

# Species Assemblage Arriving at and Emerging from Trees Colonized by *Ips pini* in the Great Lakes Region: Partitioning by Time Since Colonization, Season, and Host Species

BRIAN H. AUKEMA,<sup>1,2</sup> GREG R. RICHARDS,<sup>1</sup> STEVEN J. KRAUTH,<sup>1,3</sup> AND KENNETH F. RAFFA<sup>1</sup>

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**ABSTRACT** The pine engraver, *Ips pini* (Say), colonizes jack, red, and white pines in the Great Lakes region. Males select suitable hosts, bore through the bark into phloem tissue, and emit aggregation pheromones. Pheromones attract conspecifics, which aid in overcoming tree defenses, and predators, which exploit these cues as kairomones. Sampling was conducted over 2 yr to characterize the assemblage of insects that arrive at and reproduce in trees colonized by *I. pini*, and how this assemblage is partitioned by host species, time after colonization, and seasonal phenology. Over 70 species from three orders were obtained. *I. pini* was most abundant, especially during late summer. The first natural enemy to arrive was *Medetera bistrata* Parent, which came simultaneously with *I. pini*. Other Diptera such as *Lonchaea corticis* Taylor and *Zabrochia polita* Coquillett were also abundant. *Roptrocerus xylophagorum* (Ratzeburg), a late instar parasitoid, arrived last. Its emergence most closely coincided with *I. pini* emergence, whereas the other species emerged substantially after *I. pini*. Host species did not affect total *I. pini* emergence but strongly affected natural enemies. Most *R. xylophagorum* and *Monochamus* spp. emerged from white pine, and most *Z. polita* emerged from red pine. *I. pini* had the highest ratio of emergence to arrival per log. Only the predator *T. dubius* and the parasitoid *R. xylophagorum* showed numerical responses to the number of emerging *I. pini*. Exclusion of insects during the first 2 wk of colonization decreased reproduction of *I. pini* and other wood borers in the spring, but not summer.

**KEY WORDS** host species, natural enemies, resource partitioning, tritrophic interactions, kairomones

THE PINE ENGRAVER, *Ips pini* (Say) (Coleoptera: Scolytidae), is endemic across North America and colonizes weakened or dead pines and sometimes spruce (Anderson 1948, Thomas 1961). Males select suitable hosts, bore into the bark, and construct subcortical “nuptial” chambers in which they mate. While boring, males emit a regionally specific stereoisomeric blend of ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol) and lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) that function as aggregation pheromones (Lanier et al. 1972; Birch et al. 1980; Wood 1982; Seybold et al. 1992, 1993; Miller et al. 1997). *I. pini* is polygynous (Kirkendall 1983), with males typically mating with two or three females (Thomas 1961, Schenk and Benjamin 1969). Females establish ovipositional galleries radiating from the nuptial chamber. Eggs are laid along the gallery, and the larvae tunnel laterally, girdling the sapwood. The brood pu-

pate in oval chambers before the adults chew through the bark and seek new hosts.

*I. pini* cause relatively low economic losses under natural forest conditions, but can be a pest during harvesting operations and in forest plantations. Wisconsin possesses 64 million m<sup>3</sup> of growing stock in jack, *Pinus banksiana* Lamb; red, *P. resinosa* Aiton; and white, *P. strobus* L. pine plantations (Wisconsin Division of Forestry Forest Health Protection Staff 2001). The abundance of brood material after thinning operations or natural windthrow may promote a rapid increase in beetle numbers, allowing healthy trees to be attacked (Thomas 1961, Schenk and Benjamin 1969, Livingston 1979, Gara et al. 1999).

The use of natural enemies as biological control agents is of great interest because the applicability of chemical insecticides is limited by environmental considerations, the marginal economic return of tree production, and the inaccessibility of subcortical insects. The most studied predators in the Great Lakes region are *Thanasimus dubius* (F.) (Coleoptera: Cleridae) and *Platysoma* spp. (Coleoptera: Histeridae) (Herns et al. 1991, Raffa 1991, Erbilgin et al. 2002). Our relatively higher knowledge of these species partly reflects methodological advances. These beetles are eas-

<sup>1</sup> Department of Entomology, 345 Russell Laboratories, 1630 Linden Drive, University of Wisconsin, Madison, WI 53706.

<sup>2</sup> Biometry Program, 345 Russell Laboratories, 1630 Linden Drive, University of Wisconsin, Madison, WI 53706.

<sup>3</sup> Insect Research Collection, 346 Russell Laboratories, 1630 Linden Drive, University of Wisconsin, Madison, WI 53706.

ily sampled using funnel traps, which are ideal for capturing hard-bodied insects (Lindgren 1983), and they respond to synthetic pheromone baits (Raffa and Dahlsten 1995; Aukema et al. 2000a,b).

Although behavioral responses of some predators to *I. pini* pheromones have been studied in detail, interactions among *I. pini* and other associates are less well understood. Relatively little is known about the diversity of insects arriving at or reproducing in logs colonized by *I. pini* or how host tree species affects this assemblage or its performance (Erbilgin and Raffa 2000). Furthermore, little is known about arrival patterns to logs after pheromone production by the primary herbivore ceases, when natural enemies may arrive and prey on life stages other than adults. As bark beetle broods and natural enemies develop, competitive or predatory balances within the tree may also change. We also lack data on how the assemblage of natural enemies may change throughout the flight season. Likewise, little is known about natural enemy developmental times, which could affect *I. pini* population dynamics within seasons, among years, and among pine species.

The objectives of this research were to 1) characterize the species assemblage responding to and emerging from host trees colonized by *I. pini* in the Great Lakes region; 2) evaluate the effects of host tree species, time since colonization, and seasonal phenology on the composition and numbers of this complex; and 3) assess the impacts of these associates by conducting exclusion experiments, modeling within-plant development, and estimating ratios of emerging to arriving insects on a per log basis.

## Materials and Methods

**Temporal and Host Tree Partitioning.** Jack, red, and white pine trees of  $\approx 20$  cm in diameter at breast height (dbh) were removed from a mixed plantation near Mazomanie, WI, cut into 1-m lengths, and taken to the laboratory. Four to eight male *I. pini* from a laboratory colony reared on similar host trees were placed evenly along each section, covered with gelatin capsules, and allowed to bore for 24 h. The colonized logs were taken to two neighboring red pine plantations ( $\approx 45$  yr) in Sauk County, Wisconsin (latitude N 43° 33.41', longitude W 89° 50.61'; latitude N 43° 33.43', longitude W 89° 50.61'). The logs were deployed in groups containing one log from each species, with 10–15 m between each log and a minimum of 100 m between groups. In 2000, three 1-m sections were collected from each of four jack, red, and white pines, and in 2001 seven 1-m sections were collected from one red and one white pine tree each. The two sites received eight and four groups in 2000, and four and three, respectively, in 2001.

Insects arriving at the infested logs were sampled with fiberglass screens that were sprayed with Tangle-Trap (The Tanglefoot Co., Grand Rapids, MI) and placed on the logs, and 12-funnel traps (Lindgren 1983). A 2 by 2-cm piece of Revenge bug strip (18.6% 2-2-dichlorovinyl dimethyl phosphate; Roxide Inter-

national, Inc., New Rochelle, NY) was placed in each cup to kill arriving insects and prevent destruction of trap contents by predators. The cups were emptied and the screens were replaced at approximate 3-d intervals for six or seven sample periods. At the end of sampling, the logs were taken back to the laboratory and placed in 30-cm-diameter construction Sonotubes (Potter Form and Tie, Co., Madison, WI), which served as insect rearing chambers. Collections were performed three times per week for 204 d. The logs were kept within the tubes for at least 298 d, at which time all insects that had emerged but not reached the collection cups were collected. Dissection of a subset of logs revealed no distinguishable insects that had died before emergence.

This experiment was performed three times: 21 July–16 August 2000, 31 May–26 June 2001, and 2 August–27 August 2001. Jack pine was not used in 2001, and only screen traps were used in the spring of 2001.

