

# Kairomonal Responses of Natural Enemies and Associates of the Southern *Ips* (Coleoptera: Curculionidae: Scolytinae) to Ipsdienol, Ipsenol and *Cis-Verbenol*

Jeremy D. Allison · Jessica L. McKenney ·  
Daniel R. Miller · Matthew L. Gimmel

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**Abstract** Bark beetle infested pines are an ephemeral habitat utilized by a diverse assemblage of insects. Although many bark beetle insect associates have little or no measurable impact on bark beetle brood production, some reduce brood production by either competing with brood for the limited phloem tissue or by feeding on brood. Several studies have observed synchrony between the colonization of hosts by bark

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J. D. Allison · J. L. McKenney · M. L. Gimmel  
Department of Entomology, Louisiana State University Agricultural Center, LSU Campus, Baton Rouge, LA 70803, USA

D. R. Miller  
United States Department of Agriculture, Forest Service, Southern Research Station, 320 Green Street, Athens, GA 30602, USA

*Present Address:*

J. D. Allison (✉)  
Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre, 1219 Queen Street East, Sault Ste Marie, ON P6A 2E5, Canada  
e-mail: Jeremy.Allison@NRCan.gc.ca

*Present Address:*

M. L. Gimmel  
Division of Entomology, Department of Ecology & Evolutionary Biology, University of Kansas, 1501 Crestline Drive, Suite 140, Lawrence, KS 66045, USA

beetles and the arrival of insect associates. Some insect associates mediate synchrony with bark beetle mass attacks with kairomonal responses to bark beetle aggregation pheromones. The objectives of this study were to document the community of Coleoptera associated with the southern *Ips* (*Ips avulsus*, *Ips calligraphus* and *Ips grandicollis*) and to test the hypothesis that synchrony of insect associates with the southern *Ips* is mediated by kairomonal responses to aggregation pheromones. A large community of Coleoptera (109 species) was recorded from traps baited with southern *Ips* pheromones. A significant treatment effect was observed for the guilds of meristem feeders, natural enemies and woodborers. The southern *Ips* pheromone ipsenol was broadly attractive to meristem feeders, natural enemies and woodborers and in general blends were more attractive than individual compounds. These results demonstrate that a diverse community of Coleoptera is associated with the southern *Ips* and that several members of this community facilitate synchrony with kairomonal responses to southern *Ips* aggregation pheromones.

**Keywords** Ipsenol · ipsdienol · *cis*-verbenol · kairomone · bark beetle natural enemies · bark beetle associates

## Introduction

In the southeastern United States, southern pines colonized by bark beetles are an ephemeral habitat utilized by a diverse assemblage of insect associates (Overgaard 1968; Moser et al. 1971; Camors and Payne 1973; Dixon and Payne 1979). Although many bark beetle associates have little or no measurable impact on bark beetle brood production, some reduce brood production by either competing with brood for the limited phloem tissue or by feeding on brood. Significant reductions in bark beetle brood production by insect associates have been demonstrated with life table and exclusion studies in several ecosystems (e.g., Linit and Stephen 1983; Amman 1984; Riley and Goyer 1986; Schroeder and Weslien 1994). Studies with the southern pine beetle, *Dendroctonus frontalis* Zimmermann (hereafter SPB) (Linit and Stephen 1983) and *Ips avulsus* (Eichhoff), *Ips calligraphus* (Germar) and *Ips grandicollis* (Eichhoff) (hereafter the southern *Ips*) (Miller 1984; Riley and Goyer 1986) reported reductions from 30–40 % to 82 % in brood production associated with concomitant colonization of host material by insect associates.

The degree of synchrony with prey is one factor that influences the impact of natural enemies on prey. The significance of synchrony is particularly acute for bark beetle insect associates because the presence of bark beetle infested trees is highly variable in space and time (Price et al. 1998). Several studies have observed a high degree of synchrony between the initiation of bark beetle mass attacks and the arrival of insect associates (see Payne 1989). One mechanism that would facilitate synchrony is kairomonal responses of associates to semiochemicals associated with bark beetle infested trees (e.g., aggregation pheromones). For example, strong correspondence between the aggregation of natural enemies and the period of peak pheromone production has been reported in the SPB system (Camors and Payne 1973; Dixon and Payne 1979, 1980). Electrophysiological studies have demonstrated that bark beetle natural enemies (Payne et al. 1984; Shepherd et al. 2005) and competitors

(Allison et al. 2001) are capable of detecting bark beetle aggregation pheromones. Field trapping studies have demonstrated attraction of natural enemies (Payne 1989) and competitors (Allison et al. 2004) to bark beetle aggregation pheromones.

The community of insects associated with SPB infested trees has been well described (e.g., Overgaard 1968; Moser et al. 1971; Camors and Payne 1973; Dixon and Payne 1979) and kairomonal responses to SPB pheromones have been reported for several members of this community (e.g., Vité and Williamson 1970). Fewer studies have documented the community of insects associated with the southern *Ips* (Riley and Goyer 1986; Kulhavy et al. 1989), although several studies have documented kairomonal responses to southern *Ips* pheromones (Turnbow and Franklin 1981; Billings and Cameron 1984; Shepherd and Goyer 2003; Shepherd et al. 2005; Miller and Asaro 2005). The objective of this study was to document the community of Coleoptera associated with the southern *Ips* and to test the hypothesis that synchrony of colonization is mediated by kairomonal responses to southern *Ips* pheromones. Specifically, certain non-*Ips* Coleoptera captured in a study of the effects of ipsdienol, ipsenol and *cis*-verbenol on catches of the southern *Ips* (Allison et al. 2012) were processed and analysed for this study. The pheromone components ipsdienol, ipsenol and *cis*-verbenol were chosen because electrophysiological studies have demonstrated that males and females of all three southern *Ips* can detect all three (Smith et al. 1988; Ascoli-Christensen et al. 1993) and chemical analyses have documented the production of *cis*-verbenol by all three species, ipsdienol by *I. avulsus* and *I. calligraphus* and ipsenol by *I. grandicollis* (Vité and Renwick 1971; Renwick and Vité 1972; Vité et al. 1972; Hughes 1974).

## Materials and Methods

### Semiochemical Release Devices

Bubble cap lures loaded with (±)-ipsdienol (= racemic ipsdienol, 50:50 mix of the plus and minus enantiomers), (±)-ipsenol (= racemic ipsenol, 50:50 mix of the plus and minus enantiomers), or *cis*-verbenol (= 13:87 mix of the plus and minus enantiomers) were purchased from Contech Enterprises Inc. (Victoria, British Columbia, Canada) (formerly Phero Tech Inc., Delta, British Columbia, Canada). The chemical purities for all three pheromones was >98 % (Contech Enterprises Inc.). The release rates were estimated to be 0.1–0.2 mg/d at 25 °C for ipsdienol and ipsenol and 0.3–0.6 mg/d at 22 °C for *cis*-verbenol (all release rates were supplied by the manufacturer).

### Field Experiments

Two identical experiments were conducted to characterize the community of insect associates in selected families of Coleoptera attracted to the southern *Ips* pheromone components ipsdienol, ipsenol and *cis*-verbenol. Both experiments used the same design of 48 eight-unit multiple-funnel traps (Contech Enterprises Inc.) deployed in a linear array of six replicate blocks of eight traps per block. In each experiment the following treatments were assigned randomly within each replicate block: 1) unbaited

control, 2) ipsdienol, 3) ipsenol, 4) *cis*-verbenol, 5) ipsdienol plus ipsenol, 6) ipsdienol plus *cis*-verbenol, 7) ipsenol plus *cis*-verbenol, and 8) ipsdienol, ipsenol and *cis*-verbenol.

Experiment 1 was conducted in the Bob R. Jones-Idlewild Research Station, LSU AgCenter, near Clinton, Louisiana from 12 June to 7 August 2009. Experiment 2 was run in the Oconee National Forest, near Eatonton, Georgia from 21 April to 30 June 2009. The stands used for both experiments were predominantly loblolly pine (*Pinus taeda* L.) and each had experienced a prescribed burn within the 12 months preceding trap deployment. Funnel traps were suspended individually on rope strung between two trees such that each trap was  $\geq 2$  m from any tree and the collection cup of each trap was 0.5–1.5 m above ground level. All traps were equipped with a wet collection cup with 150–200 ml of a solution of polypropylene glycol and water, and were spaced ca. 15 m apart within and between blocks. Trap catches were collected every 2–3 weeks. Individuals from most species of the following families of Coleoptera were identified and counted: Bothrideridae, Buprestidae, Cerambycidae, Cleridae, Colydiidae, Curculionidae (*Pachylobius* only), Disteniidae, Histeridae, Passandridae, Phalacridae, Tenebrionidae (*Corticeus* only), Thanerocleridae, Trogossitidae, and Zopheridae. These families were selected because they contain species either known or suspected to be associates of bark beetles. The natural enemy and competitor associates were sorted exhaustively, the fungivores were not (i.e., many species of fungivores were not processed). Species were identified using primary literature and specialized guides and keys, including Nelson (1975) and Wellso and Manley (2007) for Buprestidae; Lingafelter (2007) for Cerambycidae and Disteniidae; Stephan (1989) for Bothrideridae and Colydiidae; Triplehorn (1990) for *Corticeus*; Leavengood (2008, unpublished) for Cleridae and Thanerocleridae; Barron (1971) for Trogossitidae. For instances when published keys proved inadequate or did not exist (e.g., many Histeridae), direct comparisons were made with authoritatively identified specimens in the Louisiana State Arthropod Museum (LSAM), Baton Rouge, LA. Pinned or pointed voucher specimens of all species represented in this study were deposited in the same museum and the remaining specimens were sorted and retained in vials with 95 % ethanol.

### Statistical Analyses

Experimental designs were identical for both experiments (six randomized complete blocks with eight treatments) so the data were analyzed similarly. Both experiments had four collection dates, which were summed for analysis. Total associate abundance of each guild (ectoparasites, fungivores, meristem feeders, natural enemies and woodborers) was analysed first [the ectoparasites and fungivore guilds each had only a single species captured in a high enough abundance for inclusion in the analyses ( $\geq 1$  individual per trap, 48 total)] using a blocked multiresponse permutation procedure (MRBP; McCune et al. 2002). Data were subsequently subjected to separate MRBP analysis for each species within these groups with  $\geq 1$  individual per trap (48 total). Insect trap count data are often non-normal and frequently transformations fail to meet the assumptions of normal theory statistics. MRBP has the benefit that assumptions regarding the distribution of dependent variables are relaxed. All analyses were conducted with PC-ORD 6.0 (MjM Software Design, Gleneden Beach, OR) using Euclidean distances to construct the distance matrix and blocks were aligned before

analysis (McCune et al. 2002). To control the multiplicity effect, researchers typically attempt to control the probability of committing any type I error in families of comparisons under simultaneous consideration (e.g., Bonferroni method). The limitations of this approach include a substantial loss of power with increasing numbers of treatments (see Garcia 2004). Benjamini and Hochberg (1995) present an alternative approach, which controls the false discovery rate (hereafter step-up FDR). The false discovery rate (FDR) is equivalent to the family-wise error rate when all hypotheses are true but is smaller otherwise. As a result, use of step-up FDR can have substantially more power than traditional methods (see Benjamini and Hochberg 1995), particularly when the number of tests is large (Garcia 2004). This study used step-up FDR to control the false discovery rate when “n” (28 in this study) hypotheses were simultaneously tested.

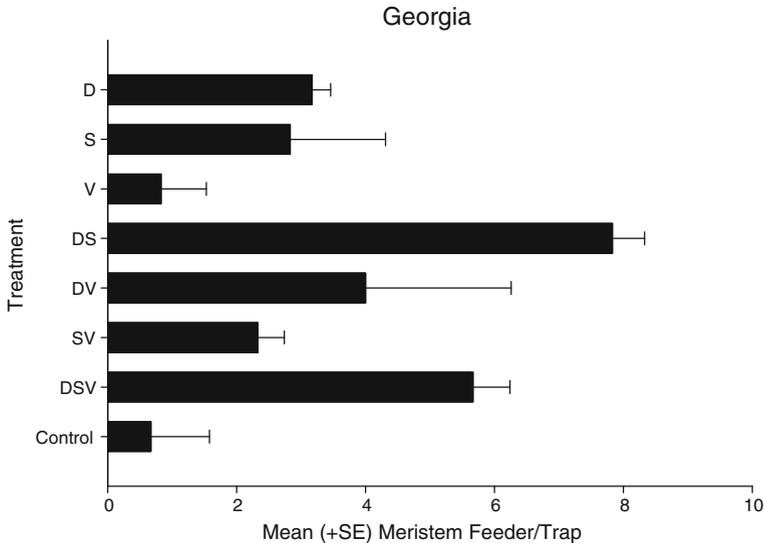
## Results

In total, 12,910 specimens were recorded from a total of 109 species of Coleoptera from target groups, including 1 meristem feeder (Curculionidae), 2 ectoparasites (Bothrideridae and Passandridae), 5 fungivore species (Phalacridae and Zopheridae), 53 natural enemy species (Cleridae, Colydiidae, Histeridae, Tenebrionidae, Thanerocleridae and Trogossitidae) and 49 woodborer species (Buprestidae, Cerambycidae and Disteniidae), (Supplementary Tables 1–3).

**Ectoparasites** A total of 119 ectoparasites were identified from 2 species of Bothrideridae (4 specimens of *Bothrideres geminatus*) and Passandridae (115 specimens of *Catogenus rufus*) (Supplementary Table 1). There were insufficient ectoparasite captures in Louisiana for analyses and only *C. rufus* was captured in high enough numbers for analysis in the Georgia total ectoparasites analysis (i.e., the total ectoparasites and *C. rufus* analysis are the same). Analysis of *C. rufus* did not detect a significant treatment effect in Georgia ( $T=-0.64$ ,  $P<0.23$ ).

**Fungivores** From the fungivores that were examined, five species (367 specimens) were recorded from 5 species of Phalacridae (80 specimens of *Gorginus rubens*) and Zopheridae (287 specimens from 4 species) (Supplementary Table 1). Analysis of total fungivore abundance did not detect a significant treatment effect in Georgia ( $T=0.87$ ,  $P<0.81$ ) or Louisiana (only *Hyporhagus punctulatus* was captured in high enough numbers for inclusion in the analysis) ( $T=1.75$ ,  $P<0.98$ ). Analysis of individual fungivores (species with a mean  $\geq 1.0$  per trap) did not detect a significant treatment effect in *Gorginus rubens* in Georgia ( $T=0.52$ ,  $P<0.67$ ) or *H. punctulatus* in Georgia ( $T=-0.95$ ,  $P<0.16$ ).

**Meristem Feeders** One hundred and seventy meristem feeders were recorded from 1 species of Curculionidae (*Pachylobius picivorus*) (Supplementary Table 1). Analysis of total meristem feeder abundance indicated a significant treatment effect in Georgia ( $T=-3.54$ ,  $P<0.004$ ) (Fig. 1). Louisiana captures had a mean  $\leq 1.0$  per trap and were not analysed. Although a significant treatment effect was detected for *P. picivorus* in Georgia no significant differences were detected among treatment means (Table 1).



**Fig. 1** Effect of *cis*-verbenol (V), ipsdienol (D) and ipsenol (S) on trap catches of meristem feeders in Georgia. There were six replicates per treatment. Means ( $\pm$  SE) are shown. Although a significant treatment effect was detected no significant differences were detected among treatment means

**Natural Enemies** A total of 10,390 natural enemies were recorded from 53 species from the families Cleridae (765 specimens from 9 species), Colydiidae (2,106 specimens from 13 species), Histeridae (3,671 specimens from 19 species), Tenebrionidae (72 specimens from 3 species), Thanerocleridae (2 specimens from 1 species), and Trogossitidae (3,774 specimens from 8 species) (Supplementary Table 2). The most abundant natural enemy was *Temnoscheila virescens* (Trogossitidae,  $N=3,243$ ) in Georgia and *Lasconotus pusillus* (Colydiidae,  $N=930$ ) in Louisiana. Analysis of total natural enemy abundance (species with a mean  $\geq 1.0$  per trap) indicated a significant treatment effect in both Georgia ( $T=-11.28$ ,  $P<0.0001$ ) and Louisiana ( $T=-12.47$ ,  $P<0.0001$ ).

In Georgia 8,333 natural enemies from 43 species of Cleridae (753 specimens from 6 species), Colydiidae (881 specimens from 11 species), Histeridae (3,292 specimens from 14 species), Tenebrionidae (45 specimens from 3 species), Thanerocleridae (2 specimens from 1 species), and Trogossitidae (3,360 specimens from 8 species) were identified (Supplementary Table 2). All of the pheromone-baited treatments captured significantly more natural enemies than the unbaited controls (Fig. 2a). Traps baited with blends including ipsenol all captured significantly more natural enemies than all of the other treatments. The binary blend of ipsdienol plus *cis*-verbenol captured significantly more natural enemies than all of the trap treatments except the two binary blends including ipsenol and the tertiary blend. There were no significant differences in the treatments ipsdienol and ipsenol alone, and both captured significantly more natural enemies than *cis*-verbenol alone and unbaited controls (Fig. 2a).

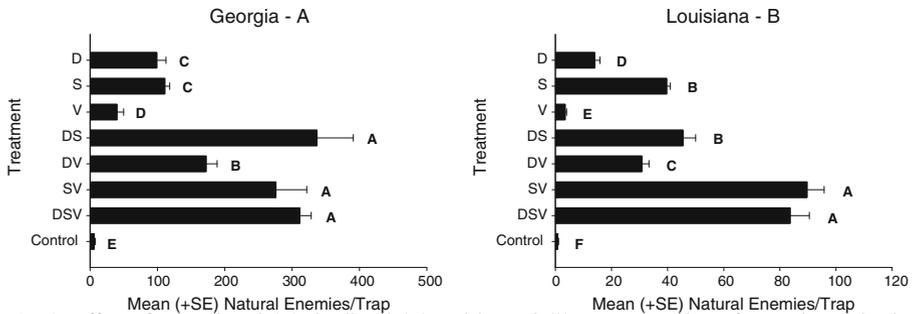
In Louisiana a total of 2,057 natural enemies from 32 species of Cleridae (12 specimens from 4 species), Colydiidae (1,225 specimens from 10 species), Histeridae (379 specimens from 12 species), Tenebrionidae (27 specimens from 3 species), and Trogossitidae (414 specimens from 3 species) were recorded (Supplementary Table 2).

**Table 1** Georgia

Guild	Family	Species	Treatment (mean±SE)									
			Ipsdienol (D)	Ipsenol (S)	cis-Verbenol (V)	D+S	D+V	S+V	D+S+V	Unbaited Control		
Meristem Feeder Natural Enemies	Curculionidae	<i>Pachyllobius pichivorus</i> <sup>a</sup>	3.17±0.91	2.83±0.57	0.83±0.41	7.83±2.26	4.00±0.50	2.33±0.70	5.67±1.48	0.67±0.29		
	Cleridae	<i>Enoclerus nigripes</i>	3.83±0.91 <sup>B</sup>	3.83±1.33 <sup>B</sup>	0±0 <sup>C</sup>	13.0±1.86 <sup>A</sup>	5.33±1.73 <sup>B</sup>	6.17±1.82 <sup>AB</sup>	5.83±2.20 <sup>B</sup>	0±0 <sup>C</sup>		
		<i>Thanasimus dubius</i>	0.50±0.22 <sup>G</sup>	4.50±2.16 <sup>E</sup>	4.0±1.63 <sup>BFG</sup>	9.0±2.03 <sup>CD</sup>	12.17±2.99 <sup>BDE</sup>	35.67±13.98 <sup>AB</sup>	19.17±3.32 <sup>AC</sup>	0.17±0.17 <sup>G</sup>		
Colydidae		<i>Lasconotus pusillus</i>	1.0±0.37 <sup>D</sup>	18.0±1.57 <sup>B</sup>	0.50±0.50 <sup>DE</sup>	13.83±2.54 <sup>B</sup>	4.0±1.03 <sup>C</sup>	30.33±3.75 <sup>A</sup>	18.67±4.27 <sup>B</sup>	0.17±0.17 <sup>E</sup>		
		<i>L. referendarius</i>	3.17±1.01 <sup>CD</sup>	7.0±1.24 <sup>AB</sup>	0.17±0.17 <sup>DE</sup>	7.67±0.95 <sup>AB</sup>	4.67±0.92 <sup>BC</sup>	12.33±1.84 <sup>A</sup>	5.67±1.41 <sup>BC</sup>	0±0 <sup>E</sup>		
		<i>Microsicus parvulus</i> <sup>b</sup>	1.00±0.45	3.17±1.30	0.33±0.21	1.17±0.60	0.67±0.33	0.83±0.48	0.17±0.17	1.17±0.48		
Histeridae		<i>Platysoma attenuatum</i>	57.67±6.21 <sup>C</sup>	22.50±4.92 <sup>D</sup>	0±0 <sup>E</sup>	216.33±43.04 <sup>A</sup>	17.67±2.86 <sup>D</sup>	16.33±5.81 <sup>D</sup>	88.0±10.06 <sup>B</sup>	0±0 <sup>E</sup>		
		<i>P. cylindricum</i>	0.17±0.17 <sup>B</sup>	11.33±0.92 <sup>A</sup>	0±0 <sup>B</sup>	7.0±2.27 <sup>A</sup>	0.33±0.21 <sup>B</sup>	12.0±2.35 <sup>A</sup>	7.83±1.38 <sup>A</sup>	0±0 <sup>B</sup>		
		<i>P. parallelum</i>	4.50±0.62 <sup>B</sup>	1.83±0.48 <sup>CD</sup>	1.0±0.37 <sup>DE</sup>	5.00±1.15 <sup>BC</sup>	31.17±4.59 <sup>A</sup>	22.17±2.44 <sup>A</sup>	18.17±2.95 <sup>A</sup>	0.17±0.17 <sup>E</sup>		
Trogossitidae		<i>Tenmoscheila virescens</i>	25.67±6.92 <sup>D</sup>	37.67±5.93 <sup>D</sup>	32.0±8.01 <sup>CD</sup>	62.67±7.57 <sup>C</sup>	95.0±10.15 <sup>B</sup>	139.5±19.78 <sup>A</sup>	145.5±12.82 <sup>A</sup>	2.50±1.12 <sup>E</sup>		
		<i>Tenebroides corticalis</i> <sup>b</sup>	1.67±0.76	1.50±0.76	2.00±0.68	1.67±0.33	1.33±0.67	0.83±0.40	2.50±0.76	2.00±0.68		
		<i>Buprestis lineata</i> <sup>b</sup>	1.17±0.65	1.83±0.70	0.50±0.34	0.83±0.31	1.83±0.31	1.33±0.56	2.00±0.93	0.50±0.34		
Woodborer		<i>Chalcophora virginianis</i> <sup>b</sup>	1.17±0.31	0.83±0.48	1.00±0.63	2.00±0.89	0.67±0.33	1.83±1.05	0.83±0.48	0.33±0.21		
		<i>Acanthocinus obsoletus</i>	1.33±0.42 <sup>AB</sup>	2.33±0.42 <sup>A</sup>	0±0 <sup>C</sup>	2.50±0.50 <sup>AB</sup>	1.33±0.61 <sup>BC</sup>	2.0±0.68 <sup>AB</sup>	2.67±0.88 <sup>AB</sup>	0±0 <sup>C</sup>		
		<i>Monochamus carolinensis</i>	1.17±0.65 <sup>CD</sup>	11.17±1.60 <sup>AB</sup>	0±0 <sup>D</sup>	10.50±1.84 <sup>AB</sup>	1.33±0.42 <sup>C</sup>	13.50±2.66 <sup>AB</sup>	14.67±2.68 <sup>A</sup>	0±0 <sup>D</sup>		
		<i>M. titillator</i>	5.17±1.28 <sup>D</sup>	12.70±1.2 <sup>BC</sup>	0.50±0.34 <sup>F</sup>	18.80±2.85 <sup>AE</sup>	8.33±1.94 <sup>CDE</sup>	18.80±2.79 <sup>AB</sup>	30±4.60 <sup>A</sup>	0.17±0.17 <sup>F</sup>		
		<i>Typocerus zebra</i> <sup>b</sup>	2.67±0.56	2.17±0.65	1.33±0.95	1.50±0.56	2.50±1.06	4.50±1.20	2.17±0.87	3.00±0.52		

<sup>a</sup> Significant treatment effect detected but no significant differences were detected among treatment means

<sup>b</sup> Significant treatment effect was not detected



**Fig. 2** Effect of *cis*-verbenol (V), ipsdienol (D) and ipsenol (S) on trap catches of natural enemies in Georgia (a) and Louisiana (b). There were six replicates per treatment. Means ( $\pm$  SE) followed by the same letter are not significantly different at  $P=0.05$

All of the pheromone-baited treatments captured significantly more natural enemies than the unbaited controls (Fig. 2b). Traps baited with the binary blend of ipsenol plus *cis*-verbenol or the tertiary blend captured significantly more natural enemies than all other trap treatments (Fig. 2b). The binary blend of ipsenol plus ipsdienol and ipsenol alone captured significantly more natural enemies than all other treatments except the blend of ipsenol plus *cis*-verbenol and the tertiary blend. The blend of ipsdienol plus *cis*-verbenol was significantly more attractive than either component alone, and traps baited with ipsdienol were more attractive than traps baited with *cis*-verbenol (Fig. 2b).

Analyses of individual natural enemies indicated that there was a significant treatment effect in eight species in Georgia (*Enoclerus nigripes*, *Thanasimus dubius*, *Platysoma attenuatum*, *P. cylindricum*, *P. paralelum*, *T. virescens*, *Lasconotus pusillus*, and *L. referendarius*) and five species in Louisiana (*Platysoma coarctatum*, *P. paralelum*, *T. virescens*, *Lasconotus pusillus*, and *L. referendarius*) (Tables 1 and 2). Although there were some differences in the pattern of treatment effects in Georgia and Louisiana, two generalities were evident. Firstly, for all of the species with treatment effects in Georgia and Louisiana, in all but two the most attractive treatments included ipsenol (in all cases at least one of the most attractive treatments contained ipsenol). The treatments ipsdienol plus *cis*-verbenol, ipsenol plus *cis*-verbenol and the tertiary blend all captured significantly more *P. paralelum* in Georgia and *T. virescens* in Louisiana than all other treatments (Tables 1 and 2). Second, the most attractive treatments for 6 of the 8 natural enemies in Georgia and all of the natural enemies in Louisiana were blends of two or more pheromone components. For the natural enemies *P. cylindricum* and *L. referendarius* in Georgia, there were no differences in the captures of traps baited with ipsenol alone and blends including ipsenol and these treatments were significantly more attractive than all other treatments (Tables 1 and 2).

**Woodborers** A total of 1,654 woodborers were recorded from 49 species from the families Buprestidae (237 specimens from 12 species), Cerambycidae (1,416 specimens from 36 species), and Disteniidae (1 specimen) (Supplementary Table 3). In both states *Monochamus titillator* was the most abundant woodborer. Analysis of total woodborer abundance (species with a mean  $\geq 1.0$  per trap) indicated a significant treatment effect in both Georgia ( $T=-9.12$ ,  $P<0.0001$ ) and Louisiana ( $T=-4.23$ ,  $P<$

**Table 2** Louisiana

Guild	Family	Species	Treatment (mean±SE)							
			Ipsdienol (D)	Ipsenol (S)	cis-Verbenol (V)	D+S	D+V	S+V	D+S+V	Unbaited Control
Natural Enemies	Colydiidae	<i>Lasconotus pusillus</i>	2.33±0.84 <sup>E</sup>	26.0±1.13 <sup>C</sup>	0.17±0.17 <sup>F</sup>	20.17±2.55 <sup>C</sup>	8.33±0.99 <sup>D</sup>	57.33±4.67 <sup>A</sup>	40.67±2.76 <sup>B</sup>	0±0 <sup>F</sup>
		<i>L. referendarius</i>	3.17±1.11 <sup>BC</sup>	3.67±0.49 <sup>C</sup>	0.17±0.17 <sup>D</sup>	10.67±2.03 <sup>A</sup>	4.67±0.84 <sup>BC</sup>	5.83±0.60 <sup>B</sup>	12.0±1.86 <sup>A</sup>	0±0 <sup>D</sup>
	Histeridae	<i>Platysoma coarctatum</i> <sup>a</sup>	3.17±1.14	4.17±1.30	0±0	7.00±2.50	1.67±0.56	3.17±1.17	4.67±1.80	0.17±0.17
		<i>P. parallelum</i>	0.67±0.33 <sup>CD</sup>	1.17±0.48 <sup>BC</sup>	0±0 <sup>D</sup>	2.33±0.56 <sup>B</sup>	3.0±0.73 <sup>B</sup>	6.33±1.48 <sup>A</sup>	9.83±1.66 <sup>A</sup>	0±0 <sup>D</sup>
Trogossitidae		<i>Temnoscheila virescens</i>	4.67±2.08 <sup>B</sup>	4.67±1.20 <sup>B</sup>	3.17±0.65 <sup>BC</sup>	5.33±1.52 <sup>B</sup>	13.17±2.30 <sup>A</sup>	16.50±1.95 <sup>A</sup>	0.67±0.21 <sup>C</sup>	
Woodborer	Cerambycidae	<i>Acanthocinus obsoletus</i> <sup>a</sup>	1.0±0.26	0.67±0.21	0±0	2.08±8.20	1.0±0.26	1.0±0.45	3.17±1.30	0±0
		<i>Monoctonus titillator</i> <sup>a</sup>	0.67±0.49	1.67±0.92	0±0	1.17±0.48	1.50±0.50	1.67±0.92	2.67±0.71	0±0

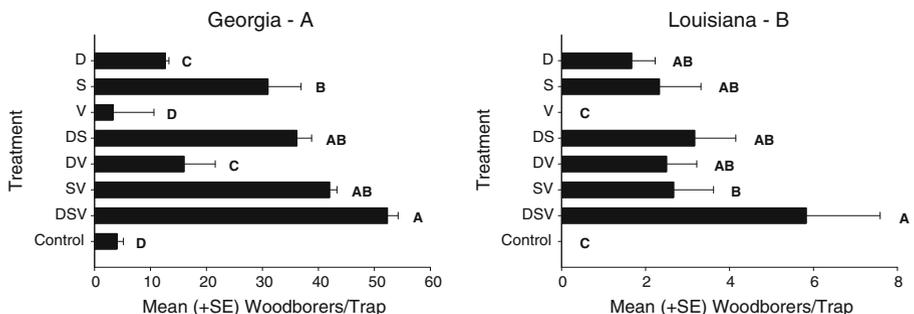
<sup>a</sup> Significant treatment effect detected but no significant differences were detected among treatment means

0.00094). In both states unbaited controls and traps baited with *cis*-verbenol only captured the fewest woodborers and traps baited with the tertiary blend captured the most (Fig. 3). The overall pattern of mean total woodborer trap captures was similar in Georgia and Louisiana.

In Georgia, 1,445 woodborers from 41 species of Buprestidae (204 specimens from 11 species) and Cerambycidae (1,241 specimens from 30 species) were identified (Supplementary Table 1). Traps baited with the tertiary blend captured significantly more woodborers than all other trap treatments except the ipsenol plus *cis*-verbenol and ipsdienol plus ipsenol treatments (Fig. 3a). Traps baited with ipsenol alone or either of the binary combinations including ipsenol all captured significantly more woodborers than traps baited with ipsdienol or *cis*-verbenol alone, ipsdienol plus *cis*-verbenol, and unbaited control traps (Fig. 3a). Traps baited with ipsdienol alone or ipsdienol plus *cis*-verbenol both captured significantly more woodborers than traps baited with *cis*-verbenol alone or unbaited traps (Fig. 3a).

In Louisiana, 209 woodborers from 21 species of Buprestidae (33 specimens from 4 species), Cerambycidae (175 specimens from 16 species) and Disteniidae (1 specimen) were captured (Supplementary Table 1). Traps baited with the tertiary blend captured significantly more woodborers than traps baited with *cis*-verbenol alone, ipsenol plus *cis*-verbenol and unbaited control traps. Unbaited control traps and traps baited with *cis*-verbenol alone both captured significantly fewer woodborers than all other trap treatments (Fig. 3b).

Subsequent analyses by species indicated that there was a significant treatment effect in three species in Georgia (*Acanthocinus obsoletus*, *Monochamus carolinensis*, and *M. titillator*) and two species in Louisiana (*A. obsoletus* and *M. titillator*) (Tables 1 and 2). Although there were some differences among species in the pattern of treatment effects in Georgia, some generalities were evident. Significantly more *A. obsoletus*, *M. carolinensis* and *M. titillator* were captured by traps baited with ipsenol alone, either of the binary combinations including ipsenol and traps baited with the tertiary blend than unbaited controls (Table 1). Traps baited with the tertiary blend captured significantly more *M. titillator* than traps baited with ipsenol only. In Georgia, mean trap catches were lowest for the unbaited control, *cis*-verbenol alone and *cis*-verbenol plus ipsdienol treatments and there was no significant difference in the mean trap catch of unbaited controls and traps baited with *cis*-verbenol (Table 1).



**Fig. 3** Effect of *cis*-verbenol (V), ipsdienol (D) and ipsenol (S) on trap catches of woodborers in Georgia (a) and Louisiana (b). There were six replicates per treatment. Means ( $\pm$  SE) followed by the same letter are not significantly different at  $P=0.05$

In Louisiana although a significant treatment effect was detected for *A. obsoletus* and *M. titillator*, no significant differences were detected among treatment means (Table 2).

## Discussion

This study documented a large community of Coleoptera captured in southern *Ips* pheromone baited traps (Supplementary Tables 1–3) including ectoparasites ( $N=2$  species), fungivores ( $N=5$  species), meristem feeders ( $N=1$  species), natural enemies ( $N=53$  species) and woodborers ( $N=49$  species). A significant treatment effect was observed for meristem feeders in Georgia and both natural enemies and woodborers in Georgia and Louisiana (Figs. 1, 2 and 3). In general, traps baited with the binary blends containing ipsenol or the tertiary blend captured more insect associates than the binary blend of ipsdienol and *cis*-verbenol and ipsenol, ipsdienol or *cis*-verbenol alone (Figs 2 and 3).

These results strongly suggest that some associates synchronize their presence at southern *Ips* mass-attacked host material via exploitation of bark beetle aggregation pheromones. The most common direct evidence of exploitation of chemical signals is the capture of illicit receivers in baited traps (Haynes and Yeorgan 1999). The results of these trapping studies are consistent with the hypothesis of illicit reception of signals; however, this type of evidence can be confounded because the exploited species are also usually captured in the baited traps, creating the potential for the presence of other cues associated with the exploited species. Although this study also captured large numbers of southern *Ips* (Allison et al. 2012), the use of wet cups to kill all captured insects shortly after capture in traps would significantly reduce the potential for the presence of additional confounding cues.

A significant treatment effect was observed for a total of thirteen species in Georgia and Louisiana (Tables 1 and 2). For seven of these thirteen species, kaironomal responses have already been reported. Attraction of the meristem feeder *Pachylobius picivorus* to traps baited with ipsdienol or ipsenol alone has been reported and although not statistically significant, captures of *P. picivorus* appeared to be higher to blends of bark beetle pheromones than to individual pheromones (Miller and Asaro 2005). Several studies have reported attraction of the natural enemy *Thanasimus dubius* to bark beetle (SPB and *Ips*) pheromones (e.g., Billings and Cameron 1984; Reeve et al. 2009). The natural enemy *T. virescens* is attracted to traps baited with the tertiary blend of ipsdienol, ipsenol and *cis*-verbenol (Billings and Cameron 1984) and to the binary blends of  $\alpha$ -pinene plus each of ipsdienol, ipsenol or frontalin (Reeve et al. 2009). Reeve et al. (2009) also demonstrated that for *T. virescens* the  $\alpha$ -pinene plus ipsdienol and  $\alpha$ -pinene plus ipsenol treatments both captured more individuals than the  $\alpha$ -pinene plus frontalin treatment. Attraction of the natural enemies *Platysoma cylindricum* and *Platysoma parallelum* to traps baited with some enantiomeric ratios of ipsdienol (with and without the pheromone lanierone) has been reported (Raffa and Klepzig 1989; Aukema et al. 2000). Shepherd et al. (2005) reported attraction of *P. parallelum* to frontalin and ipsenol, but not ipsdienol in laboratory walking bioassays. Traps baited with either ipsdienol or ipsenol alone captured significantly more *Acanthocinus obsoletus* than unbaited controls (Miller and Asaro 2005) (this study also provides some evidence that blends are more

attractive than individual compounds). Similarly, traps baited with  $\alpha$ -pinene, ethanol, ipsdienol and ipsenol captured significantly more *A. obsoletus* than traps baited with the binary combinations of  $\alpha$ -pinene plus ethanol or ipsdienol and ipsenol (Miller et al. 2011). The tertiary blend of ipsdienol, ipsenol and *cis*-verbenol (Billings and Cameron 1984), ipsenol alone or combined with either or both lanierone or ipsdienol (Miller and Asaro 2005) and traps baited with  $\alpha$ -pinene, ethanol, ipsdienol and ipsenol (Miller et al. 2011) all had significant effects on *Monochamus titillator* trap catches.

To our knowledge this study is the first to demonstrate kairomonal responses for the natural enemies *E. nigripes*, *Platysoma attenuatum*, *Platysoma coarctatum*, *Lasconotus pusillus* and *Lasconotus referendarius* and the woodborer *Monochamus carolinensis* to southern *Ips* pheromones. Although previously unknown, these responses are not surprising. Kairomonal responses of the natural enemy *E. nigripes* have been reported for the cone beetle pheromone pityol (de Groot and DeBarr 2000; Miller 2007). Zhang et al. (2008) reported electrophysiological responses of *Lasconotus tuberculatus* to ipsenol and *trans*-verbenol and attraction of *Lasconotus laqueatus* (Steed and Wagner 2008) and *Lasconotus intricatus* (Bowers and Borden 1992) to bark beetle pheromones has been reported. Finally, several congeners of *Monochamus carolinensis* are attracted to bark beetle pheromones (see Allison et al. 2001, 2003, 2004; Miller and Asaro 2005) and some literature exists that suggests that *M. carolinensis* is attracted to ipsdienol (Raffa 1991) and ipsenol (Erbilgin and Raffa 2000).

The existing literature is consistent with the main result of this study, that kairomonal responses to aggregation pheromones appear to be an important mechanism for facilitating synchrony of some southern *Ips* associates (Tables 1 and 2). In general, ipsenol appears broadly attractive and blends containing ipsenol appear more attractive than individual pheromones (Turnbow and Franklin 1981; Shepherd et al. 2005; Miller and Asaro 2005; Reeve et al. 2009; