

Landscape-Scale Habitat Selection Patterns of *Monochamus scutellatus* (Coleoptera: Cerambycidae) in a Recently Burned Black Spruce Forest

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Environ. Entomol. 33(6): 1703–1710 (2004)

ABSTRACT The host selection process of most phytophagous insects can be described as a sequence of behaviors leading from landscape-scale habitat location to host-plant scale, microsite selection. For the whitespotted sawyer, *Monochamus scutellatus* (Say), a fire-associated xylophagous cerambycid, host location and acceptance patterns have been relatively well described, whereas landscape-scale distribution patterns in recently disturbed areas have received virtually no attention. In a 5,097-ha recently burned black spruce forest of Quebec, Canada, we evaluated the variability of larval density of 569 trees in 114 plots, by using entry hole counts. This variability was then related to environmental variables ranging from tree- to landscape-scale. Both diameter at breast height (positive relationship) and fire severity (negative relationship) were significant at explaining larval density at tree scale. At larger scales, altitude had a negative effect on larval density, whereas plots having a higher percentage of unburned forest in a 500-m radius were more intensely colonized. The importance of the proximity of unburned stands could be linked to the feeding requirements of the adults, which should show preference for stands offering both egg-laying and feeding substrata, because several species of *Monochamus* have been shown to feed while being reproductively active. In our models, large-scale variables explained more variability in entry hole counts than did tree-scale variables. Thus, our results suggest that large-scale habitat location mechanisms may play an important role in the host selection process of the whitespotted sawyer.

RÉSUMÉ (FRENCH). La sélection d'hôte des insectes phytophages comporte plusieurs étapes allant de la localisation d'un habitat à l'échelle du paysage jusqu'à la sélection d'un microsite de ponte à l'échelle de la plante hôte. La localisation et l'acceptation d'hôte ont été relativement bien décrites pour le longicorne noir *Monochamus scutellatus* (Say); cependant, la localisation d'habitat à grande échelle a retenu peu d'attention. Dans un feu ayant eu lieu en pessière noire au Canada, nous avons évalué la densité de larves dans 569 arbres de 114 parcelles d'échantillonnage par décompte de trous d'entrée. Ces densités ont été confrontées à des variables environnementales à échelles multiples. À l'échelle de l'arbre, la densité de larves était liée au diamètre de l'arbre et à la sévérité du feu. À plus grande échelle, l'altitude a eu un effet négatif sur la densité de larves, alors que les peuplements ayant davantage de forêt verte dans un rayon de 500 mètres ont été plus intensément colonisés. L'importance de la proximité de massifs verts peut être liée aux exigences nutritionnelles des adultes, qui devraient préférenciellement coloniser des peuplements comportant à la fois des sites d'oviposition et d'alimentation, puisque plusieurs espèces de *Monochamus* continuent de s'alimenter lorsque sexuellement actifs. Les variables à grande échelle ont expliqué plus de variabilité dans nos modèles que les variables à l'échelle de l'arbre. Il semble donc que les mécanismes de localisation d'habitat à grande échelle jouent un rôle important dans le processus de sélection d'hôte chez le longicorne noir.

KEY WORDS *Monochamus scutellatus*, habitat location, host selection, forest fire, boreal forest

THE WHITESPOTTED SAWYER, *Monochamus scutellatus* (Say), is a deep-boring xylophagous cerambycid species. In the eastern boreal forests of North America, it

is known to thrive on several members of the pine family (Pinaceae): balsam fir, *Abies balsamea* (L.) (Belyea 1952, Vallentgoed 1991); jack, red, and white pine, *Pinus banksiana* Lambert, *Pinus resinosa* Aiton, and *Pinus strobus* (L.), respectively (Gardiner 1957, Vallentgoed 1991, Vlasak and Vlasakova 2002); and black and white spruce, *Picea mariana* (Miller) and *Picea glauca* (Moench) (Vallentgoed 1991, Vlasak and Vlasakova 2002, Saint-Germain et al. 2004a). It is a stressed-host species (sensu Hanks 1999), because its

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reproduction can only be successful on heavily stressed or recently dead trees in which inner bark is still moist (Raske 1972, Vallentgoed 1991). This species reproduces in great numbers in disturbed stands, whether they are affected by fire, windthrow, or insect epidemics (Belyea 1952; Gardiner 1957; Raske 1972; Saint-Germain et al. 2004a, b).

Larvae of the first and second instars feed in the inner bark and only weakly score the sapwood. However, at the third instar, the larvae penetrate the sapwood and start excavating deep galleries (Rose 1957, Raske 1972, Vallentgoed 1991). These galleries have been known to reach >20 cm in length (Cerezke 1977, Vallentgoed 1991). Also, woodborer larval activity facilitates wood colonization by blue and brown stain fungi (Ascomycota: Ophiostomatales) and wood rots (Raske 1972, Vallentgoed 1991). The whitespotted sawyer is a serious problem in North America after fire when salvage logging is considered, because the wormholes and stains considerably reduce the commercial value of the timber. However, the sawyer also plays important ecological roles, for its mining hastens wood decay and nutrient cycling (Edmonds and Eglington 1989), and its larvae are an important food source for predators such as the blackbacked woodpecker, *Picoides arcticus* Swainson, an uncommon bird species mainly observed in recently burned forests (Murphy and Lenhausen 1998, Imbeau et al. 1999, Nappi et al. 2003). Other sawyer species around the Northern hemisphere also are considered as pests, especially when acting as vectors for pine wilt nematodes of the genus *Bursaphelenchus* (Mamiya and Enda 1972, Wingfield and Blanchette 1983, Jikumaru and Togashi 2001).

The host selection process of insects can be subdivided in four successive steps: habitat location, host location, host acceptance, and host use. At each of these steps, several environmental stimuli or events will affect the behavior of the insect. Factors driving host location, acceptance, and use by *Monochamus* have been the subject of several studies (Gardiner 1957; Rose 1957; Raske 1972; Hughes 1979, 1981; Peddle et al. 2002; Saint-Germain et al. 2004a). However, mechanisms leading to habitat location at larger scale are still largely unknown. If the habitat location step plays an important role in the overall host selection process for the whitespotted sawyer, between-stand larval density variations could be significant. Given the important role played by the sawyer in wood decay, such variations in local colonization densities could impact large-scale snag dynamics and nutrient cycling processes.

In this article, we examine larval density patterns of the whitespotted sawyer and its relationships with potential explanatory variables in a 5,097-ha burned black spruce forest from central Quebec, Canada. Five of such potential factors were fully or partially explored in this study.

1. Thermal environment quality: Several authors have stressed that sunny and warm exposures stimulate reproductive activity and oviposition of *M. scutellatus* (Ross 1960, Raske 1972). Topographic factors

such as aspect, slope, and altitude affect the local thermal environment and thus could affect reproductive activity and subsequent larval density, or play a direct role in habitat selection. Strong winds also could deter these insects from reaching highly exposed stands.

2. Compromise between nutritional requirements of larvae and adults: Adults of some *Monochamus* species must feed on twig bark or needles of healthy trees several days after their emergence to reach their maturity (Rose 1957), and at least some species continue to do so while being reproductively active (Alya and Hain 1985). Shibata (1987) suggested that the distribution of adults of *Monochamus alternatus* Hope could represent a compromise between the nutritional needs of the adults and the larvae. This compromise could be a widespread strategy in cerambycids whose adult and larval feeding habits diverge significantly. If this hypothesis is true for *M. scutellatus*, burned stands situated near edges or unburned patches could be more intensely populated, thus allowing reproducing adults to feed on nearby living trees.
3. Distance of colonization from the unburned matrix: As colonizers come from the adjacent unburned matrix to colonize the newly killed trees, they should stop as soon as they encounter favorable habitat ("first encountered habitat, first used"). As the nearest habitat saturates, new colonizers have to go further in the disturbance to find unused habitat. This scenario should result in a density gradient exhibiting highest densities near the disturbance/matrix edge.
4. Effect of the smoke plume on colonization dynamics: Smoke is used by several species of cerambycids as attractants to locate fire-created habitats (Schütz et al. 1999, Suckling et al. 2001). Smoke contains high concentrations of physiologically active compounds and is likely to travel longer distances than host volatiles, being at first carried at high elevations by the updraft caused by the intense heat; more colonizing adults could originate from unburned stands covered by the smoke plume and create a directional density gradient. Hypotheses three and four are nonexclusive; colonization dynamics might be a combination of a short-range diffuse, multidirectional colonization process driven by host volatiles and a simultaneous long-range unidirectional colonization process driven by the smoke plume.
5. Within-stand high-quality substrate availability: A tree situated in a stand harboring numerous high-quality hosts might end up with lower larval density (dilution effect among the possible hosts) or with higher density if the high-quality stand attracts more adults (concentration effect).

Materials and Methods

Study Area. Sampling was conducted in August 2001 in the Grands-Jardins Provincial Park and in the adjacent des Martres controlled harvesting zone (fishing

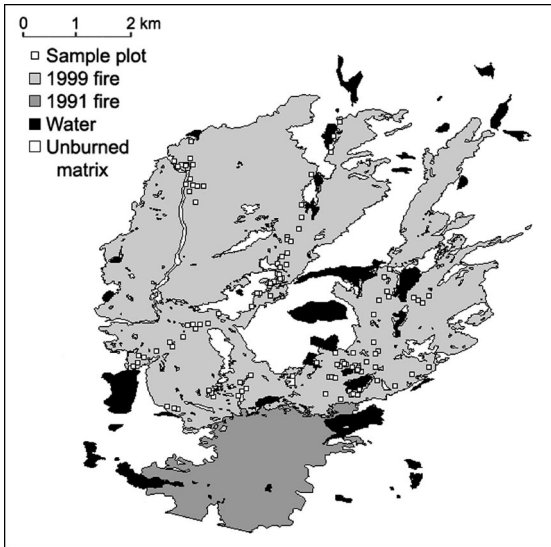


Fig. 1. Distribution of sample plots in the 1999 5,097-ha fire (Grands-Jardins provincial park).

and hunting area) (province of Quebec, Canada; 47° 41' N; 70° 43' W). Both territories are located on a plateau averaging 800 m in altitude in the Laurentian Mountains. Recent fires have occurred within the park's boundaries in 1991, 1995, and 1999 (Payette et al. 2000). Pure black spruce, *Picea mariana* (Miller), stands dominate the landscape, with the occasional presence of balsam fir, *Abies balsamea* (L.); trembling aspen, *Populus tremuloides* Michaux; and tamarack, *Larix laricina* (Du Roi). Sampling specifically took place in a 5,097-ha fire that occurred between 30 May and 5 June 1999. It was a strikingly uniform, high-intensity fire, with very few lightly burned areas. After the fire, the ground vegetation layer was dominated by fire-resistant shrubs such as *Ledum groenlandicum* Oeder and *Vaccinium* spp.

Sample Plot Establishment and Characterization. A total of 114 plots was established in the burned forest to cover the widest possible range of topographic and spatial contexts (Fig. 1). Sample plots were mostly established along transects, in which they were distanced by 300–400 m from each other. Plots were characterized on 225 m². Fire severity was recorded for each stem (diameter at breast height [dbh] \geq 5 cm) as an index by estimating the percentage of charred bark from base to top (1, uncharred; 2, < 5%; 3, 6–40%; 4, 41–60%; 5, 61–95%; 6, 96–99%; and 7, 100% of the bark charred).

Our first hypothesis was partially tested using altitude. Altitude was measured using a global positioning system (GPS) and then cross-checked with topographical maps. When GPS and map data diverged, the value obtained from the maps was retained.

Digitalized aerial photographs taken in 1999 after the fire were used to generate geographic information system data. These data were used to compute three spatial context variables with which hypotheses 2, 3,

and 4 were tested. First, to test our second hypothesis (availability of feeding substrate for both larvae and adults), we calculated the percentages of unburned forest area within radii of 100, 250, and 500 m from each sample plot center. Burned stands having some percentage of unburned forest around would allow adults to feed on living trees while being reproductively active. To test our third hypothesis (first habitat encountered, first used), we calculated the shortest distance to continuous unburned matrix to assess a potential density gradient exhibiting highest densities near the disturbance/matrix edge. To exclude small unburned fragments disseminated at the edges of the fire that were too small to be considered as significant sources of adults at the time of the fire, we added a 500-m buffer to the burned polygons. This buffer allowed us to make objective decisions on where these shortest distances were. The 500-m scale was chosen as the most appropriate considering the spatial configuration of the fire/unburned matrix edge. To test our fourth hypothesis (effect of smoke plume), distance from continuous unburned matrix also was calculated in the average orientation of winds during the fire from each sampled stand. The average diurnal orientation of winds for the time of the fire (coming from the southwest) was calculated from local meteorological station data (Pikauba Lake weather station, maintained by the Quebec Natural Resources Ministry). Actual satellite imagery of the smoke plume was unavailable, because a heavy cloud cover was present during the fire. Computation of spatial context variables was performed using the software Arcview GIS 3.1 (Environmental Systems Research Institute, Inc., Redlands, CA).

The fifth hypothesis was tested using densities of fire-killed black spruce stems with dbh \geq 8 cm and dbh \geq 12 cm for each plot. Balsam fir was uncommon in the sampled plots, and none showed any markings indicating use by the whitespotted sawyer. Thus, they were not included in stem density because they could not be considered as usable substrate.

Larval Density Estimation. Larval density was estimated using entry hole counts. Entry hole counts are a convenient way to obtain a precise estimation of the third instar population for the whitespotted sawyer (Rose 1957, Cerezke 1977). It is from this point onward that their gallery excavation behavior becomes a serious commercial devaluation factor for the wood (Raske 1972, Vallentgoed 1991). Approximately 80% of the total larval mortality occurs before the third instar (Rose 1957). Some unknown fraction of mortality occurring before the excavation of the entry holes is probably density-dependent (i.e., cannibalism; Rose 1957); such mortality factors might have added some level of unexplainable variability to our data. Entry holes are easily recognizable by their oblong form and their wood penetration angle. We are confident that most entry holes counted were made by *Monochamus scutellatus*, because no other *Monochamus* species were collected on the site. Two other deep-boring cerambycid species were present on the site, *Asemum striatum* (L.) and *Tetropium cin-*

Table 1. Summary of measured explanatory variables, with mean +1SD, minimum, maximum, and probabilities obtained from multiple and simple linear regressions (significant ones in bold)

Variable	Mean	Standard deviation	Minimum	Maximum	Significant at last step	Relation	Simple regression
Larval density	92.78/m ²	69.14	0	378.19	–		
At tree level							
Diameter at breast ht	12.55 cm	3.93	8	24.83	<0.001	+	<0.001
Fire severity index	6.44	1.01	1	7	0.015	–	0.106
At sampling-plot level							
Altitude	751.34 m	48.30	660	900	<0.001		0.001
% Unburned forest (radius 100 m)	7.33%	12.71	0	63.90	–		0.549
% Unburned forest (radius 250m)	10.78%	13.69	0	62.95	0.141		0.021
% Unburned forest (radius 500m)	16.41%	16.81	0	68.60	0.015	+	0.008
Distance from nearest unburned matrix	2,066.61 m	1,059.87	519	4179	0.041	+	0.015
Distance from unburned matrix (dominant winds)	6,148.96 m	2,816.13	1,242	12,288	0.003	+	0.002
No. of trees with dbh >8 cm	25.99	13.37	4	79	–		0.418
No. of trees with dbh >12 cm	12.04	9.51	0	37	–		0.683
Latitude	47.7194	0.0238	47.6890	47.7735	–		0.461
Longitude	–70.7576	0.0245	–70.8023	–70.7105	0.447		0.002
Latitude * longitude	–3,376.5118	2.2935	–3,381.2743	–3,373.1522	–		0.310

namopterum Kirby, but in small numbers (Saint-Germain et al. 2004a, b). However, their larvae are significantly smaller than most *Monochamus* third instars and hence produce smaller entry holes (Gardiner 1957).

In each sample plot, from four to six trees were selected: the closest tree to each plot corner (north, east, south, and west) having a dbh of at least 8 cm, and the two trees having the largest remaining diameters in the plots. In total, 569 trees were sampled. The bark of the first meter from the ground was removed around the entire circumference for each of these trees. The base of the trunk usually exhibits higher larval density and might be more representative of the overall abundance than other sections of the trunk (Saint-Germain et al. 2004a). Every entry hole was marked with lumber crayons and counted. Bark area of the first meter was estimated using two diameter measurements: one at 1 m and one at the base of the tree, above any significant root flare. Larval density was calculated using entry hole counts and this estimation of bark area.

Statistical Analyses. The relationships between measured variables and larval density were assessed using multiple linear stepwise regressions (entry at $P \leq 0.05$; removal at $P > 0.10$). First, to evaluate the impact of tree-level variables, a first regression was done incorporating dbh and the fire severity index of trees as explanatory variables in a model, including larval densities recorded from the 569 sampled trees ($n = 569$). Then, to evaluate the effect of plot-level variables, the residuals obtained from the first regression were pooled by sample plot. We thus obtained a new plot-level larval density estimation. The plot-level variables were first independently tested using simple linear regressions on larval density. Variables with an $\alpha \leq 0.10$ in the simple linear regressions were then used in a second multiple linear stepwise regression, including the plot-level larval density estimation as the dependant variable ($n = 114$) (Hosmer and Lemeshow 1989). All analyses were performed using SPSS 10.0.5 for Windows (SPSS Inc., Chicago, IL).

Results and Discussion

Significance of Tree-Level Variables. Before the identification of larger scale ecological variables affecting habitat location in the whitespotted sawyer, we first removed as much variability as possible related to host location and host acceptance. Measured larval density varied widely between trees (from 0 to 378, 19 entry holes per m²; Table 1). Both measured tree-level variables were found to be significant in the first regression model (i.e., tree diameter and fire severity). The tree-level model is summarized in Table 2.

The dbh had a positive effect on larval density in our model. Large-diameter requirements of the whitespotted sawyer have been well documented. This species generally does not oviposit on trees having diameters <8–10 cm (Rose 1957, Raske 1972, Vallentgoed 1991, Saint-Germain et al. 2004a). The reason for such selection is unclear. Late instars need a certain wood volume to support their gallery-excavating behavior. However, the length of these galleries varies widely (Cerezke 1977), and some low-diameter trees occasionally show high larval densities. A more probable explanation could be linked to the thickness of cortical and/or subcortical tissues. Thicker bark could offer better conditions for egg laying, and thicker phloem may enhance early larval development, because phloem constitutes, with cambium, the basis of early instar nutrition (Rose 1957). Higher diameters are generally correlated with thicker bark and phloem (Reid and Glubish 2001). The quality of this microhabitat could be evaluated by the female as it cuts the oviposition slit and probes the inner bark tissues with its mouthparts (Hughes 1979). If this is the case, di-

Table 2. Summary of the tree-level model obtained from multiple regression on entry hole counts

Variable	Step	<i>t</i>	<i>r</i> ² Change	Significance
dbh	1	8.837	0.121	$P < 0.001$
Fire severity index	2	–2.450	0.009	$P = 0.015$
Total model		$n = 568$	$r^2 = 0.130$	

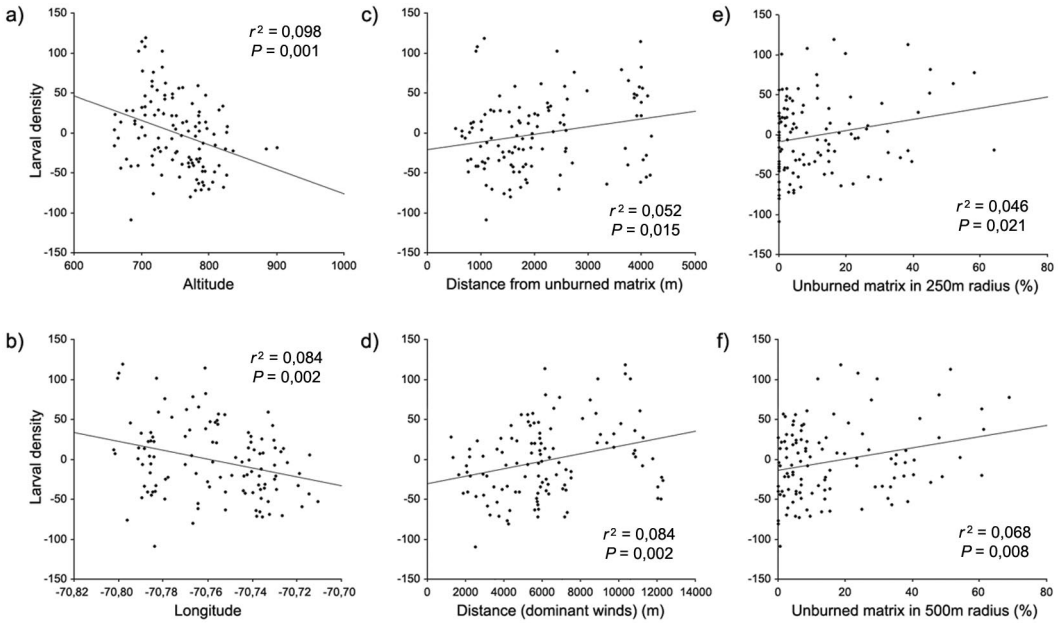


Fig. 2. Simple linear regression plots with stand-level larval density estimation as the dependant variable and (a) altitude, (b) longitude, (c) distance from the unburned matrix, (d) distance from the unburned matrix in the direction of dominant winds, (e) percentage of unburned forest in a 250-m radius; and (f) percentage of unburned forest in a 500-m radius as the independent variable.

iameter plays only an indirect role; the correlated phloem thickness is the factor having a direct influence on host selection.

