4. The vertical distribution of trapped spruce beetles on 20-cm-wide sticky boards attached to the north aspects of two spruce trees baited with pheromone and treated with insecticide in 1979 (trees EA and EI) and 1980 (trees EA and EH). Figures represent total catches over 19 days in 1979 and 15 days in 1980.

Midpoint of Height interval (m)	Tree and Year			
	EA-1979	EI-1979	EA-1980	EH-1980
	spruce beetles trapped			
0.75	81	203	41	27
1.05	143	332	96	75
1.35	235	362	101	120
1.65	365	312	179	97
1.95	356	387	186	97
2.25	461	277	154	79
2.55	437	236	142	85
2.85	199	168	151	54
3.15	249	129	108	33
3.45	252	83	105	35
3.75	166	78	114	25
4.05	88	41	125	22
4.35	79	-	99	24
4.65	106	-	74	26
4.95	132	-	70	19
5.25	106	-	44	10
5.55	72	-	45	6
5.85	87	-	42	1
Totals	3614	2608	1876	835

Table 5. Total numbers of spruce beetles caught in screen baskets (Nb), and the estimated numbers of spruce beetles that landed (Tp) on the boles of trap trees between the rim of the basket and the maximum height of insecticide treatment (4 m).

Tree and year	Tot. no. beetles Baskets (Nb)	Landed(1)[1/] (Tp)	Landed(2)[2/] (Tp)
EA-1979	4 511	25 119	-
EI-1979	2 857	24 694	-
EA-1980	5 359	9 788	3 379
EH-1980	2 832	6 562	3 276
Totals	15 559	66 433	6 655

1/ Estimates based on the same relative frequency of beetles landing on all aspects of the bole as on the north side.

2/ Estimates based on the same relative frequencies of beetles landing at the various aspects on the bole at a given height as those observed at 1.5 m.

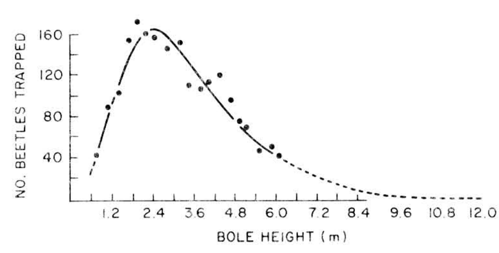

FIG. 1. Relationship between total numbers of spruce beetles caught on 20 cm x 30 cm sticky board areas and height on the bole for trap tree EA in 1980. Solid line is the graph for a three-parameter model (Table 3) fitted to the data (dots).

Table 6. Linear correlations (r) between corresponding catches of spruce beetles in screen baskets at two baited and insecticide-treated spruce trees in 2 years and between numbers of beetles caught in screen baskets and on 20-cm-wide and 6.0-m-high sticky boards attached to the north sides of the bole[1/]

Comparisons	r[1/]	n
1979:		
Tree EA & EI baskets	0.64**	18
EA basket & EA board	0.75*	9
EI basket & EI board	0.84**	9
EA board & EI board	0.89**	18
1980		
Tree EA & EH baskets	0.88**	21
EA basket and EA board	0.98**	10
EH basket & EH board	0.11[NS]	10
EA board & EH board	0.56**	21

1/ Beetles trapped on sticky boards below maximum insecticide treatment height (4 m) were used in calculating r-values.

2/ ** = significant at $p \leq 0.01$, * = significant at $p \leq 0.05$, ns = not significant.

$$Y = -0.0036 + 1.037X \quad (4)$$

$$n = 142,\ r^2 = 0.689,\ Sy.x = 0.039$$

$$Y = 0.0484 + 0.194X \quad (5)$$

$$n = 142,\ r^2 = 0.125,\ Sy.x = 0.065$$

where Y = [No. beetles trapped/tree/collecting period]/[Tot. no. beetles trapped/day]

X = [No. degree hours above threshold temp./collecting period]/[Cumulative degree hours/day].