A Poisson generalized linear mixed model was used to examine the fixed effect of tree species on total arrival and emergence of each species on a per log basis, by using a penalized quasi-likelihood approach, glmmPQL (Breslow and Clayton 1993, Venables and Ripley 2002) implemented in R (Ihaka and Gentleman 1996). The total number of insects arriving at the log was the sum of the screen and funnel trap catches. Groups nested within each plantation were used as random effects. The suitability of these models was confirmed by examination of residual plots.

To examine the effect of time on the arrival and reproduction of insects, we standardized all values to a constant surface area of bark. Although small variations in log size did not affect total reproduction ( $P > 0.05$  for most species examined), standardizing both arrival and reproduction facilitates comparisons among them. The average catch per day per 10 dm<sup>2</sup> was centered on each sample period. Arrival and emergence curves were then constructed using regression splines on  $\sqrt{y}$  transformed data to satisfy assumptions of normality (Venables and Ripley 2002).

The relative reproductive increase (ratio of emergence to arrival) and emergence models (functions of various insects with arriving and emerging associates) were examined using the data set from summer 2000. We focused our analyses on that year because  $>90\%$  of *I. pini* and 70% of all insects sampled were obtained then, there were significant year  $\times$  experiment interactions ( $P < 0.05$ ), and a portion of 2001 did not include funnel traps. All estimates of reproductive increase should be viewed as of relative value only: although emergence is standardized by containerization, trapping efficiencies surely vary among insect species. Moreover, emergence values provide full censuses of brood per female for insects such as *Ips* spp. that construct single ovipositional galleries, but only a subset for species that oviposit in multiple trees or parts of trees.

We evaluated relationships of insect emergence to the arrival and emergence of other species on a per-log basis using multiple regression. Because the number of administered *I. pini* that actually entered the logs

varied slightly (range of four to eight) among replicates, we included the number of initial borers as a variable to test whether this could potentially affect recruitment and emergence. Again, predictors were standardized to the total number of insects arriving and reproducing per 10 dm<sup>2</sup> for a given log. Models were constructed using backwards elimination from a full model comprising the most abundant insects. Species that showed significant host tree effects were examined with a model restricted to that host tree.

**Effect of Natural Enemies on Reproduction of *I. pini*.** We conducted an exclusion screening experiment to examine how temporarily restricting access to logs infested with *I. pini* affected the reproduction of *I. pini* and associates. One red and one white pine ( $\approx 20$  cm dbh) were felled in Mazomanie, WI, and cut into 23-cm logs. Each log received four male beetles on 25 May 2001 and then eight females the next day to simulate an active infestation. The logs were grouped into quartets of two red pine and two white pine logs. Each pair of the same species in a quartet came from adjacent positions in the tree.

One log in each pair was randomly selected and enclosed in aluminum screening. This screening was stapled to a lengthwise slice of foam pipe insulation wrapped around the top and bottom of the log, so the screen did not touch the log and predators could not oviposit into the bark. On 27 May, four quartets were deployed in each of the two red pine plantations as described above. Each quartet was arranged in a random square at 2-m spacing in a site, and each group was separated by a minimum of 50 m. Seven cm wide fiberglass screening sprayed with Tangle-Trap was wrapped around the middle of each log and held in place with a binder clip. The screens were sampled 31 May, 4 June, 8 June, 12 June, 16 June, and 20 June.

On 8 June, 12 d postdeployment, the aluminum screening was moved to the other bolt in each pair, thus restricting access for the second 12 d of colonization. On 20 June, the bolts were retrieved from the field. All screening was removed, and the logs were placed in 19-liter rearing cans. Black cloth and a tight fitting mesh lid sealed the cans. Insects were collected as they emerged into glass emergence jars, three times per week.

This experiment was conducted a second time, with field deployment from 26 July–20 August, by using similar sample intervals and 12-d exclusion intervals.

The total numbers of insects reared from each log were analyzed with a Poisson generalized linear mixed model, again by using group within site as a random effect and a penalized quasi-likelihood approach (Breslow and Clayton 1993). Fixed effect factors were tree species (red or white pine), time of exclusion (first or second 12-d interval), and their interaction.

## Results

**Overall Diversity and Seasonal Trends.** A diverse group of more than 70 insect species from three orders was obtained arriving to or emerging from the logs colonized with *I. pini* (Aukema 2003). Of these, 27

emerged from logs after time intervals consistent with known developmental periods, indicating reproduction within this habitat. A summary of the insects obtained and their likely association with the colonized logs is given in Table 1. This assemblage includes herbivores, which compete with *I. pini* for phloem resources, fungivores, predators, and parasitoids.

There were significant year  $\times$  season and within-year interactions for most insects, including *I. pini* ( $P < 0.05$ ). Therefore, relationships of arrival and emergence with host tree species were analyzed separately by year and are shown for 2000 and 2001 in Tables 2 and 3, respectively. Seventy percent of all insects were obtained in 2000. Overall, the primary herbivore, *I. pini*, was the most abundant, with a total of 769 arriving at and 7,781 emerging from infested logs (Tables 2 and 3). In 2001, when we performed both spring and summer assays, there was a significant effect due to phenology. Therefore, relationships of arrival and emergence with host tree species were analyzed separately by segment of the flight season and are shown for early spring and late summer in Table 3A and B, respectively. *I. pini* were more abundant in the summer than spring, with 91.2% of 1,879 *I. pini* emerging from logs deployed in the field during the summer trial (Table 3).

Overall, a total of 3,731 insects other than *I. pini* were obtained arriving at the infested logs, and 1,447 emerged from the logs in the laboratory (Tables 2 and 3). Funnel traps were most effective for sampling arriving hard-bodied insects (such as Coleoptera), and sticky screens were more effective for trapping soft-bodied insects (primarily Diptera and Hymenoptera).

**Effect of Host Species on Composition of Arriving Insects.** Statistically significant relationships ( $P < 0.05$ ) due to host tree species were observed for 26 species (Tables 2 and 3). *I. pini* were more attracted to conspecifics tunneling in white pine than red or jack pine, with a 1.7 times difference among these host species in 2000 (Table 2). This effect was significant among females but not males. The southern pine sawyer, *Monochamus titillator* (F.), the second most abundant phloeophagous herbivore, was obtained arriving at white and red pine more than jack pine (Table 2). Other herbivores arriving at the pines over both years included *Ips grandicollis* (Eichhoff) (5), *Dendroctonus valens* LeConte (12), *Dryocoetes autographus* (Ratzeburg) (19), *Dryophthorus americanus* Bedel (18), *Monochamus carolinensis* (Olivier) (3), *Monochamus scutellatus* (Say) (1), *Orthotomicus caelatus* (Eichhoff) (2), and *Orthosoma brunneum* (Forster) (9).

Five species of predacious Cleridae were captured arriving at the logs, including *Enoclerus muttkowki* (Wolcott) (7), *Enoclerus nigrifrons* (Say) (22), *Enoclerus nigripes* (Say) (1), *Thanasimus undulatus* (Say) (1), and *Zenodosus sanguineus* (Say) (4). The red-bellied checkered beetle, *Thanasimus dubius* (F.), was the most prevalent, with  $\approx 4$  times more arriving at white and red pine than jack pine (Table 2). Other coleopteran predators included *Platysoma cylindrica* (Paykull) (7), *Platysoma parallelum* (Say) (2), *Cor-*

Table 1. Insects obtained arriving to or emerging from logs of jack, red, and white pine colonized by *I. pini* in the summers of 2000 and 2001 in red pine plantations in Wisconsin

Order/Family	Insect	Association	References <sup>a</sup>
Coleoptera			
Scolytidae	<i>I. pini</i>	Phloeophagous	1–3
	<i>I. grandicollis</i>	Phloeophagous	3–5
	<i>D. valens</i>	Phloeophagous on lower stem, roots	3
	<i>D. autographus</i>	Phloeophagous on lower stem, roots	6, 7
	<i>G. materarius</i>	Fungivorous; subcortical in stumps	7, 8
	<i>Hylastes</i> spp.	Root herbivore	3
	<i>O. caelatus</i>	Fungivorous; subcortical in stumps	3, 7, 9
Cerambycidae	<i>A. pusillus</i>	Phloeophagous	8 <sup>b</sup>
	<i>M. titillator</i>	Phloeophagous early, then xylophagous	3, 9–11
	<i>O. brunneum</i>	Phloeophagous, decaying logs	3, 12
Curculionidae	<i>D. americanus</i>	Under bark of logs	3, 13–15
	<i>Pissodes</i> spp.	Phloeophagous	3, 8, 9, 16, 17
Carabidae	<i>P. pallens</i>	Predator	8 <sup>b</sup>
Cleridae	<i>E. nigrifrons</i>	Predator of adult and larval bark beetles	8, 18, 19
	<i>E. nigripes</i>	Predator of adult and larval bark beetles	3, 7, 8
	<i>E. muttkowski</i>	Predator of adult and larval bark beetles, weevils, and wood borers	17
	<i>T. dubius</i>	Predator of adult and larval bark beetles	3, 8, 20, 21
Histeridae	<i>P. cylindrica</i>	Predators under bark	8, 9
	<i>P. parallelum</i>	Predators under bark	8, 9
Nitidulidae	<i>E. labilis</i>	Attracted to flowers and sap flow	22 <sup>a</sup> , 23, 24 <sup>b</sup>
Silvanidae	<i>S. bidentatus</i>	Under bark of logs	8, 13
Staphylinidae	Staphylinidae	Fungivores and predators	3, 7
Tenebrionidae	<i>C. parallelus</i>	Fungivore; larvae are egg predators	8, 25, 26
Trogossitidae	<i>T. marginatus</i>	Predators under bark	27
	<i>T. collaris</i>	Predators under bark	8, 9
Diptera			
Asilidae	Asilidae	Generalist predators; bark surface	3, 28
Clusiidae	<i>C. johnsoni</i>	Saprophagous/fungivorous in moist, rotting wood	29
	<i>C. melanostoma</i>	Saprophagous/fungivorous in moist, rotting wood	29
Dolichopodidae	<i>M. bistrata</i>	Larval predators under bark	3, 8, 30, 31
	<i>G. politus</i>	Predator under moist bark	32
Lonchaeidae	<i>L. corticis</i>	Necrophagous, predator, possibly parasitic on <i>Pissodes strobi</i> Peck	7, 33–35
Mycetophilidae	<i>Sceptonia</i> spp.	Larvae associated with fungi	36
Stratiomyidae	<i>Z. polita</i>	Scavenger and predator in stumps	3, 7, 37, 38
Hymenoptera			
Braconidae	<i>Coeloides</i> sp. <sup>c</sup>	Bark beetle parasitoid	39–42
	<i>Spathius</i> sp. <sup>c,d</sup>	Bark beetles parasitoid	40, 43–45
Pteromalidae	<i>Rhopalicus pulchripennis</i> <sup>c</sup>	Bark beetle parasitoid	46, 47
	<i>R. xylophagorum</i>	Parasitoid of late instar bark beetles	48–51
	<i>T. tibialis</i>	Parasitoid of adult <i>Ips</i> , <i>Orthotomicus</i> , <i>Pityophthorus</i> spp.	47, 52–53

Only species of which five or more were captured, or those with definite associations with *I. pini*, are listed. For a list of all species, including Hymenoptera, see Aukema (2003).

<sup>a</sup> 1 (Thomas 1961); 2 (Schenk and Benjamin 1969); 3 (Drooz 1985); 4 (Ayres et al. 2001); 5 (Erbilgin and Raffa 2001); 6 (Johansson et al. 1994); 7 (Thomas 1955); 8 (Howden and Vogt 1951); 9 (Savely 1939); 10 (Dodds et al. 2001); 11 (Aly and Hain 1985); 12 (Yanega 1996); 13 (Downie and Amett 1996); 14 (Blatchley and Leng 1916); 15 (Kissing 1964); 16 (Graham 1925); 17 (Boucher et al. 2001); 18 (Mawdsley 1999); 19 (Aukema and Raffa 2000); 20 (Thatcher and Pickard 1966); 21 (Mignot and Anderson 1969); 22 (Schroeder and Weslien 1994); 23 (Parsons 1943); 24 (Schroeder 1996); 25 (Smith and Goyer 1980); 26 (Goyer and Smith 1981); 27 (Lescher 2002); 28 (Wood 1987); 29 (Caloren and Marshall 1971); 30 (Williamson 1971); 31 (Bickell 1985); 32 (Robinson and Vockerth 1987); 33 (Hulme 1990); 34 (Hulme 1989); 35 (MacAloney 1930); 36 (Laffoon 1965); 37 (Kraft and Cook 1961); 38 (James 1965); 39 (Kenis 1997); 40 (Townes 1969); 41 (Petterson et al. 2001); 42 (Mason 1978); 43 (Sullivan et al. 1997); 44 (Langor 1991); 45 (Matthews 1970); 46 (Espelie et al. 1990); 47 (Burks 1979); 48 (Samson 1984); 49 (Petterson et al. 2000); 50 (Sullivan et al. 2000); 51 (Grissell 1979); 52 (Senger and Roitberg 1992); 53 (Rice 1968).

<sup>b</sup> Reference indicates different species within same genus.

<sup>c</sup> Collected from white pine infested with *I. pini* in August 2002, in red pine plantation in Mazomanie, WI. Collections were not part of experiments described in this article.

<sup>d</sup> Reared from *I. pini* larvae.

*ticeus parallelus* (Melsheimer) (3), *Grynocharis quadrilineata* (Melsheimer) (2), *Tenebroides* spp. (predominantly *marginatus* Beauvois) (5), two cucujids, and 24 staphylinids not identified to species. Among Diptera, the most prevalent predator was the dolichopodid *Medetera bistrata* (Parent). *M. bistrata* showed slightly higher arrival rates on white than red pine in the spring of 2001 (Table 3A), but otherwise showed no preferences among the three host species infested with *I. pini* (Tables 2 and 3B). The dolichopodid *Gymnopternus politus* Loew was present in lower

numbers than *M. bistrata*, in an approximate 1:4 ratio, and showed no host tree preferences (Table 2). Approximately 20 *Zabrachia polita* Coquillett were captured landing on each red pine log in the summer of 2000, whereas only 15 total were obtained the following year (Table 2). *Z. polita* preferred red pine over jack or white pine. Host tree species did not affect landing rates by the other Diptera sampled in high numbers in the summer of 2000: *Clusoides albimana* Meigen, *Clusoides melanostoma* (Loew) (Diptera: Clusiidae), and *Sceptonia* spp. (Diptera: Mycetophili-



**Table 2.** Mean  $\pm$  SEM numbers of insects captured (A) arriving at and (B) emerging per log from jack, red, and white pine infested with *I. pini* and deployed in a red pine plantation from 21 July–16 August 2000