Fire severity, in some circumstances, can exacerbate this diameter effect. The effect of fire severity on host use by woodborers has been shown to vary extensively, primarily between tree species, and has been linked to bark thickness variations (Saint-Germain et al. 2004a). During the fire, cortical and sub-cortical tissues are exposed to intense heat. This heat can cause excessive water loss from the phloem and cambium when the bark's insulating potential is low (Furniss 1965). In smaller trees, the thinner bark exhibit lower insulating potential. In such trees, it is plausible that water loss can degrade the subcortical microhabitat to a point that it becomes unattractive to ovipositing females. Although fire severity was significant in our model, it explained a fairly small amount of variability. The 1999 Grands-Jardins fire was generally very intense, with few areas that were not severely burned. In a more heterogeneous fire, this factor could probably be much more significant.

Although diameter and water content of subcortical tissues have a documented effect on the oviposition behavior of the female and hence on larval densities, the lower densities observed in small or heavily scorched trees also may be partially explained by differential survival rate in larvae between the egg stage and the third instar. The effects of host characteristics on larval survival have not been extensively documented, but because ovipositing females are generally not always optimal in their host choice (Scheirs and De Bruyn 2002), the importance of unequal mortality

of young larvae along the ecological gradients we measured cannot be discarded.

Significance of Larger Scale Variables. Six large-scale variables, when tested using simple linear regression on the plot-level larval density estimation, gave significant results (Fig. 2a-f). Stem density (fifth hypothesis) was rejected as an explanatory variable (Table 1). The six variables were included in the second multiple regression. Of these six variables, four were retained: altitude, percentage of unburned matrix in a 500-m radius, distance to unburned matrix in direction of dominant winds, and distance to nearest unburned matrix. The plot-level model is summarized in Table 3.

Altitude was the first one to be selected. Altitude has been recognized to play a role in habitat selection and/or insect performance in different contexts. Markalas (1992) studied the relationships between site- and stand-related variables and tree mortality patterns under the combined effects of severe drought and insect attack (in this case, cerambycid *Acantho-*

Table 3. Summary of the landscape-level model obtained from a multiple regression on residuals from the tree-level model pooled by sample plot

Variable	Step	t	r^2 Change	Significance
Altitude	1	-3.937	0.098	$P < 0.001$
% Unburned matrix (500-m radius)	2	2.460	0.083	$P = 0.015$
Distance (dominant winds)	3	3.063	0.059	$P = 0.003$
Distance (nearest matrix)	4	2.067	0.029	$P = 0.041$
Total model		$n = 113$	$r^2 = 0.268$	

cinus reticulatus Razoumowsky and buprestid *Phaenops knoteki* Reitter) in Greek fir forests. Mortality rates were lowest at high altitude and on steepest slopes, probably because of lower insect attack rates. However, no direct measurements of insect attack intensity were taken. In western North America, it has been shown that spruce stands located at lower elevations are more susceptible to several invasive species of bark beetles (mostly the genus *Dendroctonus*) (Safranyik 1985, Reynolds and Holsten 1994). Gilbert et al. (2003) obtained similar trends for *Dendroctonus micans* (Kugelann) in the United Kingdom. Our results showed a significant negative response to altitude in sawyer larval density, even if our altitude gradient was limited (between 660 and 900 m). In rugged landscapes, stands higher in altitude are generally more exposed to wind, and this could reduce their accessibility to dispersing adults. Also, the thermal environment of mountaintops and northern aspects may not be very stimulating for reproducing sawyer adults, which prefer warm microclimates (Rose 1957, Raske 1972).

Three spatial context variables were selected in the model in steps 2 through 4. We submitted two non-exclusive hypotheses on how neighboring unburned forest may affect local sawyer larval density in a recently burned forest, one being described as the first quality habitat encountered, first used hypothesis, to be tested using sheer distance from the matrix, and the other one referring to the nutritional requirements of the adults, to be tested using the percentage of unburned forest in a delimited radius. Both variables yielded significant results. Poor correlation between these two variables ($r^2 = 0.083$ for distance from the matrix versus percentage of unburned forest in a 500-m radius) may indicate that their respective effects emerge from distinct habitat selection mechanisms.

The percentage of unburned forest in a 500-m radius was the first spatial context variable to be selected. More entry holes were counted in stands that had more neighboring unburned forests. This pattern may be related to the feeding requirements of the adults, which may incite them to reproduce in habitats close to living trees on which they can feed. Newly emerged *M. scutellatus* adults feed on the bark of shoots or small branches up to 2 wk before reaching sexual maturity; no oviposition is observed during this period (Alya and Hain 1985, Walsh and Linit 1985). Adults of *Monochamus carolinensis* (Olivier) and *Monochamus titillator* (F.) continued to feed for several weeks after reaching sexual maturity (Alya and Hain 1985). If *M. scutellatus* has the same feeding behavior, habitat location for this species may indeed represent a compromise between adult and larval habitat requirements (Shibata 1987). Under this hypothesis, burned stands neighboring a single, small, and isolated unburned fragment should have the same value as burned stands located near the continuous unburned matrix, a pattern that fits with our results. Other cases of parent-offspring conflict have been reported in plant-insect research (Scheirs 2000,

Scheirs et al. 2000). It has been suggested that such conflicts are potentially widespread in phytophagous insects (Prokopy et al. 1996) and have been used in several cases as an explanation for significant divergences from optimality models in host use patterns (Mayhew 1997, Scheirs and De Bruyn 2002).

Two vectorial distances from the unburned matrix were selected in the model: distance in the direction of dominant winds in step 3 and distance from nearest unburned matrix in step 4. However, in opposition to our predictions, these distances had a positive effect on larval density. The positive effect of distance in the direction of dominant winds indicates that areas that burned first were more intensely colonized, because fire necessarily traveled in the same general direction of the winds. Some insects are known to colonize burned stands very rapidly, in some cases even before the fire has burned out (Evans 1966). However, because the 1999 Grands-Jardins fire took place several weeks before the peak of *Monochamus* adult flight, this observed pattern is unlikely to be explained by a very fast response from the insects.

The Grands-Jardins 1999 burn was relatively small ($\approx 5,000$ ha) compared with the dispersal capacities of the whitespotted sawyer. It has been estimated that *M. scutellatus* could easily travel >10 -km during its adult life (Raske 1972). Ross (1966) even alleged that *Monochamus maculosus* LeConte could travel up to 100 km in a 5-wk period. It is thus not surprising that no real limitations related to distance from unburned matrix were detected in our study. Different patterns could be observed in larger fires, which can sometimes exceed several hundreds of thousand hectares in North American northeastern boreal forests.

Unmeasured Factors and Future Research. The variability explained by our overall models may seem limited, but we succeeded in identifying significant landscape-scale variables for habitat location for the whitespotted sawyer. Host selection in wood-feeding insect is an extremely complex process in which numerous factors may play a part. Several potentially relevant factors could not be measured in our study. The adult population levels found around the burn and acting as source populations after the fire were certainly not equal throughout, and those differences probably added to the variability in entry hole density unexplained by our models. Allison et al. (2001) showed that *M. scutellatus* responded to kairomones produced by several bark beetle species and kairomone-mediated secondary host selection by the whitespotted sawyer possibly contributed to overall variability in larval density. Also, more precise ways of estimating the smoke-plume effect and thermal environment variations linked to topography could be developed. Although patterns of host location and acceptance could vary between tree species, habitat location mechanisms should be constant between fire events. Further research should aim at corroborating our results in other fire events and at improving the accuracy of our models. Improved models could be adapted to produce predictive geographical information system models of larval density spatial pattern.

Such models could have applications in planning salvage logging operations by identifying areas of high commercial and/or conservation value.

Acknowledgments

We thank Annie-Ève Gagnon, Marie-Pierre Brunet (field-work), Antoine Nappi, Alain Leduc (statistical analyses), Chris Buddle (comments on the manuscript), the Natural Sciences and Engineering Research Council of Canada–Université du Québec en Abitibi-Témiscamingue–Université du Québec à Montréal Industrial Chair in Sustainable Forestry Management (financial assistance), and the SEPAQ (Société des établissements de plein air du Québec) for facilitating our work in the Grands-Jardins provincial park.

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Received 23 February 2004; accepted 11 August 2004.