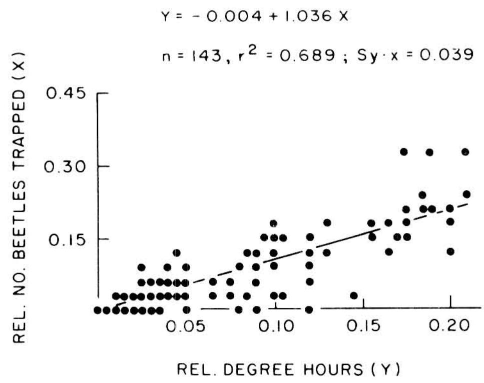

FIG. 2. Relationship between the relative numbers of spruce beetles trapped during 1-2 hr trapping periods (Y) and the relative numbers of degree-hours above a base temperature in the stand of 13.3°C (X).

The intercept of Eq. 4 was not significantly different from 0 ($p > 0.05$) and the intercept of Eq. 5 was highly significant ($p < 0.01$). Eq. 4 was forced through the origin and had the following form (Eq. 6):

$$Y = 1.005X \quad (6)$$

On three typical days, spruce beetle landing on the sticky boards started at mid-morning, peaked between 1500 and 1600 hours and ceased about 2000 hours (Fig. 3).

Discussion

The large variation in the daily catches on sticky boards and in screen baskets is directly related to the effects of temperature on emergence and flight activity. Emergence from hibernating sites and flight began after shade temperatures exceeded the approximate flight threshold of 16°C (Dyer 1973) for several days. The spruce beetles trapped in the experimental area originated mainly from windfelled trees inside the stand and along the margins. Hence, variation in the temperature conditions of the microsites undoubtedly affected the onset, magnitude and duration of daily beetle emergence and flight activity.

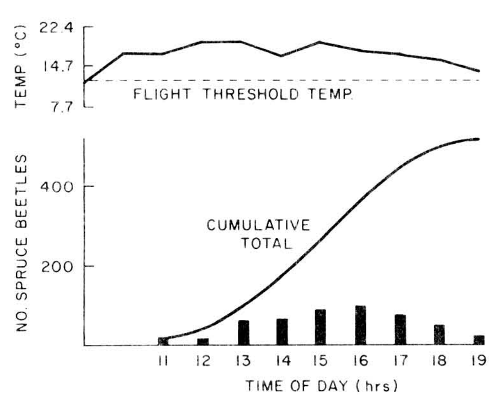

FIG. 3. Average hourly (bars) and cumulative numbers of spruce beetles trapped on sticky boards on June 04, 12, and 14, 1980 at trap tree EA. Temperature was average for the 3 days; flight threshold shown = 13.3°C.

Flying beetles generally follow attractive odours upwind to the source (Borden 1982). As the wind movement during the daily flight periods was predominantly from the south and southwest, the significantly greater numbers of beetles trapped on the north aspect at the 1.5 m level in comparison with the other aspects is partly explained by the search and attack behaviour of the beetles. The preference for landing on (Shepherd 1960) and attacking the shady sides of the host material (Dyer and Taylor 1971; Schmid 1977) could also have increased the catches on the north aspect of the bole. For these reasons, estimates of total numbers of beetles that landed on a trap tree, and on the boles below the spray height, using method 1, based on equal relative frequencies of landings on the four aspects (column 9, Table 3; column 3, Table 5) are likely to be maximum estimates. Conversely, corresponding estimates, using method 2, based on the observed frequencies of landings on the four aspects at 1.5 m (Column 10, Table 3; Column 4, Table 5) are low. This statement is supported by the observation that at Tree EA in 1980 14% more beetles were caught in the wire baskets (5359) (Table 5) than the estimated total for all landed beetles (4702) (Table 3). The beetles could crawl slowly in the stickem, and if some escaped from the small boards, lower predicted total numbers would result. Given the frequency of examination, and the fact that no stickem-coated beetles were found on the boles or in the baskets, it is unlikely that any escaped.

Vertical distributions of landings similar to those observed here (Table 4) have been reported for other bark beetles. Payne and Richerson (1977) found that the vertical distribution of landing *D. frontalis* Zimmermann generally increased to 3-5 m and then decreased with increased trap height on unbaited loblolly pines *(Pinus taeda)*. Avis (1971) found that the density of *D. ponderosae* landing on sticky boards or those caught in barrier traps on unbaited lodgepole pines *(P. contorta)* increased to a maximum between 2 and 4 m and then decreased with increasing trap height. Baiting of the host tree can affect the vertical distribution of landing beetles (Coster *et al.* 1977; Payne and Richerson 1979), but we had no indication that this occurred. At 1500 hours on 28 June, 1979, the pheromone bait was removed from tree EA. During the rest of the same afternoon, a total of 394 spruce beetles were trapped on the sticky board; the highest density (52) were taken at 2.25 m, the same height level where the maximum numbers were trapped when the bait was attached to the tree. The possibility that a few female beetles had penetrated the bark and produced pheromones was considered but no attacks were found.

The similarity of estimated parameters A and B of Eq. 1 for tree EA and the similarity of estimated attack height in both years, despite a large difference in the numbers of trapped beetles (Table 4), indicate that the vertical density gradient of landing by spruce beetles may be largely controlled by tree parameters, or by the character of the immediately surrounding stand, or by both. Beetles searching for suitable host materials tend to fly in the clear bole zone where there is minimum interference from tree crowns and ground vegetation. The estimated maxima for height of landing were not related to tree diameter and agreed closely with reported maxima for height of attack by the spruce beetle (Frye *et al.* 1977; Schmid and Frye 1977). However, as attack density, in general, is inversely related to height on the bole (Schmid and Frye 1977), and as attack density rarely exceeds 8 per 20 cm x 30 cm area, large numbers of beetles must leave the trees for lack of suitable attack sites. This is especially true of the bole zone where the highest numbers of beetles landed.

Our results show that on average about ¾ of the beetles that landed on a trap tree treated with insecticide up to 4 m, landed on the treated bole surface. Of these about ¼ were caught in the screen basket (15 559/66 443, Table 5). This is a conservative estimate owing to the method of estimating the total numbers of landed beetles discussed earlier. A main reason for this low proportion of beetles being caught in the wire baskets is that many of the beetles that were affected by the insecticide fell outside the baskets (Dyer *et al.* 1975). There was also evidence that the proportion of the total beetles that were caught in the wire basket was inversely related to the total beetles that landed on the bole (Table 5, C2÷C3). This indicates that, perhaps due to increased interference among the beetles or failure to find attack sites, or both, proportionately more beetles abandoned trees before they were incapacitated by the pesticide on trees with a high incidence of landings. Although not considered in our experiment, some beetles that fell from bark surfaces located above maximum treatment height could also have landed in the wire baskets. However, we think that such events were rare.

Spruce beetle emergence during the day was directly related to accumulated heat (degree-hours) inside the stand above a threshold temperature of 13.3°C (Fig. 2) and did not vary significantly within and between years. Beetle emergence during the day was poorly related to heat accumulation in the slash above a slash temperature threshold of 14.4°C (Eq. 5). Dyer (1973) reported a flight and attack threshold shade temperature of 15.6°C. We found that some beetles landed on the sticky boards at stand temperatures as low as 13.9°C and a slash temperature of 15.0°C. In the experimental area the only major source of beetles was from scattered windfall inside the stand. There was a difference in the diurnal pattern of temperature changes between the stand and slash. In the morning (0900 hours to 1200 hours), temperatures in the slash were up to 4°C higher than in the stand; by late afternoon the temperatures in the two locations were about the same but by 1900 to 2000 hours temperature in the stand was higher than in the slash. These are the main reasons why daily heat accumulation above the threshold temperature in the stand was more strongly related to the numbers of beetles trapped during the day than heat accumulation in the slash. During a typical day in the experimental area, landing by beetles began between 0900 hours and 1000 hours, reached its peak between 1500 hours and 1600 hours and ended by about 1900 hours (Fig. 3).

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