Order/Family	Insect	Total <sup>a</sup>	Jack <sup>b</sup>	Red <sup>b</sup>	White <sup>b</sup>	$F_{2,22}$	<i>P</i>
<b>A. Arrival</b>							
Coleoptera							
Scolytidae	<i>I. pini</i>	537	11.58 $\pm$ 2.04b	14.00 $\pm$ 1.12b	19.17 $\pm$ 1.41a	5.31	0.0131
	Males	226	4.83 $\pm$ 0.88	6.00 $\pm$ 0.86	8.00 $\pm$ 0.95	3.05	0.0676
	Females	311	6.75 $\pm$ 1.29b	8.00 $\pm$ 0.77ab	11.17 $\pm$ 1.12a	4.04	0.0320
Cerambycidae	<i>M. titillator</i>	29	0.08 $\pm$ 0.08b	1.08 $\pm$ 0.31a	1.25 $\pm$ 0.30a	10.17	0.0007
Cleridae	<i>T. dubius</i>	74	0.67 $\pm$ 0.43b	2.67 $\pm$ 0.62a	2.83 $\pm$ 0.68a	19.04	0.0000
Trogossitidae	<i>Tenebroides</i> spp. <sup>c</sup>	28	0.50 $\pm$ 0.19	0.75 $\pm$ 0.28	1.08 $\pm$ 0.26	1.61	0.2224
Diptera							
Clusiidae	<i>Clusiodes</i> spp. <sup>c</sup>	405	10.83 $\pm$ 3.64	14.08 $\pm$ 4.68	8.83 $\pm$ 3.35	2.69	0.0901
Dolichopodidae	<i>M. bistriata</i>	1,076	19.75 $\pm$ 4.91	33.00 $\pm$ 3.23	36.92 $\pm$ 6.35	3.41	0.0515
	<i>G. politus</i>	242	8.25 $\pm$ 2.17	5.08 $\pm$ 1.08	6.83 $\pm$ 1.60	1.57	0.2296
Mycetophilidae	<i>Sceptonia</i> spp.	146	5.50 $\pm$ 1.56	4.00 $\pm$ 0.67	2.67 $\pm$ 0.41	2.64	0.0939
Stratiomyidae	<i>Z. polita</i>	468	6.67 $\pm$ 1.14c	19.83 $\pm$ 2.98a	12.50 $\pm$ 1.77b	10.92	0.0005
Hymenoptera							
Pteromalidae	<i>R. xylophagorum</i>	20	0.33 $\pm$ 0.19b	0.08 $\pm$ 0.08b	1.25 $\pm$ 0.43a	6.33	0.0067
	<i>T. tibialis</i>	42	0.42 $\pm$ 0.34b	0.92 $\pm$ 0.23ab	2.17 $\pm$ 0.46a	4.97	0.0165
<b>B. Emergence</b>							
Coleoptera							
Scolytidae	<i>I. pini</i>	5,902	165.00 $\pm$ 31.72	131.83 $\pm$ 19.43	195.00 $\pm$ 26.10	1.55	0.2354
	Males	2,289	70.50 $\pm$ 13.51	52.33 $\pm$ 7.62	67.92 $\pm$ 7.95	1.16	0.3318
	Females	3,613	94.50 $\pm$ 18.45	79.50 $\pm$ 11.98	127.08 $\pm$ 18.53	2.18	0.1373
Cerambycidae	<i>Monochamus</i> spp.	91	0.17 $\pm$ 0.11b	0.50 $\pm$ 0.23b	6.92 $\pm$ 0.91a	71.28	0.0000
Cleridae	<i>T. dubius</i>	40	1.42 $\pm$ 0.36	0.83 $\pm$ 0.44	1.08 $\pm$ 0.29	0.78	0.4723
Diptera							
Dolichopodidae	<i>M. bistriata</i>	82	0.92 $\pm$ 0.36	4.33 $\pm$ 1.96	1.58 $\pm$ 0.63	2.99	0.0712
Lonchaeidae	<i>L. corticis</i>	228	3.50 $\pm$ 1.33b	12.75 $\pm$ 4.44a	2.75 $\pm$ 1.12b	4.19	0.0287
Stratiomyidae	<i>Z. polita</i>	55	0.00 $\pm$ 0.00b	4.42 $\pm$ 1.96a	0.17 $\pm$ 0.11b	10.80	0.0005
Hymenoptera							
Pteromalidae	<i>R. xylophagorum</i>	34	0.00 $\pm$ 0.00b	0.00 $\pm$ 0.00b	2.83 $\pm$ 0.96a	34.96	0.0000

Means followed by the same letter across a row are not significantly different at  $\alpha = 0.05$ . Statistical tests are limited to those species for which we obtained a minimum of 20 individuals.

<sup>a</sup> Total number of insects from all logs ( $N = 3$  host trees  $\times$  12 replicates).

<sup>b</sup> Jack pine logs were  $33.7 \pm 1.3$  dm<sup>2</sup>, red pine  $32.6 \pm 0.8$  dm<sup>2</sup>, and white pine  $37.2 \pm 1.6$  dm<sup>2</sup>.

<sup>c</sup> *C. johnsoni* and *C. melanostoma*.

dae) (Table 2). Low numbers of *Lonchaea corticis* Taylor (12) and asilids (18) were also sampled arriving to the logs.

The most prevalent parasitic Hymenoptera were the pteromalids *Roptrocercus xylophagorum* (Ratzeburg) and *Tomicobia tibialis* Ashmead. These insects were most abundant in summer 2000 and oriented most strongly to colonized white pine (Tables 2 and 3). On average, we captured one *R. xylophagorum* on each white pine log and two *T. tibialis* on each white pine log, all on sticky screens. Other Hymenoptera arriving at pine logs included bethylids such as *Disomphalus apertus* Kieffer (1) and *Pristocera armifera* (Say) (1); braconids such as *Euphoriella* sp. (1), *Distatrix* spp. (2), and *Apanteles* sp. (1); diapiids such as *Aclista* spp. (3), *Basalys* sp. (1), *Belyta* spp. (3), and *Pantoclis* spp. (2); and ichneumonids such as *Hyposoter pilosulus* (Provancher) (1), *Phobocampe bicin-gulata vernalis* (Viereck) (1), *Gnotus* sp. (1), *Arotrepes pusillus* (Cresson) (1), *Lissonota acrobasis* Ashmead (1), *Mesochorus curvulus* Thomson (1), *Demopheles corruptor matorus* (Provancher) (1), *Eusterinx bispinosa* Stroble (1), and *Stenomacrus ulmicola* (Ashmead) (2). Two siricids, *Tremex columba* (L.), were also sampled.

**Effect of Host Species on Composition of Emerging Insects.** Although *I. pini* were most attracted to conspecifics tunneling in white pine, host tree species had

no effect on the total number of *I. pini* that emerged. The relative reproductive increase of *I. pini* (ratio of emergence to arrival per log) ranged from 9.4 in red pine to 14.2 in jack pine (Table 4). The relative rate of increase in white pine was  $\approx 34\%$  higher for females than males. Between 112 and 195 *I. pini* emerged from each log in the July and August trials, but fewer than 20 *I. pini* emerged per log in the May trial of 2001. More species of scolytids were reared from logs in this spring trial. *Ips grandicollis* (Eichhoff), *Gnathotrichus materarius* (Fitch), and *Orthotomicus caelatus* (Eichhoff) were present in low numbers (Table 3A), and their reproduction did not vary among tree species. More *Monochamus* spp. emerged from white pine than jack or red pine in summer 2000, with almost seven per log (Table 2). Their relative reproductive success in white pine was double that in red pine, but only one half that of *I. pini* (Table 4). High numbers of *Acanthosinus pusillus* Kirby emerged from logs in spring 2001 (Table 3A), although reproduction was highly heterogeneous: 138 of 189 emerged from two red pine logs. The most prevalent subcortical borers in the spring of 2001 were *Pissodes* spp. weevils, with an average of 46 per white pine log and 13 per red pine (Table 3A). Other emerging herbivores included *Dryophthorus americanus* (1), *Dryocoetes autographus* (1), *D. valens* (1), and *Monochamus notatus* (Drury) (1), and *Rhagium in-quisitor* (L.) (2).

Table 3. Mean ± SEM numbers of insects per log captured at and emerging from red and white pine infested with *I. pini* and deployed in a red pine plantation in (A) spring and (B) summer 2001

Order/Family	Insect	Arrival				Emergence					
		Total <sup>a</sup>	Red <sup>b</sup>	White <sup>c</sup>	F <sub>1,6</sub>	P	Total <sup>a</sup>	Red <sup>b</sup>	White <sup>c</sup>	F <sub>1,6</sub>	P
<b>A. Early spring (30 May–26 June)</b>											
Coleoptera											
Scolytidae	<i>I. pini</i>	0	0.00 ± 0.00	0.00 ± 0.00	NA	NA	20.43 ± 14.26	3.14 ± 2.82	3.32	0.1182	
	Males	0	0.00 ± 0.00	0.00 ± 0.00	NA	NA	11.71 ± 8.50	1.71 ± 1.55	3.04	0.1320	
	Females	0	0.00 ± 0.00	0.00 ± 0.00	NA	NA	8.71 ± 5.80	1.43 ± 1.27	3.50	0.1104	
	<i>I. grandicollis</i>	0	0.00 ± 0.00	0.00 ± 0.00	NA	NA	2.86 ± 2.23	0.14 ± 0.14	3.70	0.1027	
	<i>C. maderatus</i>	0	0.00 ± 0.00	0.00 ± 0.00	NA	NA	0.43 ± 0.30	4.43 ± 4.26	2.75	0.1481	
	<i>O. caelatus</i>	1	0.14 ± 0.14	0.00 ± 0.00	NA	NA	2.43 ± 1.78	0.29 ± 0.18	2.95	0.1369	
Cerambycidae	<i>A. pusillus</i>	0	0.00 ± 0.00	0.00 ± 0.00	NA	NA	20.71 ± 12.89	6.29 ± 3.30	1.72	0.2375	
Curculionidae	Pissodes spp.	42	0.29 ± 0.18	5.71 ± 2.99	8.44	0.0272	13.29 ± 5.83	45.86 ± 16.02	4.80	0.0709	
Cleridae	<i>Enoclerus</i> and <i>Thanasimus</i> spp.	2	0.29 ± 0.18	0.00 ± 0.00	NA	NA	1.43 ± 0.30	0.71 ± 0.36	2.57	0.1600	
Tenebrionidae	<i>C. parallelus</i>	0	0.00 ± 0.00	0.00 ± 0.00	NA	NA	3.29 ± 3.29	0.00 ± 0.00	4.00	0.0923	
Diptera											
Dolichopodidae	<i>M. bistriata</i>	389	34.71 ± 10.28	20.86 ± 6.49	8.60	0.0262	0.86 ± 0.86	0.00 ± 0.00	NA	NA	
	<i>C. politus</i>	66	6.00 ± 3.41	3.43 ± 1.66	2.74	0.1490	0.00 ± 0.00	0.00 ± 0.00	NA	NA	
<b>B. Late summer (02 August–27 August)</b>											
Coleoptera											
Scolytidae	<i>I. pini</i>	232	11.29 ± 3.10	21.86 ± 5.67	6.00	0.0498	132.43 ± 31.33	112.43 ± 25.15	0.25	0.6338	
	Males	91	4.86 ± 1.56	8.14 ± 2.10	2.09	0.1989	50.00 ± 11.50	40.71 ± 10.22	0.37	0.5670	
	Females	141	6.43 ± 1.74	13.71 ± 4.14	5.87	0.0517	82.43 ± 19.87	71.71 ± 15.09	0.19	0.6801	
Cleridae	All species	44	3.43 ± 1.25	2.86 ± 1.01	0.13	0.7328	2.14 ± 1.18	1.14 ± 0.55	0.56	0.4831	
	<i>T. dubius</i>	26	2.43 ± 1.15	1.29 ± 0.52	0.95	0.3670	2.14 ± 1.18	1.14 ± 0.55	0.56	0.4831	
	<i>C. parallelus</i>	4	0.43 ± 0.30	0.14 ± 0.14	NA	NA	1.86 ± 1.86	0.57 ± 0.30	0.35	0.5756	
Diptera											
Dolichopodidae	<i>M. bistriata</i>	390	29.57 ± 6.50	26.14 ± 9.31	0.09	0.7754	1.29 ± 0.42	2.71 ± 0.94	2.05	0.2024	
	<i>C. politus</i>	20	1.00 ± 0.58	1.86 ± 0.59	5.08	0.0651	0.00 ± 0.00	0.00 ± 0.00	NA	NA	
	<i>L. corticis</i>	0	0.00 ± 0.00	0.00 ± 0.00	NA	NA	9.86 ± 3.11	1.86 ± 0.96	48.60	0.0004	

Statistical tests are limited to those species for which we obtained a minimum of 18 individuals. NA, not applicable.

<sup>a</sup> Total number of insects from all logs (N = 2 host trees × 7 replicates).

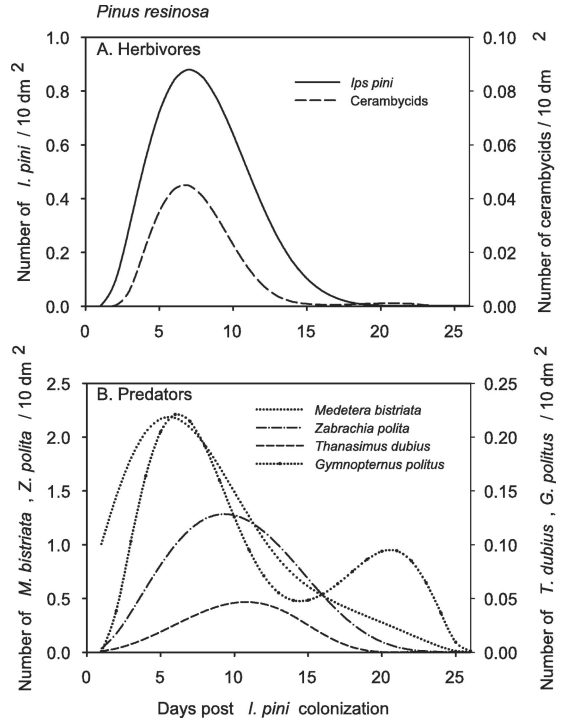
<sup>b</sup> Red pine logs were 50.8 ± 2.4 dm<sup>2</sup> in (A) spring experiment and 55.5 ± 1.0 dm<sup>2</sup> in (B) summer experiment; white pine logs were 53.0 ± 2.1 dm<sup>2</sup> in (A) spring experiment and 51.1 ± 1.9 dm<sup>2</sup> in (B) summer experiment

**Table 4.** Effect of host tree species on relative rate of increase (ratio of emergence to arrival) per log of *I. pini* and associates in red pine plantations, Wisconsin

Insect	Jack	Red	White
Herbivores			
<i>I. pini</i>	14.24	9.42	10.17
Males	14.59	8.72	8.49
Females	14.00	9.94	11.38
<i>Monochamus</i> spp.	2.00	0.43	4.88
Predators and parasitoids			
<i>T. dubius</i>	2.12	0.31	0.38
<i>M. bistrriata</i>	0.05	0.13	0.04
<i>L. corticis</i>	10.50	25.50	16.50
<i>Z. polita</i>	0.00	0.22	0.01
<i>R. xylophagorum</i>	0.00	0.00	2.27

The relative rate of increase of *T. dubius* was highest in jack pine, where the emergence/arrival ratio was 2.1 (Table 4). Other emerging beetles included *T. undulatus* (1), *E. nigripes* (3), *P. cylindrica* (8), *Silvanus bidentatus* (F.) (3), *Corticus parallelus* (Melsheimer) (7), and *Plochionus pallens* (F.) (10). The highest relative rate of increase for all predators was 25.5, for the dipteran *L. corticis* in red pine. *L. corticis* also had emergence/arrival ratios >10 per log in the other hosts, in contrast to *M. bistrriata* and *Z. polita*, which had relative reproductive ratios <1 in all pine species. The highest mean numbers of *M. bistrriata* (4), *Z. polita* (4), and *L. corticis* (13) emerged from colonized red pine logs (Table 2). Of parasitoids, *R. xylophagorum* had higher emergence and relative reproductive increase in white pine than red or jack pine in 2000 (Table 2). On average, three *R. xylophagorum* emerged from each log (Table 2). Three *T. tibialis*, all from white pine, were reared in 2000.

**Sequence of Arrival to and Emergence from Colonized Logs.** The various insect species associated with *I. pini* showed distinct arrival sequences relative to the time of colonization by the primary herbivore (Figs. 1-3). Because of host tree effects on the large number

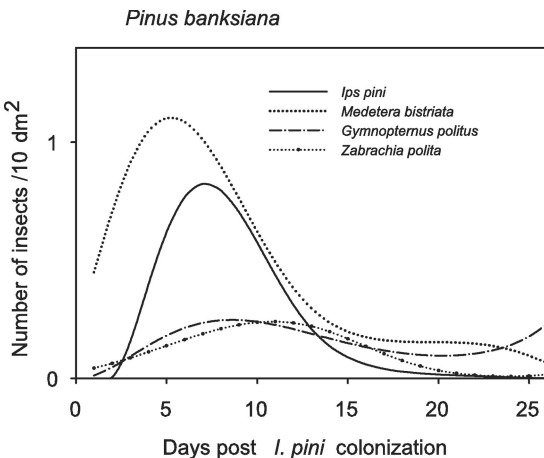


**Fig. 2.** Arrival of (A) herbivores and (B) predators to *P. resinosa* colonized with *I. pini* and deployed in a red pine plantation for 25 d. The bolts were colonized on day 0 and taken to the plantation on day 1.

of species arriving at red and white pines (Figs. 2 and 3), we display herbivores, predators, and parasitoids on separate panels to facilitate visual comparisons. The first responders to all logs were *I. pini*, *M. bistrriata*, *G. politus*, and *T. dubius*. In particular, most *M. bistrriata* typically were captured before most *I. pini*. The majority of cerambycids arrived during the first 12 d after field deployment. *Z. polita* began to arrive in red pine during the first 12 d after colonization of the logs by *I. pini* (Fig. 2B) and *R. xylophagorum* began to arrive ≈2 wk after colonization, in white pine (Fig. 3C).

Figure 4A-C shows the emergence patterns of insects reared from the logs. *I. pini* began to emerge at ≈30 d. Peak *M. bistrriata* and *L. corticis* emergence occurred at ≈55-60 d, although there was a more extended emergence pattern for *L. corticis* than other species. *Z. polita* exhibited an apparently bimodal emergence pattern in red pine, with a small peak at ≈60 d and a larger one after 80 d (Fig. 4B). The parasitoid *R. xylophagorum* emerged shortly after *I. pini*, when present in white pine (Fig. 4C). Most *T. dubius* emerged from the logs after 80 d. All cerambycids emerged after 100 d.

**Effect of Numbers of Arriving and Emerging Associates of *I. pini* on Insect Emergence.** The emerging numbers of clerids and *R. xylophagorum* were good predictors of the number of emerging *I. pini*:  $y = 31.54 + 39.63 \text{ clerids} + 10.85 \text{ pteromalids}$  ( $F_{2,33} = 11.74, P < 0.0001, R^2 = 0.38$ ). Similarly, the number of emerging



**Fig. 1.** Arrival of *I. pini* and predators to *P. banksiana* colonized with *I. pini* and deployed in a red pine plantation for 25 d. The bolts were colonized on day 0 and taken to the plantation on day 1.

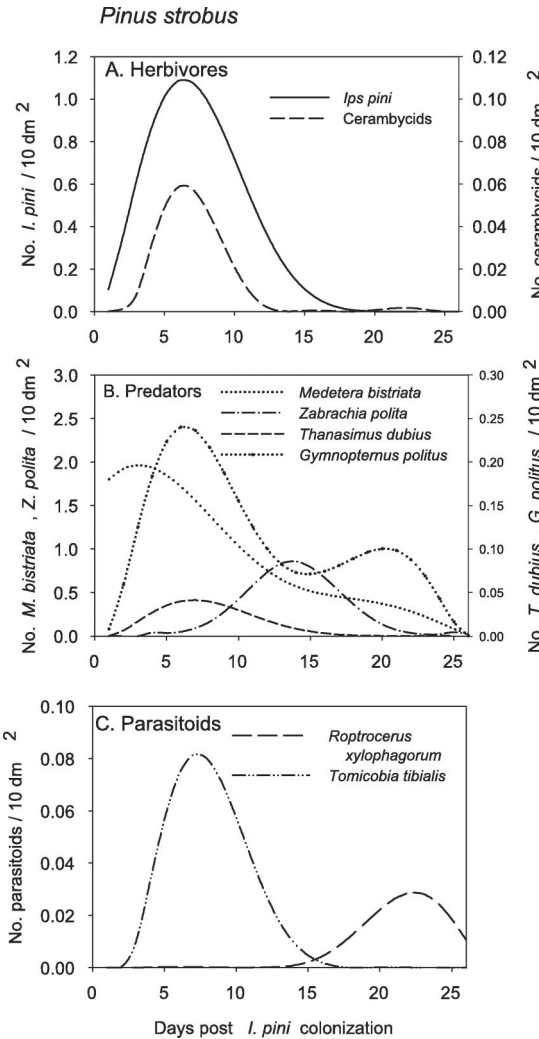


Fig. 3. Arrival of (A) herbivores, (B) predators, (C) parasitoids to *P. strobus* colonized with *I. pini* and deployed in a red pine plantation for 25 d. The bolts were colonized on day 0 and taken to the plantation on day 1.

*T. dubius* could be predicted by the number of emerging *I. pini*:  $y = -0.068 + 0.008 I. pini$  ( $F_{1,34} = 17.18, P = 0.0002; R^2 = 0.32$ ). Within white pine, the number of emerging *R. xylophagorum* could be predicted by the number of arriving *I. pini*:  $y = 0.390 + 0.023 I. pini$  ( $F_{1,10} = 17.14, P = 0.0201, R^2 = 0.59$ ).

**Exclusion Screening Experiments.** *O. caelatus* and *I. pini* comprised 80% of the 4,893 insects that emerged from the logs in the exclusion screening experiment conducted in the spring (Table 5A). Exclusion of insects during the first 2 wk after the administered *I. pini* colonized the logs decreased reproduction of *I. pini* by 37%, *Dryocoetes autographus* (Ratzeburg) by 78%, and *O. caelatus* by 87% (Table 5A). The most prevalent predators were *Corticteus parallelus* (Melsheimer), *Platysoma* spp., and *T. dubius*. More *C. parallelus* emerged in red than white pine, although there was

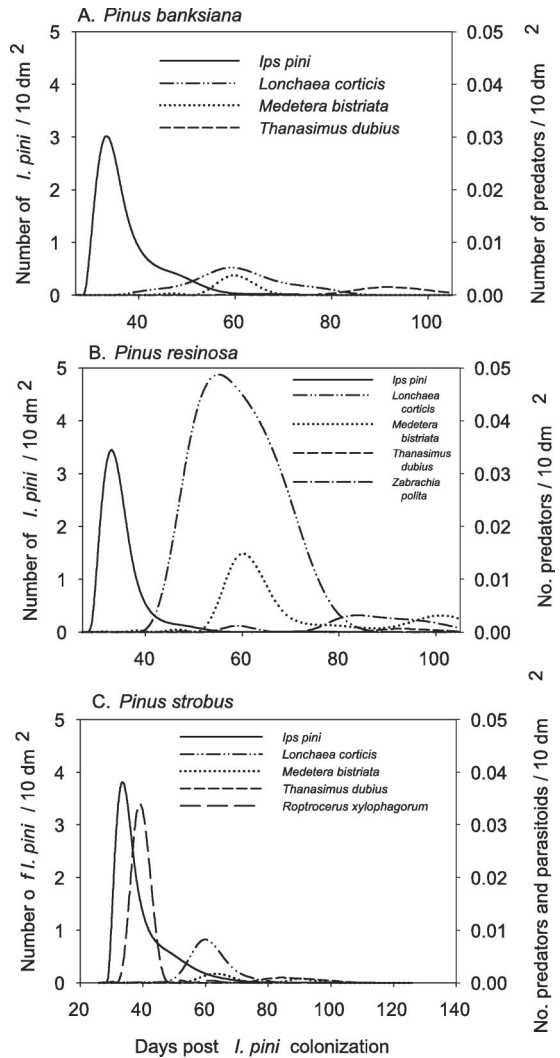


Fig. 4. Emergence of *I. pini* and associated insects from (A) *P. banksiana*, (B) *P. resinosa*, and (C) *P. strobus* colonized with *I. pini* and deployed in a red pine plantation for 25 d. The bolts were colonized on day 0 and taken to the plantation on day 1. Predators include *M. bistriata*, *G. politus*, *Z. polita*, and *T. dubius*. *R. xylophagorum* is a parasitoid.

high variation. The timing of exclusion screening did not affect *C. parallelus* development in red pine, although almost all *C. parallelus* emerged from white pine logs with unrestricted access immediately after *I. pini* colonization. Neither differential exclusion screening nor pine species affected reproduction of *Platysoma* spp. and *T. dubius*.

*I. pini* was the most abundant insect reared from the logs colonized during mid- to late summer 2001, although its total emergence was only half that in the spring (Table 5B). Most insects emerged from red pine, and exclusion screening did not affect reproduction. Predator emergence was much lower than in the spring. The most abundant predator was *Sivlanus bidentatus* (F.), of which all 31 were reared from the



Table 5. Effect of host tree species, time of exclusion screening (days 1–12 or days 13–24), and their interaction on the reproduction of insects (mean  $\pm$  SEM per log) in red and white pine ( $n = 8$  replicates each) colonized during early and late flight season

Order Family	Insect	Total	Red pine		White pine		Tree		Time		Tree $\times$ Time	
			1–12 d	13–24 d	1–12 d	13–24 d	$F_{1,21}$	$P$	$F_{1,21}$	$P$	$F_{1,21}$	$P$
Coleoptera Scolytidae	<i>I. pini</i>	1,912	46.75 $\pm$ 9.02	64.38 $\pm$ 8.74	45.50 $\pm$ 10.55	82.38 $\pm$ 17.97	0.45	0.5094	5.99	0.0233	0.54	0.4700
	Males	873	21.13 $\pm$ 4.85	30.88 $\pm$ 4.70	19.00 $\pm$ 5.30	38.13 $\pm$ 9.30	0.12	0.7340	5.88	0.0244	0.48	0.4951
	Females	1,039	25.63 $\pm$ 4.61	33.50 $\pm$ 4.24	26.50 $\pm$ 5.61	44.25 $\pm$ 9.08	0.95	0.3410	5.23	0.0327	0.54	0.4705
	<i>I. grandicollis</i>	161	0.50 $\pm$ 0.50	0.00 $\pm$ 0.00	7.13 $\pm$ 3.61	12.50 $\pm$ 10.08	11.53	0.0027	0.01	NA	0.94	0.3444
	<i>D. valens</i>	2	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.13 $\pm$ 0.13	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
	<i>D. autographus</i>	55	0.63 $\pm$ 0.38	2.25 $\pm$ 1.66	0.63 $\pm$ 0.26	3.38 $\pm$ 1.51	0.21	0.6543	5.60	0.0276	0.21	0.6543
	<i>C. materarius</i>	25	0.00 $\pm$ 0.00	0.25 $\pm$ 0.25	0.38 $\pm$ 0.26	2.50 $\pm$ 1.67	7.32	0.0132	5.50	0.0290	0.59	0.4503
	<i>Hylastes</i> spp.	10	0.13 $\pm$ 0.13	0.25 $\pm$ 0.25	0.25 $\pm$ 0.25	0.63 $\pm$ 0.50	NA	NA	NA	NA	NA	NA
	<i>O. caelatus</i>	2,026	19.63 $\pm$ 13.16	89.38 $\pm$ 37.32	10.38 $\pm$ 5.74	133.88 $\pm$ 37.92	0.09	0.7721	18.69	0.0003	1.16	0.2946
	<i>D. americanus</i>	24	0.00 $\pm$ 0.00	0.88 $\pm$ 0.61	0.00 $\pm$ 0.00	2.13 $\pm$ 1.34	1.47	0.2391	23.76	0.0001	1.47	0.2391
	<i>Pissodes</i> spp.	98	2.38 $\pm$ 1.08	7.75 $\pm$ 4.57	1.13 $\pm$ 0.48	1.00 $\pm$ 0.33	5.89	0.0243	1.61	0.2190	1.95	0.1770
	Total	70	1.75 $\pm$ 0.53	1.25 $\pm$ 0.75	3.13 $\pm$ 0.91	2.63 $\pm$ 0.73	4.53	0.0454	0.66	0.4274	0.05	0.8305
	<i>E. nigripes</i>	13	0.25 $\pm$ 0.16	0.00 $\pm$ 0.00	0.88 $\pm$ 0.52	0.50 $\pm$ 0.33	NA	NA	NA	NA	NA	NA
	<i>T. dubius</i>	56	1.50 $\pm$ 0.46	1.25 $\pm$ 0.75	2.25 $\pm$ 0.70	2.00 $\pm$ 0.80	1.82	0.1916	0.33	0.5696	0.01	0.9427
	<i>T. undulatus</i>	1	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	NA	NA	NA	NA	NA	NA
<i>Platysoma</i> spp.	91	2.63 $\pm$ 0.92	2.50 $\pm$ 1.21	2.38 $\pm$ 0.89	3.88 $\pm$ 1.23	0.55	0.4653	0.47	0.4993	0.93	0.3461	
<i>P. cylindrica</i>	50	1.38 $\pm$ 0.60	1.00 $\pm$ 0.68	2.13 $\pm$ 0.91	1.75 $\pm$ 0.80	1.10	0.3069	0.25	0.6236	0.01	0.9412	
<i>P. parallelum</i>	41	1.25 $\pm$ 0.59	1.50 $\pm$ 1.10	0.25 $\pm$ 0.16	2.13 $\pm$ 0.58	0.37	0.5486	3.44	0.0776	2.73	0.1135	
<i>Enopaeae labilis</i>	7	0.00 $\pm$ 0.00	0.25 $\pm$ 0.16	0.38 $\pm$ 0.38	0.25 $\pm$ 0.25	NA	NA	NA	NA	NA	NA	
<i>S. bidentatus</i>	20	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	1.88 $\pm$ 1.74	0.63 $\pm$ 0.50	9.23	0.0063	0.67	0.4228	0.67	0.4228	
Total	4	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.25 $\pm$ 0.16	0.13 $\pm$ 0.13	NA	NA	NA	NA	NA	NA	
<i>C. parallelus</i>	216	0.25 $\pm$ 0.16	11.75 $\pm$ 7.78	7.38 $\pm$ 4.83	7.63 $\pm$ 7.06	9.59	0.0055	14.71	0.0010	15.73	0.0007	
Diptera Dolichopodidae Lonchaeidae	<i>M. bistrriata</i>	6	0.38 $\pm$ 0.68	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.25 $\pm$ 0.25	NA	NA	NA	NA	NA	NA
	<i>L. corticis</i>	1	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
	Total	1	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
Hymenoptera Ichneumonidae Coleoptera Scolytidae	<i>Orgillus</i> sp.	1	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
	<i>I. pini</i>	1,082	18.75 $\pm$ 4.29	18.75 $\pm$ 6.18	52.75 $\pm$ 16.87	45.00 $\pm$ 10.27	13.02	0.0017	0.11	0.7487	0.06	0.8080
	Males	515	8.25 $\pm$ 2.15	9.25 $\pm$ 3.49	23.38 $\pm$ 6.49	23.50 $\pm$ 5.33	15.50	0.0008	0.04	0.8427	0.00	0.9898
	Females	567	10.50 $\pm$ 2.18	9.50 $\pm$ 2.98	29.38 $\pm$ 10.45	21.50 $\pm$ 5.12	9.75	0.0051	0.55	0.4647	0.22	0.6476
	<i>I. grandicollis</i>	270	8.13 $\pm$ 4.46	5.50 $\pm$ 4.54	8.25 $\pm$ 4.98	11.88 $\pm$ 7.44	0.70	0.4116	0.02	0.8970	0.64	0.4323
	<i>Hylastes</i> spp.	14	0.25 $\pm$ 0.25	0.13 $\pm$ 0.13	0.50 $\pm$ 0.38	0.88 $\pm$ 0.64	NA	NA	NA	NA	NA	NA
	<i>O. caelatus</i>	103	6.88 $\pm$ 4.00	0.88 $\pm$ 0.52	0.88 $\pm$ 0.52	4.25 $\pm$ 2.51	0.29	0.5982	0.29	0.5982	7.21	0.0139
	Total	3	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.13 $\pm$ 0.13	0.13 $\pm$ 0.13	NA	NA	NA	NA	NA	NA
	Total	6	0.13 $\pm$ 0.13	0.50 $\pm$ 0.38	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	NA	NA	NA	NA	NA	NA
	<i>T. dubius</i>	5	0.00 $\pm$ 0.00	0.50 $\pm$ 0.38	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	NA	NA	NA	NA	NA	NA
	<i>T. undulatus</i>	1	0.13 $\pm$ 0.13	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
	Total	2	0.00 $\pm$ 0.00	0.25 $\pm$ 0.16	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
	<i>Platysoma</i> spp.	3	0.00 $\pm$ 0.00	0.38 $\pm$ 0.26	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
	<i>P. cylindrica</i>	1	0.00 $\pm$ 0.00	0.13 $\pm$ 0.13	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
	<i>P. parallelum</i>	2	0.00 $\pm$ 0.00	0.25 $\pm$ 0.16	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
<i>S. bidentatus</i>	31	3.38 $\pm$ 2.59	0.00 $\pm$ 0.00	0.50 $\pm$ 0.38	0.00 $\pm$ 0.00	2.35	0.1403	11.91	0.0024	2.35	0.1403	
Total	2	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.25 $\pm$ 0.25	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA	
Diptera Lonchaeidae	<i>L. corticis</i>	4	0.13 $\pm$ 0.13	0.38 $\pm$ 0.38	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA
	Total	4	0.13 $\pm$ 0.13	0.38 $\pm$ 0.38	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	NA	NA	NA	NA	NA	NA

