

# Importance of Log Size on Host Selection and Reproductive Success of *Ips pini* (Coleoptera: Scolytidae) in Ponderosa Pine Slash of Northern Arizona and Western Montana

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**ABSTRACT** Pine engraver, *Ips pini* (Say), often use thinning slash, and their populations are known to be influenced by the condition of this material. In our study, we evaluated the importance of three log diameters (5, 10, and 20 cm) and three lengths (60, 120, and 240 cm) on various parameters of bark beetle host attack, development, and emergence. Evaluation of slash colonization in northern Arizona (near Flagstaff) and western Montana (near Missoula) over several years, during both spring and summer reproductive periods, indicated that the size of material selected by pine engraver differed by state, year, and season. However, within individual trials and over all trials, a trend in preference for larger diameter logs was apparent, whereas log length was of little effect. When evaluating only attacked logs, results indicated that the apparent preference for larger logs was not followed by significantly greater reproductive performance in the larger log sizes. Log origin was tested as a potential factor for the difference in attack densities between Arizona and Montana trials. Although male beetles in Montana and female beetles in Arizona seemed to distinguish between local-source and foreign-source logs during the attack phase, the gallery development and reproductive success of egg, larval, and new adult stages were not significantly different. Ultimately, differences among the trials both in host size selection and in reproductive success within attacked logs were closely tied to the overall population density of adult beetles. The implications of these findings for resource managers are discussed.

**KEY WORDS** *Pinus ponderosa*, pine engraver, slash management, population density, host preference

THE PINE ENGRAVER, *Ips pini* (Say), is a widely distributed, common, and important bark beetle of North American coniferous forests (Furniss and Carolin 1977). It is considered to be a moderately aggressive species, typically attacking recently dead material or weakened, dying trees (Kegley et al. 1997). However, host colonization by pine engraver can change to primary attacks on live trees when populations build to outbreak numbers. This population increase can occur in naturally produced slash or storm-damaged trees (e.g., windthrow), but more often is the result of improper slash management (Kennedy 1969, Schenk and Benjamin 1969, Parker 1991). Significant mortality of live trees may result when these large populations encounter forest stands with compromised defense systems (e.g., drought) (Kennedy 1969). Attacked trees are typically sapling and pole-sized trees (12–20 cm diameter at breast height [dbh]; 5–8 inches dbh) (Kennedy 1969, Furniss and Carolin 1977, Livingston 1979, Kegley et al. 1997). However, pine engraver will use the tops of larger trees, and under extreme drought

conditions they may attack and kill trees >33 cm (13 inches) dbh (Parker 1991). Although outbreaks of pine engraver usually last no more than 2 yr (Livingston 1979, Kegley et al. 1997), improper slash management has contributed to chronic outbreaks lasting 16 yr and killing hundreds of hectares of trees (Gara et al. 1999)

All phases of pine engraver reproduction from establishment of the male nuptial chamber and female egg galleries to larval growth and preemergence feeding by the new brood occurs in the tree phloem where nutrients are concentrated, and the bark affords a certain level of protection from predators and environmental conditions (Raffa et al. 1993). Because pine engraver beetles feed and reproduce in the phloem, any treatment that dries out this tissue before brood development is complete, or that prevents brood from emerging, will serve to prevent population increases. Current slash guidelines for prevention of outbreaks by *Ips* species recommend removal of all stems and branches 10 cm (4 inches) or greater in diameter (Wilkinson and Foltz 1982, Parker 1991). In addition, cutting of remaining material into shorter sections to

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promote drying has been recommended (Wesley 1995).

These management guidelines are generic for the western United States and are often applied to *Ips* species as a broad group. However, because pine engraver exhibits spatial and temporal differences in activity (see U.S. Department of Agriculture Forest Service, Forest Health Protection Insect and Disease Conditions reports in References), generalized recommendations may not be adequate in preventing pine engraver population increases or in assisting managers in determining the most effective and efficient control method for their situation. Regional and temporal differences in activity levels, manifest as both differences in host selection and in reproductive success, may be due to changes in host quality (Atkins 1966, Byers 1989, Redmer et al. 2001, Erbilgin et al. 2002), beetle condition (Wagner et al. 1981, Anderbrant et al. 1985, Gast et al. 1993, Wallin and Raffa 2000), intraspecific interactions (Wagner et al. 1981, Anderbrant et al. 1985, Byers 1989, Reeve et al. 1998, Wallin and Raffa 2002), interspecific competition (Birch and Wood 1975, Light et al. 1983, Hunt and Borden 1988, Poland and Borden 1998), predation (McCambridge and Knight 1972, Byers 1989, Reeve 1997, Erbilgin et al. 2002) and abiotic factors such as wind, temperature, and precipitation (Sartwell 1970, Wagner et al. 1981, Holsten and Werner 1990, Villa-Castillo and Wagner 1996, Wermelinger and Seifert 1999).

Of these factors, host quality is considered the most important in affecting population growth of bark beetles (Berryman 1982, Price 1997, Lieutier 2002). Yet, managers traditionally do not have the resources to evaluate host quality characteristics such as phloem thickness, bark thickness, or phloem moisture. However, it is possible that log diameter and log length might serve as surrogate measures. Previous studies on bark beetle utilization of slash have noted affects of log diameter and log length on host selection and reproductive success (Schenk and Benjamin 1969, Schmid 1977, Wesley 1995, Reid and Glubish 2001). Specifically, shorter log lengths may dry more rapidly from the cut ends, causing decreased reproduction (Schmid 1977), whereas smaller diameters may have thinner bark and thinner phloem, which also speed log desiccation (Amman 1969, Schenk and Benjamin 1969, Cole 1978). If log size is an important determinate of host quality, managers may be able to mitigate pine engraver population growth by removing certain log diameters or cutting slash into specific lengths.

Host quality may also differ from region to region, affecting both host selection and reproductive success. Previous studies have noted differences in bark beetle performance due to host species (Amman 1982, Lawson et al. 1995). Although ponderosa pine in our study locations are of the same species and variety (*Pinus ponderosa* P&C Lawson variety *scopulorum* Engelm.) (USDA 2002), others have noted that considerable variation exists among individual trees within the same variety (Mirov and Iloff 1958, Zaravin and Cobb 1970, Sturgeon 1979, Smith 1982, Katoh and

Croteau 1998, Linhart et al. 2001) and that environment can have an important effect on the expression of the genotype (Linhart et al. 2001). Not all differences are likely to be biologically relevant to beetle activity. Therefore, actual measures of pine engraver activity at different stages of development will provide the best indicators of regional host quality differences. If differences in pine engraver activity between two regions are caused by differences in log quality, a reciprocal exchange of host material should result in differential host selection and reproductive success.

In addition to host quality, host quantity can affect population dynamics by affecting bark beetle population densities. Specifically, competition for resources is an important source of mortality for pine engraver and other bark beetles (Mills 1986, Kirkendall 1989, Lawson et al. 1995, Reeve et al. 1998). If populations increase or if populations are concentrated in limited resources, bark beetle densities within host material will increase, resulting in decreased overall reproductive success per adult parent (Cole 1978, Anderbrant et al. 1985, Kirkendall 1989, Robins and Reid 1997, Reeve et al. 1998). In addition, attack behavior, host selection, and reproductive vigor of a population may change with increased beetle density (Cole 1978, Mills 1986, Anderbrant and Schlyter 1989, Byers 1989, Reeve et al. 1998, Wallin and Raffa 2002).

In our study, we tested several hypotheses important for developing spatially and temporally relevant guidelines for the management of slash. First, we asked two questions related to host preference: 1) How do log length and log diameter affect pine engraver host selection? and 2) Is host selection affected by the population density of adult beetles? Second, we tested three hypothesis related to pine engraver reproductive performance within colonized logs: 1) log size affects reproductive success, 2) host quality of trees from two distinct regions are different and host origin explains some of the observed differences in pine engraver activity between locations, and 3) population density of parent beetles affects colonization and reproductive success within individual logs.

## Materials and Methods

**Study Sites.** We conducted this study in ponderosa pine forests (*P. ponderosa*) of northern Arizona, within 32 km (20 miles) of Flagstaff, and western Montana, within 48 km (30 miles) of Missoula. At an elevation of 2,133 m (7,000 feet) above sea level and a latitude of 35.1° N, Flagstaff experiences four distinct seasons as does Missoula much further to the north at a latitude of 46.6° N and an elevation of 975 m (3,200 feet). With mean annual temperatures of 6.6 and 7.6°C (44 and 46°F), and mean annual precipitation of 34 and 58 cm (13.4 and 22.8 inches), respectively, Missoula and Flagstaff fall into Holdridge's cool temperate steppe/moist forest life-zone class (Smith 1986; IRI 2003; NOAA 2003a,b). In both locations, pine engraver populations are typically bivoltine with spring beetle flights beginning in early and mid-April, and summer

flights in mid- to late June, in Arizona and Montana, respectively (Livingston 1979, Parker 1991, Villa-Castillo and Wagner 1996, Kegley et al. 1997; our unpublished data).

These two locations were chosen for this study because ponderosa pine was the dominant forest cover, both sites were located in the interior west, and because overall climate and pine engraver life cycles were similar. However, pine engraver activity was generally greater around Missoula than around Flagstaff (USDA-FS FHP annual conditions reports; our unpublished data), providing an opportunity to evaluate potential factors causing different levels of pine engraver activity in slash material.

We selected similar stands of ponderosa pine in both locations. The stands used were sufficiently uneven aged that they furnished the size range of trees required for the slash trials. Most stands had been scheduled for thinning within the next 2 yr and had high basal areas of smaller diameter trees (e.g., 10–30 cm; 4–12 inches). Stands were patchy with canopy cover ranging from <20% in open patches to 98% in the denser sections. Because pine engraver will likely travel no >0.8 km (0.5 miles) in its search for slash (Livingston 1979), we chose stands that were not in proximity to active logging or thinning projects. Thus, our logs should have been the main source of host material for local beetle populations.

**Experimental Design.** A full factorial experiment with three log diameters (5, 10, and 20 cm; 2, 4, and 8 inches) and three log lengths (60, 120, and 240 cm; 2, 4, and 8 feet) was laid out in a completely randomized design. Ten replications of each of the nine combinations of diameter and length were cut for a total of 90 logs within each trial. These trials also tested the factors location (Arizona and Montana), flight season (spring and summer), and year (2000 and 2001). Individual trials were conducted at both locations in spring 2000, summer 2000, and spring 2001, resulting in six trials.

For each trial, we created a grid with 15–20 m (49–66 feet) spacing between points, and randomly assigned one of the log dimensions to each point. From within a 15-m radius around each point, we cut the smallest tree that would provide the assigned log size. In a few instances, we had to search outside the 15-m radius to find a tree with a lower bole diameter close to the diameter needed for the specific log (e.g., 5-cm logs were not cut from the tops of large trees). Thus, each log originated from a separate tree and was placed at a distance from its neighboring logs to minimize potential neighbor influences.

Green-needled branches from the cut trees were arranged around each log, without shading the log, to provide a source of foliage volatiles. To avoid excessive moisture buildup and to allow access to all log surfaces, logs were elevated 5–15 cm (2–6 inches) on sticks or rocks. We conducted the spring and summer 2000 trials in the same stands, but chose different stands for the spring 2001 trials.

In addition to published information on flight seasonality (Livingston 1979, Villa-Castillo 1994), pher-

omone traps in nearby stands were used to monitor beetle flights. However, traps were placed >0.8 km (0.5 miles) from the logs to avoid removing beetles that might potentially attack logs. In the three Arizona trials, logs were exposed 3 April–15 May (spring 2000), 15 May–5 July (summer 2000), and 27 March–8 May (spring 2001), corresponding to approximate peak flights of mid-April, 17 June, and 20 April, respectively. In Montana, logs were exposed 14 April–5 June (spring 2000), 6 June–14 July (summer 2000), and 5 April–21 May (spring 2001), corresponding to peak flights of 28 April, 23 June, and mid-April, respectively.

Six to 8 wk after logs were initially cut, 30-cm (1-foot) sections were removed from the center of each log. Sample sections were then placed in mesh bags and stored indoors for an additional 6 to 8 wk to ensure complete development and emergence of pine engraver broods and to prevent continued colonization of sections by other subcortical insects.

**Response Variables.** To facilitate data collection, bark was removed in two halves by cutting the bark longitudinally and peeling each half from the 30-cm-log sections. For each of the two bark halves, we measured the surface area, number of nuptial chambers (male attacks), the number of egg galleries per nuptial chamber (egg-laying females per male), and the length of each egg gallery. Egg galleries were labeled as complete (initiated and completed within the bark sample) or incomplete (initiated in the sample but continued beyond). Egg galleries that initiated outside of the bark sample but extended into the sample were also measured. On three or more complete egg galleries, all unhatched eggs and larval galleries (hatched eggs) were counted. Emergence holes were counted on a 10-cm-wide band of the bark circumscribing the log section. Data from the bark halves were combined for analysis of the entire log section.

Variables used in analyses included 1) attack density (number of nuptial chambers per meter squared of bark); 2) females per male ratio (average number of egg galleries per nuptial chamber); 3) egg gallery density (length in centimeters of all egg galleries, complete, incomplete, or initiated outside sample, per square meter of bark); 4) egg gallery length (average length in centimeters of all complete egg galleries); 5) fecundity (average number of eggs laid in complete egg galleries); 6) egg density (number of eggs per centimeter of egg gallery); 7) egg survival (average ratio of larval galleries to total eggs laid); 8) larva density (average number of larva per centimeter of egg gallery); 9) emergence hole density (number of emergence holes per square meter of bark); 10) egg gallery length per male (the ratio of centimeters of egg gallery per nuptial chamber); and 11) emergence holes per male (number emergence holes per nuptial chamber). Variables 10 and 11 were calculated to account for the influence of attack density on variables 3 and 9. Variables 1, 3, and 9 were calculated twice, once using all logs and again using only colonized (attacked) logs, whereas all other variables were calculated using only the colonized logs. These response variables allowed us to assess the three main stages of

host colonization by pine engraver beetles: attack (variables 1 and 2), development of the colonization (variables 3–8 and 10), and emergence of progeny (variables 9 and 11), for treatments (all logs) and for individual log sizes (colonized logs). Within the emergence stage, we have assumed that emergence hole density was directly related to the actual number of beetles that emerged (Sartwell 1971).

**Statistical Analyses.** A multiple response permutation procedure for one-factor designs (MRPP) (Mielke and Berry 2001) with multiple comparisons (Petrondas and Gabriel 1983) (computations programmed in Visual Basic for Applications within Excel 2000 by Rudy M. King, U.S. Department of Agriculture–Forest Service, Rocky Mountain Research Station Statistical Unit) was chosen for the majority of statistical analyses due to its use of actual data values (versus ranks or other transformations) and insensitivity to the unequal variance or deviations from normal distributions found in our data sets (Petrondas and Gabriel 1983). The MRPP analyses were limited to the testing of one factor. Thus, in evaluations of log size, we used the diameter categories or length categories, or the combined diameter  $\times$  length treatment as the single factor for analysis. In some cases, we analyzed data using multiple response variables. However, most analyses were conducted on single response variables because each represented a specific stage in colonization.

**Slash Colonization.** This portion of our analyses was an evaluation of the slash treatments as a whole. All experimental bolts were considered. Thus, zero values for unattacked logs were used in determining the average attack, development, and emergence of each slash size category. The average emergence hole densities within each size category indicated how many beetles were produced by all log bolts of that size. However, emergence hole density was not necessarily indicative of how successful parent beetles were in brood production. It was possible, for example, to have high brood production from few parent beetles or poor brood production from many parent beetles, yet produce the same average number of new beetles from a given slash size.

Variation in slash colonization among trials was expected. Thus, we conducted an initial analysis to evaluate the importance of log diameter and log length, along with the spatial and temporal factors of location (Arizona or Montana), year (2000 or 2001), and flight season (spring or summer) in causing variation in slash colonization. Due to unequal variance structures among the treatments and strongly non-normal distributions, these five factors were initially tested using data on the presence or absence of pine engraver within the sample logs. Hierarchical loglinear analysis was used to determine the significance of each variable and their interactions (HILOGLINEAR, SPSS Science 2000). A significant effect of diameter and length would indicate that the nine diameter-length combinations should be considered as individual treatments in further evaluations of the effect of log size on slash utilization.

Because quantitative differences in densities were lost in the use of the presence-absence data, we also evaluated the importance of each factor independently using MRPP tests on the quantitative data. The additional assessment of location, year, and season factor effects was conducted by determining if, for each size class, the factor levels (e.g., Arizona and Montana, 2000 and 2001, spring and summer) were significantly different.

Within each trial, the effect of slash size on host selection, brood development, and brood production was assessed by comparing average attack densities, egg gallery densities, and emergence hole densities, respectively (variables 1, 3, and 9 computed for all sample logs). In addition to testing the effect of each of the nine size treatments, we tested for significant differences between diameter classes and between length classes. Finally, we compared trials to determine whether differences in the density of active, flying parent beetles corresponded to differences in slash utilization.

**Reproductive Performance.** After evaluating pine engraver log size preference, we tested whether pine engraver reproductive performance within individual logs was linked to log size or was better explained by other factors such as log origin or density of adult beetles during the trial. These analyses of reproductive performance used variables 1–11 calculated using data from the attacked logs only.

**Log Size.** We used MRPP tests with multiple comparisons to detect significant differences in reproductive activity related to log size. The relationship between host size preference (previous analysis) and reproductive performance (this analysis) were assessed by visually comparing treatment similarities. We would expect that preference for a particular log size or group of sizes would be followed by greater reproductive success within those same sizes.

**Log Origin.** During the spring 2001 trials, 10 additional logs 20 cm (8 inches) in diameter by 120 cm (4 feet) in length were cut, transported to the other state, and randomly placed among the main experiment logs, preserving the 15–20-m (49–66-foot) spacing between logs. The 10 Montana logs were cut so they could be placed on-site in Arizona 1 d before cutting of logs for the Arizona main (log-size) experiment. The 10 Arizona logs were cut during setup of the Arizona main experiment and sent to Montana in time to be placed on-site during the cutting of the Montana main experiment.

These 20 logs were processed and data were collected as described in the main experimental design. The effect of log origin was tested by comparing the 10 “foreign” logs with the 10 “local” logs of the same size from the main log experiment. Two sets of comparisons were made: in Arizona, Arizona logs (local) were compared with Montana (foreign) logs, and in Montana, Montana logs (local) were compared with Arizona logs (foreign). Response variable 1 for all logs, as well as variables 1–11 for attacked logs, was used to determine whether log origin was influential at any stage of host colonization. The MRPP statistical anal-

yses were performed on variables individually, followed by a final analysis of reproductive performance by using response variables 1–8, 10, and 11. Variable 9 (larva per centimeter of egg gallery) was dropped because MRPP is limited to 10 response variables, and it was closely related to variables 7 (egg density) and 8 (egg survival).

**Beetle Population Density during the Trial.** The effect of beetle density during the trial on reproduction within colonized logs was evaluated by comparing trial ranks at each stage of colonization (variables 1–11) with the trial beetle population density. The sum of all nuptial chambers in all log samples was used as the relative measure of population density. Close correlations between trial beetle density and trial colonization variables would indicate that beetle density was important to the overall reproductive success of pine engravers. However, breaks in the similarity of trials that correspond more closely to trial location than to beetle density might indicate that other location-related factors were operative.

**Overall Effect of Log Size on Host Selection and Reproductive Success.** Our study encompassed a wide range of spatial and temporal variation in pine engraver populations. Thus, pooling of all our data were useful in clarifying the overall effect of log size on host selection patterns (all logs) and reproductive success (colonized logs) that might be expected in the intermountain west of the United States. Pooled data were subject to MRPP and multiple comparison tests on the nine log size treatments. Response variables tested included attack density, egg gallery density, and emergence hole density (variables 1, 3, and 9, respectively) calculated for both all logs and colonized logs only.

## Results

**Factors Affecting Slash Utilization.** Hierarchical loglinear analyses on presence-absence data indicated that both log diameter and log length were significant factors in determining the presence of pine engraver ( $P < 0.001$  and  $P = 0.05$ , respectively) (Table 1). Because both diameter and length were significant factors, our subsequent analyses considered each log diameter and length combination as a unique treatment.

Additional results of loglinear analyses suggested that the presence of pine engraver in the slash treatments varied between flight seasons ( $P < 0.001$ ) but not with location ( $P = 1.0$ ) or year ( $P = 0.15$ ) (Table 1). However, when values for attack density, egg gallery density, and emergence hole density were used in comparisons, we found that Montana had significantly higher levels of activity for most size treatment categories ( $P \leq 0.05$ ) (Fig. 1). Although the years 2000 and 2001 were not significantly different when locations were pooled, we did find that within each location there were several instances where attack, development, and emergence were significantly different between years. Comparison of flight season was only possible for the Montana 2000 trials. For several log size treatments, results indicated that the summer

**Table 1.** Significance of main effects and two-way interactions on the presence and absence of pine engraver beetles in all logs from slash-size trials conducted in Arizona and Montana

Factors	df	P value <sup>a</sup>
Main factors		
Diameter	2	<0.01
Length	2	0.05
Location	1	1.00
Year	1	0.15
Season	1	<0.01
Two-way interactions		
Diameter × length	4	0.52
Diameter × location	2	1.00
Diameter × year	2	0.24
Diameter × season	2	0.05
Length × location	2	1.00
Length × year	2	0.45
Length × season	2	0.70
Location × year	1	1.00
Location × season	1	1.00
Year × season	1	1.00

All three-way and higher interactions were nonsignificant ( $P > 0.05$ ).

<sup>a</sup> Significance determined using hierarchical loglinear analyses.

flight had significantly more attacks and more egg gallery construction than did the spring flight. However, the number of beetles emerging from each log size was similar. Because we detected significant differences among the trials due to location, year, and flight, we considered each state-year-flight combination (each trial) individually in our analyses of the importance of log size in host selection.

Comparison of the nine log treatments for each trial revealed a general trend for increased attack density and increased egg gallery density with increased log size (Fig. 2), although significant differences among treatments were not detected in all trials. Results for emergence hole density showed a similar trend of increased beetle emergence in the larger log sizes for the Arizona trials.

Treatment effects were more pronounced with changes in log diameter than with log length. When log diameter classes were compared, regardless of log length, we found significant differences in pine engraver activity in the slash treatments ( $P \leq 0.05$ ) (Fig. 3). Conversely, we found that attack densities, egg gallery densities, and emergence hole densities were similar among log length categories regardless of log diameter ( $P > 0.05$ ).

Apparent differences in pine engraver activity among the five trials were confirmed when multiple comparisons detected significant differences in average log attack densities among trials (Fig. 4). Additional data on activity levels within each trial suggest that the increase in mean attack densities is due to both an increase in the number of logs attacked and an increase in the density of attacks within individual logs. Specifically, we found that as the sum of nuptial chambers in all log samples increased there was increased use of smaller sized logs and an increase in maximum log attack densities for each size class (Table 2). These data supported the conclusion that trial activity levels could be ranked with activity low in

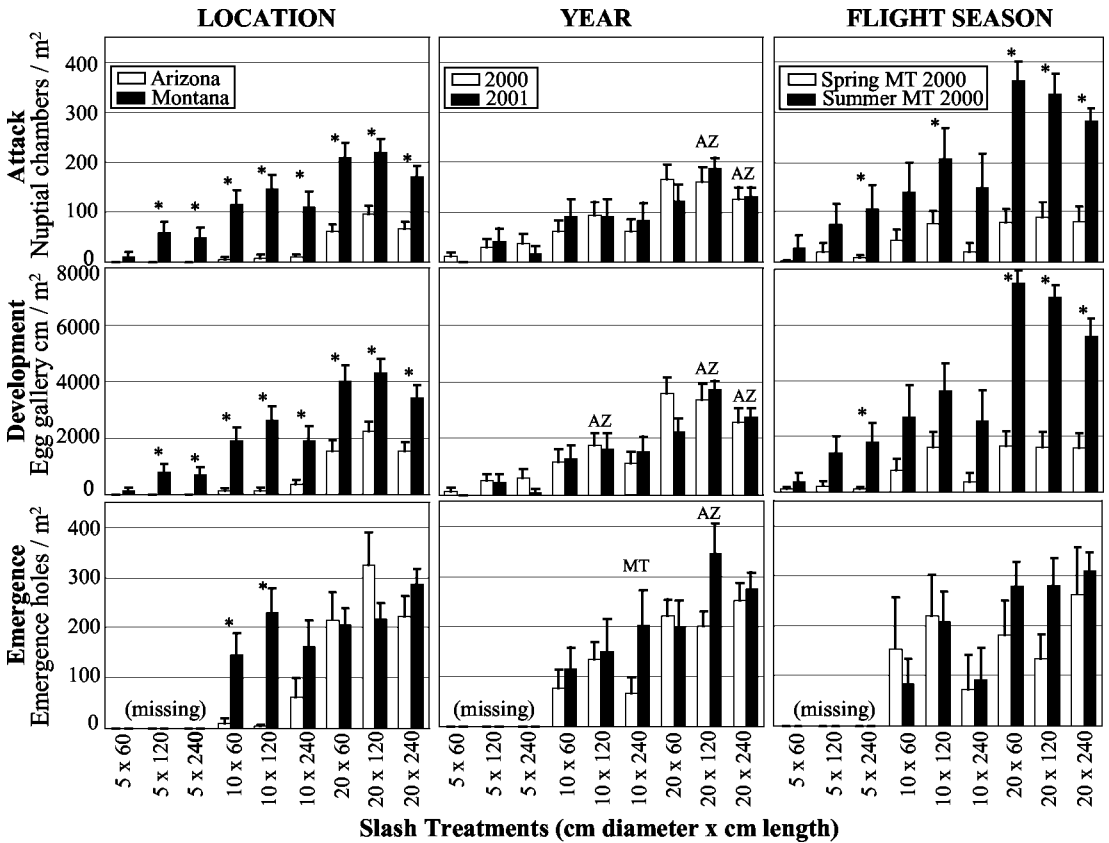


Fig. 1. Treatment means for the main factors location, year, and flight season illustrate the overall importance of the factor in determining pine engraver activity during the three host colonization stages of attack, development, and emergence. Significant differences between factor pairs for each slash treatment are indicated by an asterisk (\*). When years were compared for Arizona and Montana separately, significant yearly effects were detected as indicated by AZ and MT, respectively (multiple response permutation procedures for one-factor designs with  $P \leq 0.05$ ). Error lines are +1 SE (n varied from 10 to 30).

Arizona 2000, spring; medium in Arizona 2001, spring; and Montana 2000, spring, and higher in Montana 2001, spring; and Montana 2000, summer ( $P \leq 0.05$ ). During the summer 2000, trial in Arizona, pine engravers attacked only two of the 90 logs, so this trial was removed from analyses.

**Factors Affecting Reproduction in Attacked Logs.** Evaluation of factors affecting reproductive success during attack, development, and emergence stages (variables 1–11) are based on data from colonized logs only. Due to difficulties determining emergence holes for the small diameter logs, results are missing for emergence hole density and emergence holes per nuptial chamber (variables 9 and 11, respectively) for the 5-cm-diameter treatments.

**Effect of Individual Log Diameter and Length on Reproductive Success.** Among all cases in which attack density, egg gallery density, and emergence hole density (variables 1, 3, and 9, respectively) within colonized logs were considered, we found only three instances where log size treatments were significantly different ( $P \leq 0.05$ ) (Fig. 5). No more than one instance occurred in any one colonization phase or any

one trial. Closer evaluation of these three instances failed to reveal a distinct pattern related to log size, with the possible exception of emergence hole density in the Montana 2001 spring trial, where greater densities were found in the 10-cm-diameter logs. Evaluation of the effect of log size on the additional stages of beetle colonization (variables 2, 4–8, 10, and 11) similarly found that responses were largely similar among log size treatments and were without pattern (data not shown).

**Effect of Log Origin on Host Selection and Reproductive Success.** In the reciprocal log exchange experiment, we found that pine engraver may have differentiated between local and foreign logs during the attack stage but that log source had no significant effect on the development or emergence stages of colonization ( $P > 0.05$ ) (Table 3). Montana male pine engraver attacked local source logs significantly more often than they attacked logs from Arizona ( $P \leq 0.05$ ). However, once a log was attacked, attack densities within local and foreign logs were similar. In Arizona, male beetles did not differentiate between log sources, but significantly more females were attracted to males

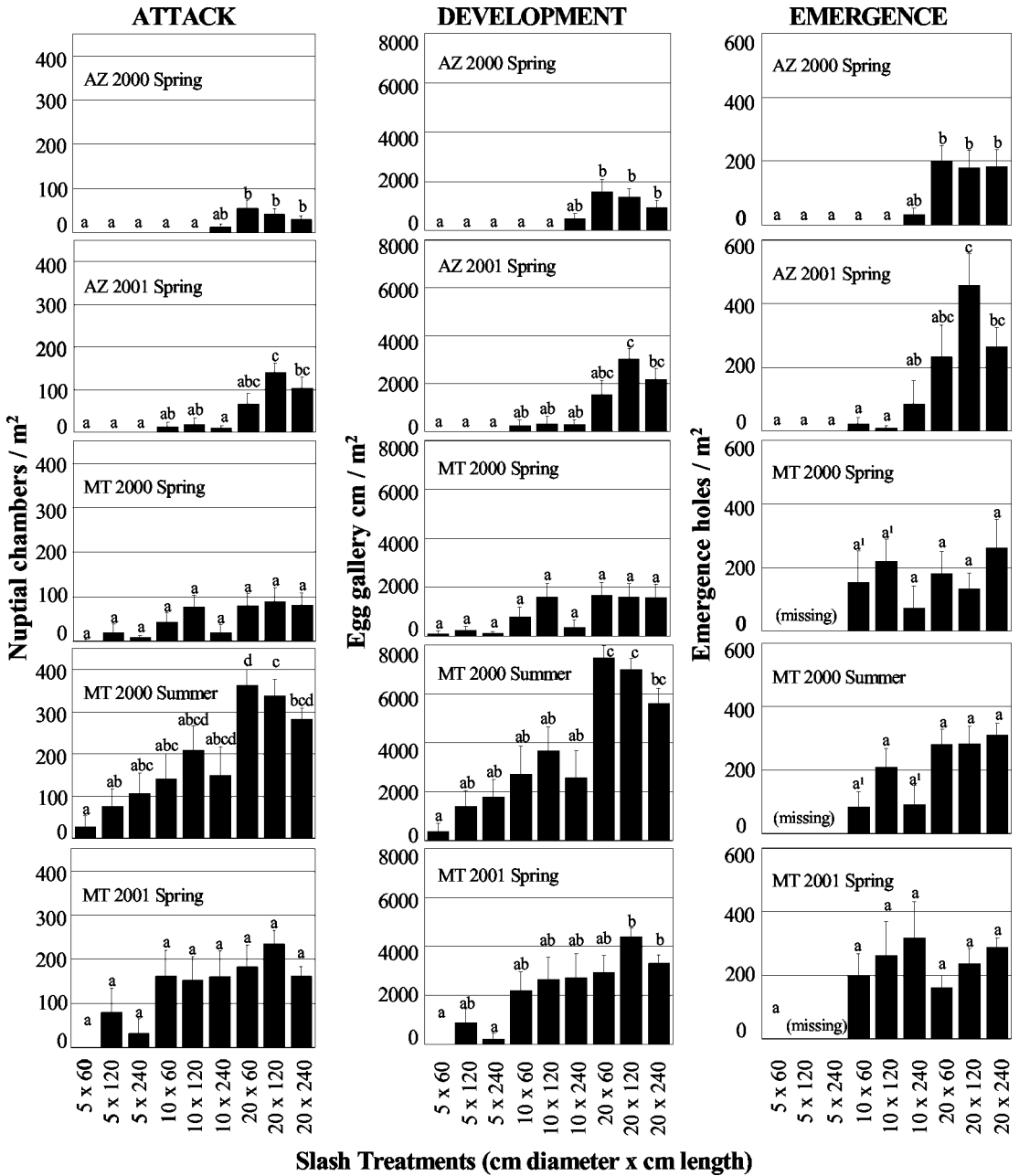


Fig. 2. Effect of slash size on average attack density, egg gallery density, and emergence hole density per log for all logs in trials conducted in Flagstaff, AZ (AZ), and Missoula, MT (MT). Similar letters within a trial indicate treatments that were not significantly different (multiple response permutation procedure for one-factor designs with multiple comparisons using an experimentwise alpha level of 0.05 for each trial). Values potentially affected by missing data (25–50% of potentially positive values) are indicated by the superscript (1). Error lines are +1 SE ( $n \approx 10$ ).

in Arizona (local) logs. Tests on all other parameters of development and emergence (variables 3–11) indicated no differences in the suitability of Arizona and Montana logs for pine engraver reproduction. Comparison of local and foreign logs using all variables (1–8, 10, and 11) in a multiple response test also

indicated that log origins were not significantly different ( $P > 0.05$ ).

*Effect of Adult Beetle Density during the Five Trials.* To test for potential effect of adult beetle density on log colonization, we pooled data for all attacked logs within each trial and used these values to compare the

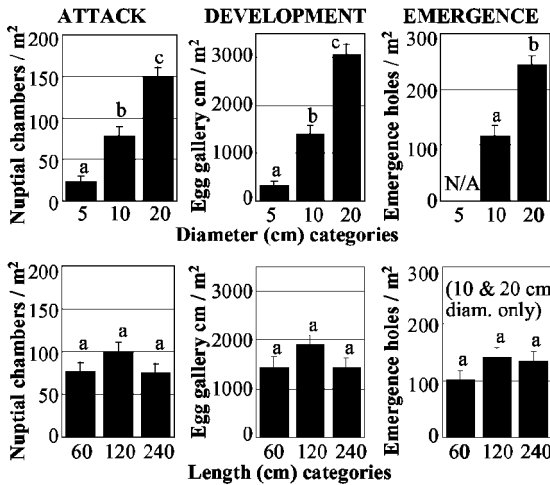


Fig. 3. Effect of log diameter and length on measures of pine engraver attack, development, and emergence for all logs. Categories with similar letters are not statistically different (multiple response permutation procedure for one-factor designs with multiple comparisons using an experimentwise alpha level of 0.05). Error lines indicate +1 SE ( $n \approx 150$ ).

trials to one another. In particular, we tested whether density of adult beetles during a trial (Fig. 5; Table 2) affected the colonization of individual logs. Results from multiple comparisons indicated that during most colonization stages, significant differences among trials corresponded closely to the ranking of trials based on the adult beetle density during the trial (Table 4). The pattern we observed was that as the population density of parent pine engraver beetles increased, attack density and egg gallery density within attacked logs also increased, but egg gallery length, fecundity, larval density, egg gallery length per male, and emergence holes per male decreased. Often, there was greater differentiation between the Montana summer 2000 and Montana spring 2001 trials than suggested by the multiple comparison in Fig. 4, with continued

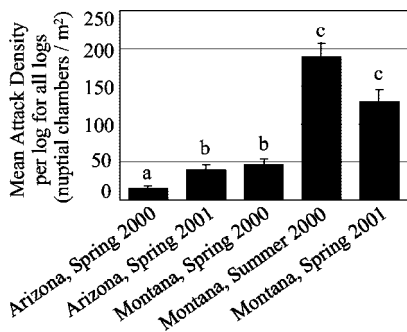


Fig. 4. Comparison of the five trials using mean attack density for all logs. Similar letters indicate trials were not significantly different (multiple response permutation procedure for one-factor designs with multiple comparisons using an experimentwise alpha level of 0.05). Error lines indicate +1 SE ( $n$  varied from 24 to 53).

Table 2. Ranking of the five slash-size trials based on the relative levels of several measures of adult pine engraver activity; trials are listed in order of increasing attack density, although AZ3 and MT1 are comparable

	Trial <sup>a</sup>				
	AZ1	AZ3	MT1	MT3	MT2
No. of logs in trial <sup>b</sup>	89	87	90	90	88
Sum of all nuptial galleries	179	495	517	1,298	1,930
Sum of all egg galleries (cm)	408	1,120	1,013	2,980	6,102
% of logs attacked	29	29	39	52	60
of 5-cm diameter	0	0	17	10	34
of 10-cm diameter	13	15	40	50	47
of 20-cm diameter	76	70	60	93	100
Max. attack density in all logs	181	267	218	493	594
in 5-cm diameter	0	0	182	444	426
in 10-cm diameter	52	131	203	482	576
in 20-cm diameter	181	267	218	493	594

<sup>a</sup> Trial names indicate location in AZ or MT, as well as the year and season (1, spring 2000; 2, summer 2000; 3, spring 2001).

<sup>b</sup> Some trials have <90 logs due to random losses.

similarity between Arizona spring 2001 and Montana spring 2000. However, in a few instances, differences seemed to be more closely related to state (AZ/MT) than to density (e.g., females per male, egg survival, and emergence hole density).

**Overall Effect of Log Size on Slash Colonization and Reproduction.** Logs in our five trials were exposed to a wide range of active pine engraver population densities. Pooling of the data from these trials provided a good picture of overall pine engraver activity and the importance of log size. Results of multiple comparisons on the nine log size treatments reinforced the conclusion that log diameter was the more important component in the colonization of the various log sizes and that the larger diameter slash, particularly the 20-cm-diameter class, was preferred by pine engraver (Fig. 6). When only attacked logs were considered, we found no significant difference in beetle performance during attack, development, or emergence stages attributable to individual log sizes.

Discussion

**Effect of Log Size on Host Selection and Reproduction.** Initial analyses of pine engraver presence-absence data suggested that both log diameter and log length were important in host selection. However, in subsequent analyses using attack density, egg gallery density, and emergence hole density, diameter was the only significant factor.

Our observed lack of significant response by pine engraver to log length during attack, development, and emergence contrasts with previous studies. In a similar experiment conducted in southern Arizona with ponderosa pine slash colonized by pine engraver and the Arizona fivespined ips, *Ips lecontei* Swaine, Wesley (1995) found that intermediate lengths (120 cm) were preferred over shorter (60-cm) or longer (240-cm) lengths and concluded that log length was more important than diameter in host selection by *Ips* species. Likewise, Schmid (1977) found spruce beetle,



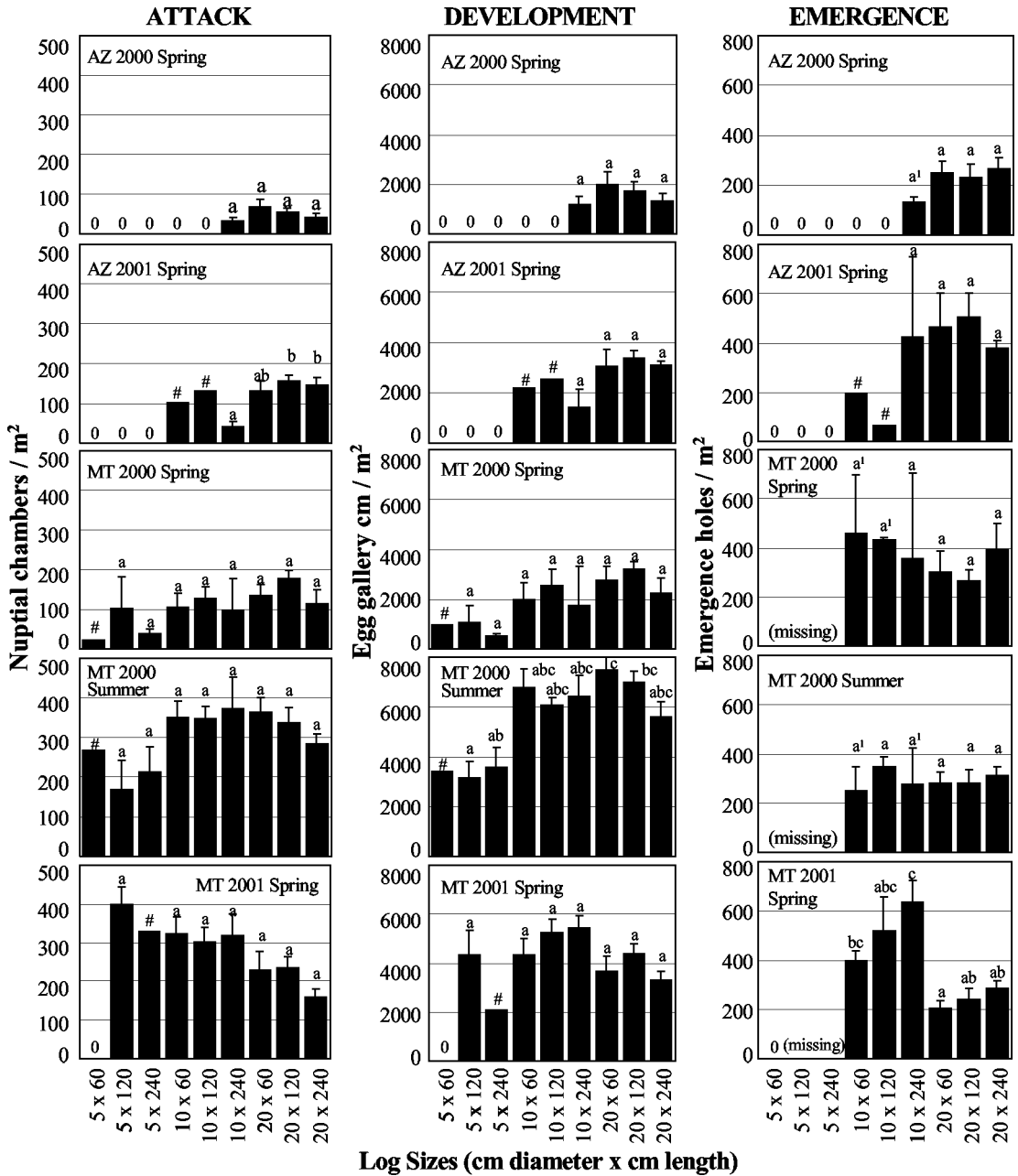


Fig. 5. Effects of log size on average attack density, egg gallery density, and emergence hole density per log for logs colonized during trials in Flagstaff, AZ (AZ) and Missoula, MT (MT). Similar letters within a trial indicate treatments that were not significantly different (multiple response permutation procedure for one-factor designs with multiple comparisons using an experimentwise alpha level of 0.05). Error lines are +1 SE (*n* varied from 2 to 10). Bars without error lines (#) were estimated from one value and were excluded from multiple comparisons. Treatments with no attacked logs are indicated by (0). Values potentially affected by missing data (25–50% of potentially positive values) are indicated by the superscript 1).

*Dendroctonus rufipennis* (Kirby), colonization was lower within spruce logs, *Picea engelmanni* Parry, shorter than 2.4 m (8 feet) compared with those longer than 2.4 m. Both studies attributed avoidance of the shorter logs to potentially faster desiccation.

If sufficient drying of phloem occurs in proximity to the cut ends, it is possible that brood production in

slash could be decreased by cutting logs into many short pieces. As support for this hypothesis, Schmid (1977) found spruce beetle egg gallery densities were reduced within 0.3–0.6 m (1–2 feet) of the cut ends. Redmer et al. (2001) tested the hypothesis that phloem desiccation from the cut ends of the log is significant by comparing logs with untreated ends to

**Table 3. Comparison of AZ and MT logs placed at both the source location (local) and at a location in the other state (foreign) (avg. ± SE)**

Log placement log source	Attack			Development					Emergence			
	Nuptial chambers/m <sup>2</sup> (all logs) <sup>a</sup>	Nuptial chambers/m <sup>2</sup> (colonized)	Egg galleries/nuptial chamber	Gallery/m <sup>2</sup> (cm)	Length of complete galleries (cm)	Eggs laid per complete egg gallery	Eggs/cm egg gallery	Larva eggs laid	Larva cm egg gallery	Egg gallery per nuptial chamber (cm)	Holes/m <sup>2</sup>	Holes/nuptial chamber
AZ/AZ <sup>b</sup> (local)	141 ± 22	156 ± 17	2.24 ± 0.11	3370 ± 288	96 ± 0.4	26.6 ± 2.3	2.3 ± 0.1	0.75 ± 0.02	1.76 ± 0.12	22.1 ± 1.2	507 ± 97	3.37 ± 0.56
AZ/MT <sup>c</sup> (foreign)	97 ± 22	138 ± 11	1.91 ± 0.12*	3102 ± 302	10.6 ± 0.7	26.4 ± 2.8	2.0 ± 0.1	0.75 ± 0.03	1.53 ± 0.05	22.6 ± 1.3	345 ± 58	2.80 ± 0.65
MT/MT <sup>d</sup> (local)	235 ± 30	235 ± 30	2.46 ± 0.09	4374 ± 393	7.7 ± 0.4	17.7 ± 1.1	1.9 ± 0.1	0.77 ± 0.02	1.47 ± 0.10	19.8 ± 1.3	237 ± 48	1.37 ± 0.39
MT/AZ <sup>e</sup> (foreign)	62 ± 29	155 ± 37	2.14 ± 0.25	2716 ± 555	8.3 ± 0.7	19.7 ± 1.4	2.0 ± 0.2	0.81 ± 0.03	1.64 ± 0.18	18.8 ± 3.6	229 ± 63	2.08 ± 0.86

<sup>a</sup> Nuptial chambers per square meter were calculated for both "all logs" and "colonized logs only". All other factors were calculated for colonized logs only.  
<sup>b</sup> *n* = 10 for all logs; *n* = 9 for colonized logs.  
<sup>c</sup> *n* = 10 for all logs; *n* = 4 for colonized logs.  
<sup>d</sup> *n* = 10 for all logs; *n* = 10 for colonized logs.  
<sup>e</sup> *n* = 10 for all logs; *n* = 7 for colonized logs.  
<sup>f</sup> Significant differences between local and foreign source logs are noted with an asterisk in the lower row (multiple response permutation procedure for one-factor designs, *P* ≤ 0.05).

**Table 4. Comparisons of attack, development, and emergence for all colonized logs within the five slash-size trials (avg. ± SE)**

Trial <sup>a</sup>	Attack			Development					Emergence		
	Nuptial chambers m <sup>-2b</sup>	Egg galleries/nuptial chamber	Gallery/m <sup>2</sup> (cm)	Length of complete galleries (cm)	Eggs laid per complete egg gallery	Eggs/cm egg gallery	Larva/eggs laid	Larva/cm egg gallery	Egg gallery per nuptial chamber (cm)	Holes/m <sup>2</sup>	Holes/nuptial chamber
AZ <sup>c</sup>	52 ± 7a	216 ± 0.13b	1604 ± 211a	12.3 ± 0.6d	34.5 ± 1.6c	2.52 ± 0.11c	0.81 ± 0.01cd	2.07 ± 0.10d	31.6 ± 1.9c	238 ± 25a	5.74 ± 0.60d
AZ <sup>d</sup>	136 ± 11b	2.26 ± 0.06b	2992 ± 204c	9.4 ± 0.4c	24.2 ± 1.6b	2.09 ± 0.07b	0.76 ± 0.01b	1.61 ± 0.06c	22.9 ± 1.0b	424 ± 51b	3.40 ± 0.53c
MZ <sup>e</sup>	116 ± 13b	1.84 ± 0.09a	2215 ± 240b	9.5 ± 0.4c	22.1 ± 1.5b	1.99 ± 0.10b	0.75 ± 0.03d	1.52 ± 0.09bc	19.1 ± 1.0a	351 ± 45ab	2.65 ± 0.29c
MT <sup>f</sup>	253 ± 17c	2.31 ± 0.05b	4170 ± 214d	7.4 ± 0.2b	15.9 ± 0.7a	1.78 ± 0.04a	0.76 ± 0.01bc	1.39 ± 0.04bc	18.0 ± 0.8a	340 ± 32ab	1.79 ± 0.23b
MT <sup>g</sup>	312 ± 17c	3.07 ± 0.07c	6004 ± 277a	6.2 ± 0.2a	16.7 ± 0.8a	2.14 ± 0.07b	0.61 ± 0.02a	1.30 ± 0.07a	20.3 ± 0.7ab	294 ± 23ab	1.01 ± 0.11a

<sup>a</sup> Trials are listed in order of increasing attack density, although AZ3 and MT1 are comparable. Trial names indicate location in AZ or MT, as well as the year and season (1, spring 2000; 2, summer 2000; 3, spring 2001).  
<sup>b</sup> Means in the columns followed by similar letters indicate the trials are not significantly different (multiple response permutation procedure for one-factor designs with multiple comparisons, *P* ≤ 0.05).  
<sup>c</sup> "attack" and "development" *n* = 26; "emergence" *n* = 24.  
<sup>d</sup> "attack" and "development" *n* = 25; "emergence" *n* = 25.  
<sup>e</sup> "attack" and "development" *n* = 33-36; "emergence" *n* = 25.  
<sup>f</sup> "attack" and "development" *n* = 46; "emergence" *n* = 43.  
<sup>g</sup> "attack" and "development" *n* = 53; "emergence" *n* = 41.

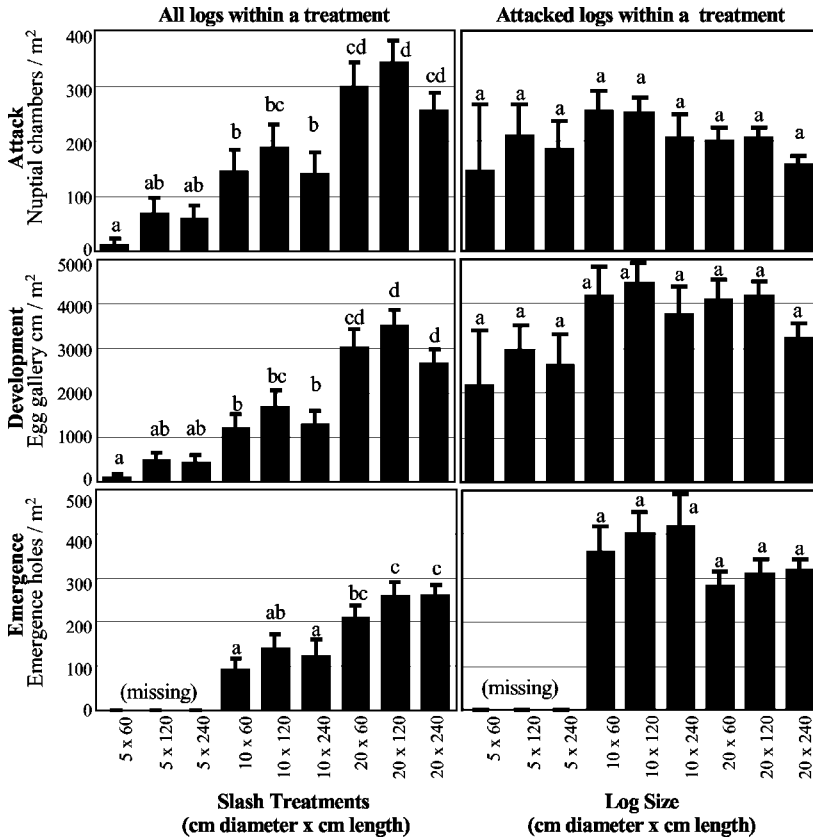


Fig. 6. Treatment means for all logs (slash treatments) and for attacked logs only (log size) during the host colonization phases of attack, development, and emergence. Similar letters indicate treatments that were not significantly different (multiple response permutation procedure for one-factor designs with multiple comparisons using an experimentwise alpha level of 0.05). Error lines are +1 SE ( $n \approx 50$  for all logs;  $n$  varied from 2 to 41 for attacked logs).

logs with 1 cm of wax applied to the cut ends. Results indicated that neither phloem moisture nor pine engraver reproductive success was significantly altered by the wax treatment. However, it is unclear how far from the cut end these phloem moisture samples were taken. We failed to detect localized effects at the log cut end because our samples were taken from the center of the log bolt. However, after our 30-cm sample sections had been in storage for  $\approx 6$  to 8 wk, we noted that only 1–3 cm (0.5–1 inches) along the log’s cut end dried rapidly enough to prevent beetle activity.

The importance of log diameter on host selection and reproduction has been noted for a number of bark beetle species (Cole 1978, Parker and Stevens 1979, Amman and Pasek 1986, Reid and Glubish 2001). Wesley (1995) found that, although log length was the more important factor, pine engraver and the Arizona fivespined ips in southern Arizona both preferred 10-cm-diameter logs over 5- or 20-cm logs. Meanwhile, Parker and Stevens (1979) found that brood production by mountain pine beetle, *Dendroctonus ponderosae* Hopkins, in northern Arizona was greatest in larger slash sizes when all logs were considered. Diameter has also been noted as the primary factor predicting

host selection by Douglas-fir beetle, *Dendroctonus pseudotsugae* Hopkins, in Douglas-fir, *Pseudotsugae menziesii* (Mirbel) Franco slash (Reid and Glubish 2001).

Despite the influence of log size on colonization of the slash treatments, our results using only attacked logs indicated that the size of a log had little or no effect on reproductive success in that log during the attack, development, or emergence phases. At least two explanations are possible for why we did not observe increased reproduction in the preferred larger log sizes.

First, beetles may have selected logs for some unmeasured characteristic that was more commonly found in the larger log sizes. Thus, we would have detected apparent selection for the larger logs. Yet, if reproductive success depended on a characteristic that also occurs in smaller logs, albeit less frequently, reproduction in colonized logs could have been similar among log sizes. Several host characteristics other than log size have been identified as important in host selection and reproduction. For example, thicker bark on the larger diameter logs may be related to higher preference and brood success (Amman 1969). Bark thickness is also correlated with phloem thickness

(Amman 1969), and several studies have attributed increased brood production in bark beetles to greater phloem thickness (Amman 1972; Cole 1978; Amman and Pasek 1986; Haack et al. 1984, 1987a,b) or phloem moisture (Redmer et al. 2001). Reid and Robb (1999) found no relationship between host colonization variables and diameter for pine engraver in jack pine, *Pinus banksiana* Lambert. They suggest that selection and reproductive success are not due to diameter or phloem thickness, per SE, but rather may be due to pre-mortem tree vigor, which is often related to, but not always directly correlated with, either phloem thickness or slash diameter.

Second, it is possible that smaller diameter logs constitute more vulnerable habitats (e.g., quicker desiccation or greater temperature increases), but the negative effect on reproduction is only apparent during strongly unfavorable environmental conditions (e.g., intense sun exposure and/or hot temperatures). Thus, beetles may avoid the risky smaller log sizes even though high reproductive success is possible in some years. Additionally, preference for smaller logs might occur when larger logs present a more immediate risk of density-induced negative feedback (e.g., decreased fecundity or increased mortality) (Berryman 1997).

In those cases where preference for particular oviposition sites does not correspond to reproductive performance (Price 1997), there may be an opportunity to attract beetles to logs that would provide low emergence; to create a "trap log." However, the poor preference-performance relationship may be related to a misidentification of mismeasurement of the log trait actually preferred by pine engraver, or it may indicate that the link between preference and performance in the sometimes eruptive pine engraver species may be weak (Leyva et al. 2000). Previous studies examining eruptive species found that for the chrysomelid beetles, *Disonycha pluriligata* (LeConte) and western spruce budworm, *Choristoneura occidentalis* Freeman, preference-performance links were not apparent (Dodge and Price 1991, Leyva et al. 2000). Although it is possible that linkages between preference and performance may not exist for eruptive species such as pine engraver (Leyva et al. 2000), it seems unlikely that host preferences would exist without the selection pressure of increased performance. If linkages are weak with selection occurring only occasionally, a strongly controlled genetic preference may persist in the population. However, if this is true we would expect pine engraver to show a clear size threshold of host acceptance, not a threshold varying with population pressure. Thus, it is more likely that log size is not a host characteristic that adequately predicts reproductive success within host material, and that some other trait such as phloem thickness or phloem moisture is more appropriate. This suggests that creation of a trap log is not a useful management option, except where attacked logs are treated to minimize pine engraver brood survival (e.g., damage colonized phloem) (Borden and Lacey 1985, Bentz and Munson 2000).

We were particularly interested in the utility of using log length and diameter in management guidelines because managers traditionally do not evaluate the specific conditions of slash phloem moisture and thickness or pre-mortem tree vigor. Unfortunately, we were unable to identify either a log length or a diameter threshold at which pine engraver populations no longer selected slash nor successfully reproduced. Instead, we discovered different thresholds of log use in each trial. We concluded that the amount and sizes of slash selected by pine engraver depended largely on the adult (parent) beetle population density. With increased populations, more slash was attacked, smaller diameter logs were selected, and densities of adult beetles within individual logs increased. Similarly, we found that reproductive success within attacked logs was not directly related to log size. However, reproductive success within individual logs corresponded to the population density of adult beetles during a trial. Increased beetle density during a trial resulted in increased attack densities in logs, greater negative density-induced feedback during brood development, and decreased reproductive success per adult.

The importance of density in the population dynamics of bark beetles has been noted in a number of studies (Cole 1978, Wagner et al. 1981, Botterweg 1983, Light et al. 1983, Anderbrant et al. 1985, Anderbrant and Schlyter 1989, Byers 1989, Kirkendall 1989). For example, host selection and attack behavior of a population may change with increased adult beetle density (Cole 1978, Gara et al. 1999, Wallin and Raffa 2002). Within logs, increased density may result in shorter egg galleries (Anderbrant 1990, Lawson et al. 1995, Robins and Reid 1997, Reeve et al. 1998), fewer eggs per egg gallery (Amman 1972, Mills 1986, Hindmarch and Reid 2001), decreased egg density within galleries (Mills 1986, Hindmarch and Reid 2001), and decreased reproductive success per adult parent (Cole 1978, Anderbrant et al. 1985, Anderbrant and Schlyter 1989, Kirkendall 1989, Robins and Reid 1997, Reeve et al. 1998, Hindmarch and Reid 2001).

**Management Implications.** The five trials in this study captured a wider range of pine engraver activity than found in previous studies. Attack densities within our colonized logs ranged from 6 to 594 male beetles per square meter with an average attack density of 200 males per square meter for all attacked logs (93 males per square meter for Arizona trials, 242 males per square meter for Montana trials). Villa-Castillo and Wagner (1996) reported an average density of 40 males per square meter in ponderosa pine logs in Flagstaff, and Sartwell (1970) reported an average of 135 males per square meter for attacked samples and a range of 67–180 males per square meter. Values for other response variables, such as ratio of egg galleries to nuptial chambers, average gallery length, and eggs per female gallery were comparable with those measured in other studies (Schenk and Benjamin 1969, Sartwell 1970, Villa-Castillo and Wagner 1996, Reid and Robb 1999). Thus, our results are representative

of the wider range of pine engraver activity within *Pinus* hosts.

Our results suggest that cutting of slash into shorter pieces (at least down to 60 cm in length) was not effective in deterring colonization or minimizing reproductive success in individual logs. We noted that beetles colonized all three of our log diameters; however, preference for the larger diameters may indicate that a greater proportion of large-diameter logs are suitable hosts. Our results support past recommendations that management efforts concentrate on removing the larger diameter material or rendering the phloem unsuitable. However, we found no support for a particular diameter threshold for material removal as has been given in the past (Wilkinson and Foltz 1982, Parker 1991). Our study demonstrates that pine engraver host selection and subsequent reproductive success within the individual logs is highly influenced by the population density of flying beetles. Thus, the use of different sized slash material will change depending on the overall population level and the amount of material locally available. The implication for slash management is that diameter thresholds for slash disposal will vary with changes in beetle and slash densities. If pine engraver densities increase without a change in available material or if adequate host material is reduced in quantity we might expect to see 1) increased colonization of smaller diameter slash pieces, and 2) increased beetle densities within the attacked logs.

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