

# Exploiting Behavioral Disparities Among Predators and Prey to Selectively Remove Pests: Maximizing the Ratio of Bark Beetles to Predators Removed During Semiochemically Based Trap-Out

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**ABSTRACT** Mass-trapping using semiochemical lures is a potentially useful control measure against bark beetle pests. A serious problem, however, is the inadvertent removal of predators that respond to these baits as kairomones. *Ips pini* (Say) infests hard pines in the western, Great Lakes, and eastern forests of North America. In Wisconsin, *I. pini* responds primarily to 50(+)/50(-) and 75(+)/25(-) blends of ipsdienol, its principal pheromone component. Its response is increased by a synergist, lanierone. Its most abundant predators in Wisconsin include *Thanasimus dubius* (F.), which responds to similar blends of ipsdienol, and *Platysoma cylindrica* (Paykull) and *P. parallelum* (Say), which respond to primarily (-) enantiomers of ipsdienol. These predators do not show increased response when lanierone is released in addition to ipsdienol. We conducted a no-choice assay using rotating blends of ipsdienol and lanierone to simulate a trap-out treatment. Lures that contain enantiomers of ipsdienol most preferred by *I. pini*, in combination with lanierone, can selectively remove up to three to six times more pests than predators during the spring. Moreover, delaying deployment of the same lures until summer can result in removal of up to 39 times more pests than predators. In contrast, lures that contain enantiomers of ipsdienol most preferred by predators can inadvertently remove two or more predators per each bark beetle trapped. Exploiting these behavioral differences between pests and predators can improve biological control by conserving predators during trap-out programs.

**KEY WORDS** *Ips pini*, *Thanasimus dubius*, *Platysoma*, biological control, coevolution, pheromones

BARK BEETLES (COLEOPTERA: Scolytidae) are among the most damaging forest pests in North America and Europe (Rudinsky 1962). Colonization of susceptible trees is mediated by aggregation pheromones emitted by pioneering beetles (Wood 1982). These pheromones may be synthesized from or synergized by host terpenes (Hughes 1974, Hunt et al. 1986, Miller and Borden 1990), and attract large numbers of beetles that collectively exhaust host defenses. Beetles establish broods in the phloem. Progeny pupate in the phloem or outer bark, and then emerge to seek new hosts. The destruction of phloem by many beetles and associated fungi usually results in tree death (Raffa and Berryman 1983).

Control tactics have historically included methods such as thinning, sanitation and salvage harvests, or insecticides (Williamson and Vité 1971, Berryman 1982, Stark 1982, Swezey et al. 1982). Pheromones also provide possible avenues for bark beetle management (Borden 1989), such as exclusion or saturation (Furniss and Livingston 1979, Tilden et al. 1981, Borden 1989). More commonly, synthetic pheromones are applied to large numbers of traps or trap trees for the purpose of mass removal of bark beetles, as has

been attempted for mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Borden and Lacey 1985), the smaller European elm bark beetle *Scolytus multistriatus* Marsham (Lanier 1979), the spruce beetle *Ips typographus* L. (Bakke 1989, Raty et al. 1995), and others.

Although mass trapping can remove large numbers of bark beetle pests, they also inadvertently remove high numbers of predators that use bark beetle pheromones as kairomones (Stephen and Dahlsten 1976, Dixon and Payne 1980, Billings and Cameron 1984, Payne et al. 1984, Grégoire et al. 1989, Payne 1989, Grégoire et al. 1992, Seybold 1993, Ross and Daterman 1995, Erbilgin and Raffa 2000). Natural enemies play an important role in regulating scolytid population dynamics (Dahlsten 1982, Kulhavy and Miller 1989, Turchin et al. 1991, Raffa 1995, Reeve et al. 1995, Stephen 1995, Reeve 1997), and contribute to self-sustaining biological control over large areas and long time frames (Miller et al. 1987, Dahlsten and Whitmore 1989). In some instances, removal of predators through mass trapping may have prolonged the outbreak (DeMars et al. 1986). The best bark beetle management strategies minimize the negative effects on natural enemies and maximize impacts on the target species (Ross and Daterman 1995, Poland and Borden 1997).

We investigated methods to reduce damage to the predator complex during trap-out of the pine en-

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graver, *Ips pini* (Say). *I. pini* is a chronic pest of plantation pines in the Great Lakes region and damages timber during harvest operations in western North America (Klepzig et al. 1991, Miller et al. 1997). *I. pini* and its associated predators respond to the principal *I. pini* pheromone, ipsdienol (2-methyl-6-methylene-2,7-octadien-4-ol), in ratios of (+) and (-) stereoisomers that vary transcontinentally (Lanier et al. 1972; Birch et al. 1980a, 1980b; Lanier et al. 1980; Seybold et al. 1992; Seybold 1993; Raffa and Dahlsten 1995; Miller et al. 1997). In Wisconsin, *I. pini* prefer a racemic (50(+)/50(-)) to 75(+)/25(-) enantiomeric ratio, whereas its principal predators *Thanasius dubius* (F.) and *Platysoma cylindrica* (Paykull) prefer slightly more (+) ratios or substantially more (-) ratios (Herms et al. 1991, Raffa 1995, Aukema et al. 2000), respectively. *I. pini* response to ipsdienol is increased by a synergist, lanierone (2-hydroxy-4,4,6-trimethyl-2,5-cyclohexadien-1-one) (Teale et al. 1991, Seybold 1993). However, responses of Wisconsin predators to ipsdienol are not synergized by lanierone (Miller et al. 1997, Aukema and Raffa 2000, Aukema et al. 2000).

These disparities in responses to enantiomeric ratios of ipsdienol and the presence or absence of lanierone may reflect a coevolving system between bark beetles and their predators (Raffa and Klepzig 1989, Herms et al. 1991, Raffa 1991). That is, predators may select for slight shifts in ipsdienol chirality or lanierone production. This model of chemically based enemy free space is supported by the observation that *I. pini* demonstrate pheromone-based assortative mating (Teale et al. 1994).

Previous research on differences between the preferences of predators versus *I. pini* to *I. pini* pheromones has been performed under behavioral choice conditions. However, this does not reflect the more stringent test of a no-choice situation that would occur during a trap-out program. The purpose of this research is to test whether an understanding of behavioral differences between herbivores and predators to herbivore pheromones can be used to conserve biological control agents during semiochemically based trap-out operations. Specifically, we tested whether removal of the predator complex could be reduced by (1) timing lure deployment to target high *I. pini* populations when predator populations are relatively low (Raffa 1991) and (2) selecting lures that target pests yet conserve natural enemies (Raffa and Klepzig 1989, Aukema and Raffa 2000).

### Materials and Methods

**Treatments.** The experiment was conducted in the field as a no-choice assay. Responses to 20 mg (AI) pheromone lures formulated in polyvinyl bubble-capsules were evaluated. The lures (Pherotech Inc., Delta, BC) consisted of three ratios of (+) to (-) ipsdienol: 75(+)/25(-), 50(+)/50(-), 03(+)/97(-), with and without lanierone, for a total of six treatments. The lures contained a 1,3-butanediol carrier solvent that is unattractive to *I. pini* (Miller 1990), and

had release rates of 110  $\mu\text{g}/\text{d}$  (ipsdienol) and 100  $\mu\text{g}/\text{d}$  (lanierone) at 25°C.

**Experimental Design.** Six isolated plots were chosen in mature red (*Pinus resinosa* Aiton) or red and white (*P. strobus* L.) mixed pine plantations (40-50 yr old) in central Wisconsin. Sites included two plots in Sauk County (N 43° 33.41', W 89° 50.61'; N 43° 33.43', W 89° 50.61'), two plots in Waushara County (N 44° 01.31', W 89° 17.88'; N 44° 01.46', W 89° 17.85'), and one plot in Marquette County (N 43° 55.33', W 89° 18.79'). An additional sixth site in Marquette County (N 43° 58.30', W 89° 17.13') was used in 1997, but replaced with a site in Sauk County (N 43° 34.61', W 89° 52.30') in 1998 because of transfer of ownership. Plots were similar in stand structure and site characteristics, and were monitored for presence of brood material such as windthrow from storms.

In each plot, nine 12-unit multiple funnel traps (Lindgren 1983) were deployed in a group such that traps were spaced  $\approx 10$  m apart. Traps were suspended from nylon twine stretched between two trees such that the trap's cup was at least 50 cm from both the ground and the nearest tree. All traps within a plot received the same treatment lure. Each trap received one lure, attached to a middle trap funnel with wire. A 3 by 3-cm block of time-released 20% organophosphate insecticide strip (Pest STRIP, Loveland Industries, Greeley, CO) was placed in each cup to kill arriving insects and prevent destruction of trap contents by predators.

Trap catches were collected every 3 d for six sample periods. An 18-d experiment was selected to ensure that insect populations remained relatively stable during each trial; this interval is half the generation time of *I. pini* and several times less than that of its predators. At each collection, the treatments were randomized across the six plots according to a Latin square design such that treatment and plot location were randomization sources. The experiment was performed twice per year for 2 yr. Assays were timed to correspond with major flight periods of *I. pini* and predators. The experiments were performed 19 May through 3 June and 14 July through 29 July 1997, and 9 May through 24 May and 25 June through 10 July 1998. Trap catches were tabulated for herbivores, predators, and the parasitoid *Tomicobia tibialis* Ashmead (Hymenoptera: Pteromalidae).

**Statistical Analyses.** All data were transformed by square root ( $y$ ) to reduce heteroscedasticity. To check for potential changes in background insect populations, we tested for autocorrelation of data points using the Mauchly test of sphericity, which was determined to be positive (i.e.,  $P > 0.05$ ; variances are not correlated and thus independent). As an additional precaution, we tested for potential site by time interactions, which were always insignificant (see *Results*). Thus, a replicated Latin squares mixed effects model was constructed consistent with the design of the experiment (PROC MIXED, SAS Institute 1996). Treatment, replication, replication by treatment interaction, sampling interval, and site, nested within the replication, were used as fixed effects. Data for

Table 1. Average number of insects caught per 3-d collection period per trap, in field trials in Wisconsin, USA

Insect	Family	1997		1998		Total (1,287)
		Spring (323)	Summer (318)	Spring (322)	Summer (324)	
Herbivores (80.8%):						
<i>Ips pini</i> (Say)	Scolytidae	4.15	13.24	4.98	25.19	15,318
<i>Ips grandicollis</i> (Eichhoff)	Scolytidae	0.01	0.00	0.02	0.02	18
<i>Ips perroti</i> Swaine	Scolytidae	0.17	0.06	0.02	0.07	103
<i>Dendroctonus valens</i> LeConte	Scolytidae	0.75	0.03	0.14	0.04	312
<i>Orthotomicus caelatus</i> (Eichhoff)	Scolytidae	0.18	0.01	0.01	0.01	66
<i>Hylastes</i> spp.	Scolytidae	0.08	0.01	0.02	0.00	35
Metallic wood borers <sup>a</sup>	Buprestidae	—	—	0.05	0.05	32
Long horned beetles <sup>b</sup>	Cerambycidae	0.02	0.21	0.05	0.11	121
Total herbivores:						16,005
Predators (19.1%):						
<i>Thanasimus dubius</i> (F.)	Cleridae	0.60	0.49	2.85	0.51	1,435
<i>Enoclerus muttkowski</i> Wolcott	Cleridae	0.00	0.00	0.00	0.00	2
<i>Enoclerus nigrifrons</i> (Say)	Cleridae	0.00	0.12	0.01	0.31	141
<i>Enoclerus nigripes</i> Say	Cleridae	0.09	0.08	0.07	0.14	125
<i>Enoclerus sphegeus</i> (F.)	Cleridae	0.01	0.16	0.28	0.22	214
<i>Phlogistosternus dislocatus</i> (Say) <sup>a,c</sup>	Cleridae	0.00	0.02	0.00	0.14	50
<i>Zenodorus sanguineus</i> (Say) <sup>a</sup>	Cleridae	0.00	0.00	0.16	0.03	62
<i>Platysoma cylindrica</i> (Paykull)	Histeridae	0.22	0.25	1.79	0.69	952
<i>Platysoma parallelum</i> (Say)	Histeridae	0.55	0.08	0.23	0.08	305
<i>Corticus parallelus</i> (Melsheimer)	Tenebrionidae	0.18	0.03	0.31	0.10	200
<i>Grynocharis quadrilineata</i> (Melsheimer)	Trogositidae	0.02	0.01	0.21	0.00	78
<i>Tenebroides</i> spp. <sup>d</sup>	Trogositidae	0.11	0.08	0.34	0.18	229
Total predators:						3,793
Parasitoid (0.1%):						
<i>Tomocobia tibialis</i> Ashmead	Pteromalidae	0.00	0.00	0.01	0.04	17
Total Insects:						19,815

Values in parentheses in headings indicate number of trap collections. Total shows sum of all trap collections.

<sup>a</sup> Not tabulated for 1997.

<sup>b</sup> Primarily *Monochamus carolinensis* Olivier and *Monochamus titillator* (F.).

<sup>c</sup> Natural history undetermined. Likely a predator (Cleridae).

<sup>d</sup> *Tenebroides* nr. *collaris* Sturm and another *Tenebroides* spp.

each species of arriving insect were subjected to analysis of variance (ANOVA). Least squared means were used to adjust for all terms in the model. Least squared means or contrasts were used for pair-wise comparison. Treatment effects were judged to be significant at  $P < 0.05$ . For ratio calculations, raw means were used.

For each collection, an average was taken across each plot for each insect, by treatment, to eliminate potential problems with missing data caused by lures blown off in storms, traps damaged by falling trees, or other reasons. However, no plot ever lost more than two of the nine traps in a sample period, and overall, <0.7% of the data were lost over 2 yr. We conducted statistical analyses on all species for which a minimum of 200 specimens over 2 yr were obtained, except for *Tenebroides* species (Coleoptera: Trogositidae) because they were not keyed to species. We grouped *Platysoma parallelum* (Say) with *P. cylindrica* as 'Platysoma' spp. for analysis purposes, because these species exhibit similar responses to *I. pini* semiochemicals (K.F.R., unpublished data).

Insects were retained in the analysis if they exhibited a treatment effect in either 1997 or 1998 and the effect was significant ( $P < 0.05$ ) when both years were pooled. Replications were pooled across seasons (by year) and across years (by season) to examine both

season and year effects as well as their treatment interactions, and data were pooled across both years by season only when treatment by year interactions were not significant.

## Results

At least eight species of herbivores, 12 predators, and one parasitoid were captured (Table 1). The highest response by a herbivore to these treatments was by *I. pini*, which comprised 77.3% of all insects caught. Of the predators, the most abundant were Cleridae (53.4%), followed by Histeridae (33.1%). The parasitoid *T. tibialis* was the only insect tabulated that was not a beetle. Most *I. pini* were caught in the summer (80.8%), whereas most of the clerids and histerids were caught in the spring (67.4%).

Because of significant seasonal and annual effects in the absolute numbers of *I. pini* and its major associates, subsequent analyses are partitioned accordingly. There were no significant treatment by year interactions for any insect. Potential time by site interactions were insignificant at  $P = 0.05$  (and never approached statistical significance) in either spring or summer for all insects (*I. pini* [ $F = 0.55$ ,  $P = 0.9183$ ;  $F = 0.58$ ,  $P = 0.8987$ ], *T. dubius* [ $F = 0.18$ ,  $P = 1$ ;  $F = 0.38$ ,  $P =$

**Table 2. Effect of overall treatment, enantiomeric composition of ipsdienol, and lanierone on responses of *I. pini* and associates in no-choice field trials in Wisconsin, USA**

Term	<i>Ips</i> spp.	<i>I. pini</i>	<i>D. valens</i>	<i>T. dubius</i>	<i>C. parallelus</i>	<i>Platysoma</i> spp.	Predators <sup>a</sup>
Spring							
1997							
Overall treatment effect							
<i>F</i>	4.65	4.90	2.05	3.49	1.10	0.52	1.43
df	5, 20	5, 20	5, 20	5, 20	5, 20	5, 20	5, 20
<i>P</i>	0.0056	0.0043	0.1142	0.0199	0.3916	0.7571	0.2549
Ipsdienol enantiomeric composition effect <sup>b</sup>							
<i>F</i>	7.97	8.12	5.00	9.48	2.79	1.09	3.13
df	2, 23	2, 23	2, 23	2, 23	2, 23	2, 23	2, 23
<i>P</i>	0.0023	0.0022	0.0158	0.0010	0.0825	0.3545	0.0626
Lanierone effect <sup>c</sup>							
<i>F</i>	3.39	3.53	1.04	0.06	0.17	0.49	0.93
df	1, 20	1, 20	1, 20	1, 20	1, 20	1, 20	1, 20
<i>P</i>	0.0803	0.0748	0.3192	0.8119	0.6846	0.4918	0.3460
1998							
Overall treatment effect							
<i>F</i>	11.76	13.14	3.20	16.72	7.16	6.73	5.30
df	5, 20	5, 20	5, 20	5, 20	5, 20	5, 20	5, 20
<i>P</i>	0.0001	0.0001	0.0277	0.0001	0.0006	0.0008	0.0029
Ipsdienol enantiomeric composition effect <sup>b</sup>							
<i>F</i>	6.80	7.73	8.96	44.60	14.44	15.48	11.62
df	2, 23	2, 23	2, 23	2, 23	2, 23	2, 23	2, 23
<i>P</i>	0.0048	0.0027	0.0013	0.0001	0.0001	0.0001	0.0003
Lanierone effect <sup>c</sup>							
<i>F</i>	21.43	23.25	0.06	0.40	3.71	0.57	2.03
df	1, 20	1, 20	1, 20	1, 20	1, 20	1, 20	1, 20
<i>P</i>	0.0002	0.0001	0.8026	0.5350	0.0684	0.4596	0.1700
1997 and 1998							
Overall treatment effect							
<i>F</i>	10.39	11.28	1.96	6.58	2.92	0.64	0.54
df	5, 45	5, 45	5, 45	5, 45	5, 45	5, 45	5, 45
<i>P</i>	0.0001	0.0001	0.1032	0.0001	0.0228	0.6740	0.7448
Ipsdienol enantiomeric composition effect <sup>b</sup>							
<i>F</i>	11.36	12.31	5.30	18.14	7.12	1.68	1.43
df	2, 51	2, 51	2, 51	2, 51	2, 51	2, 51	2, 51
<i>P</i>	0.0001	0.0001	0.0081	0.0001	0.0019	0.1967	0.2478
Lanierone effect <sup>c</sup>							
<i>F</i>	14.49	15.41	0.23	0.04	1.15	0.00	0.02
df	1, 45	1, 45	1, 45	1, 45	1, 45	1, 45	1, 45
<i>P</i>	0.0004	0.0003	0.6308	0.8369	0.2903	0.9637	0.9018
Summer							
1997							
Overall treatment effect							
<i>F</i>	11.22	11.13	0.24	9.26	0.96	2.65	0.54
df	5, 20	5, 20	5, 20	5, 20	5, 20	5, 20	5, 20
<i>P</i>	0.0001	0.0001	0.9382	0.0001	0.4644	0.0537	0.7437
Ipsdienol enantiomeric composition effect <sup>b</sup>							
<i>F</i>	16.27	16.29	0.16	20.62	2.41	4.46	0.98
df	2, 23	2, 23	2, 23	2, 23	2, 23	2, 23	2, 23
<i>P</i>	0.0001	0.0001	0.8515	0.0001	0.1122	0.0230	0.3903
Lanierone effect <sup>c</sup>							
<i>F</i>	9.63	9.44	0.02	1.45	0.15	0.02	0.05
df	1, 20	1, 20	1, 20	1, 20	1, 20	1, 20	1, 20
<i>P</i>	0.0056	0.0060	0.8801	0.2426	0.7039	0.8847	0.8318
Overall treatment effect							
<i>F</i>	22.05	22.04	0.96	5.16	1.46	6.75	2.89
df	5, 20	5, 20	5, 20	5, 20	5, 20	5, 20	5, 20
<i>P</i>	0.0001	0.0001	0.4670	0.0034	0.2473	0.0008	0.0404
Ipsdienol enantiomeric composition effect <sup>b</sup>							
<i>F</i>	11.01	11.15	1.90	11.73	0.57	12.35	5.09
df	2, 23	2, 23	2, 23	2, 23	2, 23	2, 23	2, 23
<i>P</i>	0.0004	0.0004	0.1720	0.0003	0.5755	0.0002	0.0148

Table 2. Continued

Term	<i>Ips</i> spp.	<i>I. pini</i>	<i>D. valens</i>	<i>T. dubius</i>	<i>C. parallelus</i>	<i>Platysoma</i> spp.	Predators <sup>a</sup>
Lanierone effect <sup>c</sup>							
<i>F</i>	44.55	44.20	1.10	0.47	5.13	0.29	0.39
df	1, 20	1, 20	1, 20	1, 20	1, 20	1, 20	1, 20
<i>P</i>	0.0001	0.0001	0.3064	0.5008	0.0349	0.5946	0.5380
1997 and 1998:							
Overall treatment effect							
<i>F</i>	27.91	27.94	0.93	8.07	0.78	3.67	0.63
df	5, 45	5, 45	5, 45	5, 45	5, 45	5, 45	5, 45
<i>P</i>	0.0001	0.0001	0.4726	0.0001	0.5683	0.0072	0.6750
Ipsdienol enantiomeric composition effect <sup>b</sup>							
<i>F</i>	24.70	24.92	1.56	20.37	0.94	9.03	1.34
df	2, 51	2, 51	2, 51	2, 51	2, 51	2, 51	2, 51
<i>P</i>	0.0001	0.0001	0.2192	0.0001	0.3962	0.0004	0.2719
Lanierone effect <sup>c</sup>							
<i>F</i>	42.60	42.31	0.75	1.06	1.39	0.12	0.14
df	1, 45	1, 45	1, 45	1, 45	1, 45	1, 45	1, 45
<i>P</i>	0.0001	0.0001	0.3918	0.3093	0.2450	0.7270	0.7111

<sup>a</sup> Predators include *T. dubius*, *Platysoma* spp., *C. parallelus*, *E. nigripes*, *E. nigrifrons*, and *E. spegheus*.

<sup>b</sup> Ipsdienol enantiomeric composition effect refers to significance ( $P < 0.05$ ) in a one-way ANOVA of synthetic lures grouped by three enantiomeric compositions of ipsdienol.

<sup>c</sup> Lanierone effect is a contrast of synthetic ipsdienol lures with versus without lanierone.

0.9882], *E. nigripes*, [ $F = 1.03$ ,  $P = 0.4799$ ;  $F = 0.79$ ,  $P = 0.7171$ ], *E. nigrifrons* [ $F = 0.90$ ,  $P = 0.6049$ ;  $F = 0.82$ ,  $P = 0.6863$ ], or the histerids [ $F = 0.09$ ,  $P = 1$ ;  $F = 0.29$ ,  $P = 0.9978$ ] and  $df = 25, 20$ ).

**Herbivores.** Response by *I. pini* varied among the pheromone treatments (Table 2). These treatment effects were present on all four occasions during which this experiment was conducted. There were significant effects because of both ipsdienol enantiomeric composition and lanierone. *I. pini* preferred lures with high proportions of (+) ipsdienol, but the exact preference varied within years. In both years, they preferred primarily lures with 75(+)/25(-) ipsdienol in the spring, but their preference switched to 50(+)/50(-) ipsdienol in the summer (Table 3). This treatment by season interaction was significant in both 1997 ( $F = 3.37$ ;  $df = 5, 45$ ;  $P = 0.0114$ ) and 1998 ( $F = 2.79$ ;  $df = 5, 45$ ;  $P = 0.0279$ ). *I. pini* was the only species to demonstrate a statistically significant shift in preferences. *I. pini* responses to ipsdienol lures were significantly enhanced by the presence of lanierone (Table 2). Approximately three to four times more beetles were trapped when a lanierone lure was added to the ipsdienol lure (Table 3).

The responses of *Dendroctonus valens* LeConte varied among enantiomers of ipsdienol in the spring (Table 2). Populations in the summer were too low for analysis. *D. valens* preferred those enantiomeric compositions of ipsdienol that the primary herbivore *I. pini* preferred; i.e., it responded in highest numbers to 75(+)/25(-) ipsdienol in the spring (Table 3). However, the presence of lanierone in combination with ipsdienol did not affect response by *D. valens* (Table 2).

**Predators.** Response by *T. dubius* varied among the enantiomers of ipsdienol in the spring and summer of both years (Table 2). *T. dubius* responded in highest

numbers to lures containing 75(+)/25(-) ipsdienol in the spring, although in the summer they responded in higher numbers to lures with racemic, 50(+)/50(-) ipsdienol (Table 3). In this respect, its response was consistent with the primary herbivore *I. pini*. The season by treatment interaction term was not significant, however ( $F = 0.63$ ;  $df = 5, 45$ ;  $P = 0.6752$  in 1997;  $F = 2.17$ ;  $df = 5, 45$ ;  $P = 0.0746$  in 1998), probably a result of the lower numbers in the summer. *T. dubius* response to ipsdienol was not synergized by the presence of lanierone (Table 2).

*Platysoma* spp. preference for specific enantiomers of ipsdienol was discernable in the spring of 1997 and the summer of both years (Table 2). When this preference was statistically significant, *Platysoma* spp. always responded in the highest numbers to lures emitting 03(+)/97(-) ipsdienol. *Platysoma* spp. responded in lowest numbers to lures emitting 75(+)/25(-) ipsdienol (Table 3). The addition of lanierone did not increase the responses of *Platysoma* spp. to ipsdienol (Table 2).

*Corticus parallelus* Melsheimer was present in highest numbers in the spring of 1998. During that experiment, its response varied among enantiomeric compositions of ipsdienol (Table 2). Overall, they responded in highest numbers to 75(+)/25(-) ipsdienol in the spring and to 50(+)/50(-) ipsdienol in the summer (Table 3). This pattern of the highest numbers of insects responding to 75(+)/25(-) ipsdienol in the spring and racemic ipsdienol in the summer was similar to that of *I. pini*. *C. parallelus* showed no additive or multiplicative response to the presence of lanierone in combination with ipsdienol (Table 2).

We grouped the three predators that demonstrated clear responses to specific enantiomeric compositions of ipsdienol, *T. dubius*, *Platysoma* spp., and *C. parallelus*, with other predators that have been shown to

Table 3. Average numbers of bark beetles and predators (per trap per 3-d sample period) attracted to different lures

Year/Insect	Lanierone			No Lanierone		
	75(+)/25(-)	50(+)/50(-)	03(+)/97(-)	75(+)/25(-)	50(+)/50(-)	03(+)/97(-)
Spring						
<i>I. pini</i>	8.15 (± 2.64)a	6.09 (± 2.84)ab	0.39 (± 0.14)d	7.07 (± 6.45)abc	2.54 (± 1.65)bcd	0.74 (± 0.36)cd
Other <i>Ips</i> spp.	0.19 (± 0.08)	0.15 (± 0.07)	0.09 (± 0.07)	0.46 (± 0.44)	0.17 (± 0.07)	0.02 (± 0.02)
<i>D. valens</i>	0.79 (± 0.31)	0.56 (± 0.20)	0.20 (± 0.09)	1.37 (± 1.02)	0.94 (± 0.43)	0.65 (± 0.44)
<i>T. dubius</i>	0.83 (± 0.59)a	0.96 (± 0.88)ab	0.06 (± 0.04)b	1.17 (± 0.73)a	0.52 (± 0.41)ab	0.07 (± 0.06)b
<i>Platysoma</i> spp.	0.17 (± 0.07)	0.67 (± 0.48)	1.15 (± 1.10)	0.67 (± 0.44)	0.82 (± 0.55)	1.18 (± 0.82)
<i>C. parallelus</i>	0.19 (± 0.16)	0.30 (± 0.28)	0.00 (± 0.00)	0.33 (± 0.29)	0.20 (± 0.18)	0.04 (± 0.04)
Predators	1.28 (± 0.82)	1.98 (± 1.61)	1.28 (± 1.15)	2.18 (± 1.29)	1.78 (± 1.22)	1.43 (± 0.92)
1998						
<i>I. pini</i>	16.19 (± 7.25)a	10.67 (± 3.48)a	0.19 (± 0.12)b	1.48 (± 0.53)b	1.50 (± 0.75)b	0.00 (± 0.00)b
Other <i>Ips</i> spp.	0.04 (± 0.04)	0.06 (± 0.02)	0.06 (± 0.04)	0.04 (± 0.04)	0.02 (± 0.02)	0.06 (± 0.02)
<i>D. valens</i>	0.21 (± 0.05)a	0.15 (± 0.04)ab	0.06 (± 0.04)bc	0.22 (± 0.06)a	0.18 (± 0.07)ab	0.04 (± 0.04)c
<i>T. dubius</i>	5.28 (± 1.79)a	4.15 (± 1.41)a	0.28 (± 0.17)b	4.46 (± 1.17)a	2.67 (± 0.64)a	0.28 (± 0.07)b
<i>Platysoma</i> spp.	1.08 (± 0.38)c	1.83 (± 0.79)bc	3.38 (± 1.16)a	1.18 (± 0.46)c	2.07 (± 0.91)bc	2.59 (± 1.06)ab
<i>C. parallelus</i>	0.38 (± 0.20)ab	0.30 (± 0.17)b	0.02 (± 0.02)c	0.65 (± 0.18)a	0.50 (± 0.19)ab	0.04 (± 0.02)c
Predators	7.11 (± 2.32)a	6.70 (± 2.12)a	4.28 (± 1.38)bc	6.43 (± 1.75)a	5.44 (± 1.45)ab	3.32 (± 1.20)c
1997 and 1998 pooled:						
<i>I. pini</i>	12.17 (± 3.89)a	8.38 (± 2.25)b	0.29 (± 0.10)c	4.28 (± 3.20)b	2.02 (± 0.88)bc	0.37 (± 0.21)c
Other <i>Ips</i> spp.	0.11 (± 0.05)	0.10 (± 0.04)	0.08 (± 0.04)	0.25 (± 0.22)	0.09 (± 0.04)	0.04 (± 0.02)
<i>D. valens</i>	0.50 (± 0.17)	0.35 (± 0.11)	0.13 (± 0.05)	0.80 (± 0.52)	0.56 (± 0.24)	0.34 (± 0.23)
<i>T. dubius</i>	3.06 (± 1.13)a	2.56 (± 0.92)a	0.17 (± 0.09)b	2.82 (± 0.82)a	1.59 (± 0.49)a	0.18 (± 0.05)b
<i>Platysoma</i> spp.	0.62 (± 0.23)	1.25 (± 0.47)	2.25 (± 0.84)	0.93 (± 0.32)	1.44 (± 0.54)	1.89 (± 0.68)
<i>C. parallelus</i>	0.28 (± 0.13)ab	0.30 (± 0.15)ab	0.01 (± 0.01)c	0.49 (± 0.17)a	0.35 (± 0.14)a	0.04 (± 0.02)bc
Predators	4.20 (± 1.47)	4.34 (± 1.46)	2.77 (± 0.97)	4.31 (± 1.22)	3.61 (± 1.06)	2.37 (± 0.78)
Summer						
1997						
<i>I. pini</i>	16.70 (± 6.08)b	37.36 (± 10.80)a	3.30 (± 2.03)cd	9.86 (± 4.13)bc	12.17 (± 2.65)b	0.38 (± 0.17)d
Other <i>Ips</i> spp.	0.01 (± 0.04)	0.08 (± 0.05)	0.06 (± 0.04)	0.02 (± 0.02)	0.07 (± 0.04)	0.04 (± 0.04)
<i>D. valens</i>	0.02 (± 0.02)	0.04 (± 0.02)	0.02 (± 0.02)	0.06 (± 0.04)	0.02 (± 0.02)	0.02 (± 0.02)
<i>T. dubius</i>	0.80 (± 0.27)a	0.67 (± 0.24)a	0.17 (± 0.09)b	0.54 (± 0.18)a	0.74 (± 0.24)a	0.02 (± 0.02)b
<i>Platysoma</i> spp.	0.20 (± 0.08)	0.15 (± 0.05)	0.62 (± 0.28)	0.12 (± 0.06)	0.41 (± 0.21)	0.45 (± 0.22)
<i>C. parallelus</i>	0.04 (± 0.02)	0.06 (± 0.02)	0.02 (± 0.02)	0.02 (± 0.02)	0.06 (± 0.02)	0.02 (± 0.02)
Predators	0.30 (± 0.37)	1.27 (± 0.32)	1.13 (± 0.31)	1.10 (± 0.24)	1.52 (± 0.50)	0.94 (± 0.35)
1998						
<i>I. pini</i>	49.18 (± 13.12)a	56.65 (± 11.69)a	12.50 (± 6.92)b	18.46 (± 4.35)b	13.96 (± 4.22)b	0.39 (± 0.16)c
Other <i>Ips</i> spp.	0.00 (± 0.00)	0.15 (± 0.05)	0.13 (± 0.11)	0.09 (± 0.05)	0.09 (± 0.05)	0.09 (± 0.06)
<i>D. valens</i>	0.04 (± 0.04)	0.06 (± 0.04)	0.00 (± 0.00)	0.06 (± 0.02)	0.09 (± 0.07)	0.02 (± 0.02)
<i>T. dubius</i>	0.63 (± 0.37)a	1.04 (± 0.58)a	0.09 (± 0.04)b	0.67 (± 0.28)a	0.57 (± 0.33)a	0.07 (± 0.04)b
<i>Platysoma</i> spp.	0.17 (± 0.12)c	0.91 (± 0.42)ab	1.63 (± 0.92)a	0.33 (± 0.14)c	0.54 (± 0.22)bc	1.07 (± 0.48)ab
<i>C. parallelus</i>	0.07 (± 0.07)	0.04 (± 0.02)	0.07 (± 0.06)	0.09 (± 0.06)	0.15 (± 0.07)	0.15 (± 0.07)
Predators	1.26 (± 0.56)c	2.76 (± 1.01)a	2.67 (± 1.12)ab	1.59 (± 0.55)bc	1.83 (± 0.53)abc	2.22 (± 0.69)ab
1997 and 1998 pooled						
<i>I. pini</i>	32.94 (± 8.45)b	47.19 (± 8.15)a	7.94 (± 3.71)d	14.24 (± 3.16)c	13.06 (± 2.39)c	0.38 (± 0.11)e
<i>D. valens</i>	0.03 (± 0.02)	0.05 (± 0.02)	0.01 (± 0.01)	0.06 (± 0.02)	0.06 (± 0.04)	0.02 (± 0.01)
Other <i>Ips</i> spp.	0.05 (± 0.02)	0.11 (± 0.03)	0.09 (± 0.06)	0.06 (± 0.03)	0.08 (± 0.03)	0.06 (± 0.04)
<i>T. dubius</i>	0.71 (± 0.22)a	0.86 (± 0.30)a	0.13 (± 0.05)b	0.60 (± 0.16)a	0.66 (± 0.20)a	0.05 (± 0.02)b
<i>Platysoma</i> spp.	0.18 (± 0.07)b	0.54 (± 0.23)ab	1.13 (± 0.48)ab	0.23 (± 0.08)b	0.47 (± 0.15)ab	0.77 (± 0.26)a
<i>C. parallelus</i>	0.06 (± 0.04)	0.05 (± 0.02)	0.05 (± 0.03)	0.06 (± 0.03)	0.10 (± 0.04)	0.08 (± 0.04)
Predators	1.28 (± 0.32)	2.03 (± 0.56)	1.91 (± 0.60)	1.35 (± 0.30)	1.68 (± 0.35)	1.59 (± 0.41)

Data are from no-choice field trials in red and red/white mixed pine plantations in Wisconsin, USA, 1997 and 1998. Standard errors are developed from average number of insects caught per site. Different letters indicate means are significantly different within a species at  $P < 0.05$  based on least squared means comparisons where treatment effects exist. Predators include *T. dubius*, *Platysoma* spp., *C. parallelus*, *E. nigripes*, *E. nigrifrons*, and *E. spegheus*.

respond to ipsdienol in previous choice tests in Wisconsin, *Enoclerus nigripes* Say, *E. nigrifrons* (Say), and *E. spegheus* (F.) (Miller et al. 1997, Aukema and Raffa 2000). When pooled across years, pooled predators did not show preferences for any specific enantiomeric composition of ipsdienol with or without lanierone (Table 2). Additionally, the treatment by season interaction was not statistically significant ( $F = 0.15$ ;  $df = 5, 45$ ;  $P = 0.9786$  in 1997 and  $F = 0.81$ ;  $df = 5, 45$ ;  $P = 0.5486$  in 1998).

**Ratios of Pests to Predators Removed by Simulated Trap-Out.** The ratios of pests to predators removed from the population by these simulated trap-outs are shown as a predator complex and for each of the predators individually in Table 4. The highest ratios occurred when lures containing lanierone were used, and when the lures were deployed later in the season. For example, in the spring, overall pest:predator ratios of almost 3:1 can be obtained by using 75(+)/25(-) ipsdienol with lanierone (Table 4). The same lure

Table 4. Pest:predator ratios using *I. pini* as pests and various associates as predators

Season	Year	Insect	n	Lanierone			No Lanierone		
				75(+)/25(-)	50(+)/50(-)	03(+)/97(-)	75(+)/25(-)	50(+)/50(-)	03(+)/97(-)
All Predators									
Spring	1997-1998			2.90	1.93	0.10	0.99	0.56	0.16
Summer	1997-1998			25.78	23.26	4.17	10.56	7.80	0.24
Effect of individual insect species on pest:predator ratios									
Spring	1997	<i>I. pini</i>	1,341						
		<i>T. dubius</i>	194	9.82	6.33	7.00	6.06	4.89	10.00
		<i>Platysoma</i> spp.	251	48.00	9.14	0.34	10.61	3.11	0.62
		<i>C. parallelus</i>	57	43.20	20.56	N/A	21.22	12.46	20.0
		Predators <sup>a</sup>	535	6.35	3.08	0.30	3.24	1.43	0.52
Spring	1998	<i>I. pini</i>	1,605						
		<i>T. dubius</i>	919	3.06	2.57	0.67	0.33	0.56	0.00
		<i>Platysoma</i> spp.	651	15.05	5.82	0.06	1.25	0.72	0.00
		<i>C. parallelus</i>	101	42.90	36.00	10.00	2.29	3.00	0.00
		Predators <sup>a</sup>	1,786	2.28	1.59	0.04	0.23	0.28	0.00
Summer	1997	<i>I. pini</i>	4,210						
		<i>T. dubius</i>	156	20.98	55.51	19.44	18.32	16.42	20.00
		<i>Platysoma</i> spp.	104	82.00	242.87	5.30	85.50	29.86	0.83
		<i>C. parallelus</i>	11	450.96	647.69	174.98	513.02	218.98	20.00
		Predators <sup>a</sup>	305	12.89	29.44	2.92	9.00	8.01	0.40
Summer	1998	<i>I. pini</i>	8,162						
		<i>T. dubius</i>	166	78.12	54.62	135.00	27.69	24.32	5.25
		<i>Platysoma</i> spp.	251	295.10	62.43	7.67	55.39	26.00	0.36
		<i>C. parallelus</i>	31	664.04	1529.38	168.76	199.41	94.25	2.62
		Predators <sup>a</sup>	666	39.06	20.53	4.69	11.59	7.62	0.18

Ratios are developed from raw means per trap per 3 d sample period for the experiments pooled by seasons, spring and summer. Data is taken from no-choice field trials in Wisconsin, USA, in red and red/white mixed pine plantations, 1997 and 1998. N is total number of insects caught in experiment. NA, Zero predators were caught with that lure, so a ratio could not be developed.

<sup>a</sup> Predators include *T. dubius*, *Platysoma* spp., *C. parallelus*, *E. nigripes*, *E. nigrifrons*, and *E. spegheus*.

used in the summer provides ratios that are approximately nine times higher. Up to 26 times more pests than predators can be removed by using an optimal combination of lures and season.

The seasonal and annual abundances of individual predator species (Table 4) greatly affect the overall ratios (Table 4). For example, between spring 1997 and 1998, the ratios of *I. pini* to *T. dubius* were reduced

to one-third their original value of 9.8 at 75(+)/25(-) ipsdienol plus lanierone. This occurred because *T. dubius* populations increased 4.8 times, whereas *I. pini* populations remained relatively constant. The highest ratios for individual predators can be obtained by using lures to which that predator does not respond. For example, *Platysoma* spp. do not respond in high numbers to 75(+)/25(-) ipsdienol lures with lanierone. When that lure was deployed in the summer of 1998, close to 300 times more *I. pini* were removed than *Platysoma* species. This occurred even though *Platysoma* populations were at the highest levels of the two summers.

Some pest:predator ratios were <1, indicating that more predators than *I. pini* were removed from the populations. Overall in the spring, any lure without lanierone attracted more predators than *I. pini* (Table 4). The 03(+)/97(-) ipsdienol lures without lanierone attracted higher numbers of predators than *I. pini* even in the summer, because of the large number of histerids responding to this blend (Table 4).

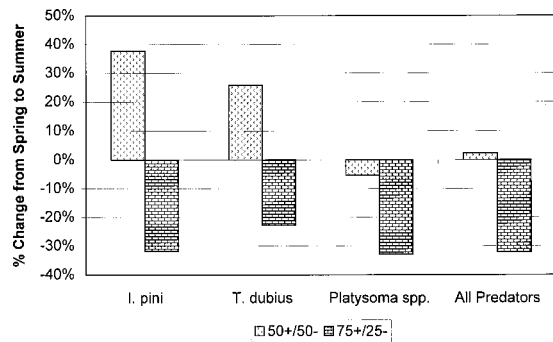


Fig. 1. Percent change in proportions of *I. pini* and associated predators captured from spring to summer in response to 50(+)/50(-) and 75(+)/25(-) ipsdienol enantiomeric compositions. *I. pini* show greatest response to these enantiomers. Each enantiomeric mixture of ipsdienol includes summed raw means of lures with and without lanierone pooled over 1997 and 1998 in no-choice field trials in Wisconsin red and red/white mixed pine plantations. Predators include *T. dubius*, *Platysoma* spp., *C. parallelus*, *E. nigripes*, *E. nigrifrons*, and *E. spegheus*.

Discussion

While some trap-out programs have been promising enough to warrant periodic large scale use over the past 20 yr (Bakke 1989, Vité and Baader 1990), the basic challenge of reducing predator mortality remains. Physical exclusion methods using screens or escape pipes in the traps have had mixed success and in some cases reduce removal of the target pest (Bakke 1989, Ross and Daterman 1998). The applicability of

physical exclusion depends largely on the specific natural enemy guild of the targeted pest. Unfortunately, *T. dubius* are very agile (Frazier et al. 1981) and *Platysoma* spp. and *C. parallelus* are small enough to exploit the same galleries as *I. pini*. We found that exploiting differences in chemical responses and phenology can be used to minimize negative impacts on the predator complex. Loss of some predators is unavoidable, but this effect can be offset if the concurrent removal of *I. pini* is greater than the numerical impact of the various predators removed. For example, a 75(+)/25(-) ipsdienol lure with lanierone removed a minimum of six times more bark beetles than predators during 1997 (Table 4). Conversely, lures such as 03(+)/97(-) ipsdienol generate pest:predator ratios of <1, and thus could be especially detrimental if the predators are caught in traps.

Conservation of predators during semiochemically based trap-out could intensify biological control on those bark beetles not responding to the treatment. Judicious selection of lures potentially could augment biological control by concentrating predators at an infestation. Before these ideas can be used in operational forestry, we need better information on the effects of each of the predator species on *I. pini* population dynamics in Wisconsin, which remains poorly understood (Raffa 1991, Aukema et al. 2000).

The timing of lure deployment has a potentially greater influence on selective pest removal than strictly exploiting behavioral disparities in chemical responses. For example, in 1997, a 50(+)/50(-) ipsdienol lure with lanierone removed three times more *I. pini* than predators in the spring but up to 29 times more *I. pini* than predators in the summer (Table 4). There are both benefits and consequences of waiting until summer before using lures for trap-out. Fewer predators would be lost if trapping were restricted to the summer months. Also, *I. pini* populations are often higher in mid to late summer than spring in Wisconsin, especially in drought years when trees progressively become more susceptible to attack (Schenk 1961). Conversely, spring trap-out could reduce *I. pini* numbers before populations build. The optimal approach may be to sample in the spring to judge relative predator and bark beetle numbers and the relative abundance of each predator species (Aukema et al. 2000), and then implement trap-out programs designed to conserve the most abundant predators in the summer (Table 4).

One challenge for designing trap-out programs concerns the plasticity of *I. pini* and predator responses. Some predators, such as *T. dubius*, can track *I. pini* shifts in pheromone response from spring to summer, although this ability differs among species (Fig. 1). Such problems can be minimized by developing monitoring tactics that more accurately reflect actual numbers of *I. pini* and predators responding to infested hosts (Aukema et al. 2000). The observed plasticity in response to various stereoisomers also suggests that *I. pini* potentially could develop resistance to mass-trapping programs (Hermes et al. 1991). However, the efficacy, frequency, and extent of trap-out programs

used in forestry may not generate the intense selection seen in agricultural systems treated with pesticides. By way of reference, Tabashnik and Croft (1982) estimated that seven consecutive generations of pesticide selection causing 90% mortality are needed to fix heritable resistance, which seems unlikely to be realized in operational forestry. In the only test of whether intensive semiochemical treatments in agriculture can cause heritable shifts (of which we are aware), Collins and Cardé (1985) found no treatment effect.

Our results suggest that new avenues for biological control can be applied in highly coevolved systems by exploiting the behavioral separation of predator and prey responses to herbivore pheromones. We currently have insufficient knowledge on the numerical or functional impacts of various predators on *I. pini*, the relative plasticities of their responses over long periods, the role of alternate prey species, and the interactions of host and microbial volatiles with pheromones to fully integrate biological and semiochemically based control. However, our demonstration suggests that pests can be selectively targeted by exploiting coevolving predator-prey kairomonal relationships, and this overall approach may be applicable to the management of other forest and agricultural ecosystems.

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