Statistical tests are limited to those species for which we obtained a minimum of 18 individuals. NA, not applicable.

set of logs that were open to colonizers during days 13–24. Emergence of *Platysoma* spp. and *T. dubius* from all logs decreased 97 and 91% from the spring to summer, respectively.

During the summer, we obtained three species not found in other experiments. Single specimens of two ichneumonids, *Dusona americana* (Ashmead) and *Cratichneumon rubricus* (Provancher), were captured arriving at red pine. We obtained one specimen each of the braconid wasp *Cyanopterus* sp. on both red and white pine bolts colonized by *I. pini* (Table 5).

### Discussion

A diverse assemblage of species from a variety of feeding guilds arrives at and exploits trees colonized by *I. pini*. However, these associates are dominated by one or a few species within each taxon and feeding guild (Table 1). The most abundant species partition the resource based on time since *I. pini* colonization, host tree species, and/or seasonal phenology.

There was strong partitioning among species in the sequence of arrival to colonized tissue. This sequence may provide clues about the chemical ecology of some natural enemies whose behavior has not been thoroughly studied. For example, *M. bistrriata* arrived concurrently with, or slightly before, conspecifics of the primary herbivore *I. pini* (Figs. 1–3). Orientation to cues associated with bark beetles by *M. bistrriata* and *G. politus* is not well understood, but these species may use pheromones and host tree volatiles to select oviposition sites (Williamson 1971). The arrival of various parasitoid species correlates with the life stage attacked. *T. tibialis* parasitizes adult *I. pini* and arrives immediately, exploiting aggregation pheromone signals (Rice 1968). *R. xylophagorum* enters galleries and parasitizes late instars (Samson 1984) and arrives predominantly 15–26 d after colonization when larvae are present (Fig. 3C). *R. xylophagorum* may use microbial volatiles or other cues particular to the preferred life stage to aid in host finding (Sullivan et al. 2000, Pettersson et al. 2000).

The total emergence of *I. pini* did not vary across host trees. In contrast, some members of the natural enemy complex, such as the competitor and facultative predator *Monochamus* spp. (Dodds et al. 2001) and the parasitoid *R. xylophagorum*, showed strong host tree associations. Host tree partitioning may be facilitated by favorable physiological properties, such as bark thickness and nutritional properties of the phloem tissue, or phytochemistry (Savely 1939, Lawson et al. 1996). For example, the soft bark of white pine may facilitate oviposition by *Monochamus* spp., which chew egg niches into the stem surface. White pine also has higher concentrations of oxygenated monoterpenes, which are attractive to *R. xylophagorum* (Pettersson et al. 2000). Partitioning among host tree species may reduce interspecific competition and intraguild predation, because many of the subcortical larval predators, such as *T. dubius* and dolichopodid flies, are feeding generalists once in the bark beetle

habitat (Thomas 1955, Dahlsten and Stephen 1974, Lawson et al. 1996, Ounap and Elberg 1999).

The numbers and distribution of insects that respond to pine logs colonized by *I. pini* are also partitioned by seasonal phenology, which could affect competition, predation, and the population dynamics of *I. pini*. Most *I. pini* emerged from logs in the summer trials (Tables 2 and 3). More potentially competitive phloeophagous species, such as *G. materarius*, *O. caelatus*, *D. autographus*, *Dryophthorus americanus* Bedel, and *Pissodes* spp., were present in the spring than summer. Resulting interspecific competition, as well as possible kairomonal attraction of predators to cues associated with these insects (Thomas 1955), could suppress *I. pini* early in the flight season. Competition from other *Ips* species present in the region, such as *Ips grandicollis* (Eichhoff) and *Ips perroti* (Swaine), was low, even though the former are often abundant (Ayres et al. 2001, Erbilgin and Raffa 2001, Wallin and Raffa 2001).

The relative rate of increase, or the ratio of emergence to arrival, varied among different host trees within insect species. *I. pini*'s relative rate of increase was highest in jack pine (Table 4), perhaps because there were fewer predators overall in this tree (Table 2; Fig. 4A). The rate of increase of *T. dubius* estimated from this field study agrees closely with that obtained from controlled laboratory studies (Aukema and Raffa 2002). In each case, replacement rates by this predator were less than one on a per log basis, indicating the need for this species to undertake multiple ovipositional events to be successful (Table 4; Aukema and Raffa 2002). Between-insect differences in ratios of emergence to arrival need to be treated with caution due to differences in relative effectiveness of various trap types and sampling efficiencies, and varying mating and ovipositional strategies.

Although exclusion experiments provide a useful tool for estimating natural enemy impacts in some systems, the concurrent arrival of predators and colonizing herbivores poses serious challenges to studies of bark beetle population dynamics (Linit and Stephen 1983). In our experiments, the reduced emergence of bark beetles after enclosure of logs during the first 2 wk post-colonization cannot be attributed solely to predation, because it also limited the number of cojoining herbivores. An alternate approach is to fully colonize the logs with herbivores in the laboratory before exposing them to field populations. However, the cessation of pheromone production under these conditions may decrease predator arrival (Miller 1984). A nonmanipulative alternative is to model numerical responses among bark beetles and associates. For example, both clerids and *R. xylophagorum* exhibited positive numerical responses to *I. pini* emergence or arrival (Aukema 2003). However, there can be pronounced multicollinearity in bark beetle–natural enemy population data, at both the plantation (Erbilgin et al. 2002) and within-tree (Aukema 2003) levels. This demands caution when inferring cause–effect relationships. Controlled laboratory-amending experiments can complement such studies (Aukema and

Raffa 2002), and the confounding effects of multiple predators may be separated by studies of individual and collective predator behaviors and impacts (Rosenheim 1998). However, like all laboratory studies, these may be less realistic than field conditions. Given the diversity of this assemblage, the responses by several species to common chemical signals, and the interactions among these insects at several levels of scale, a combination of approaches seems necessary.

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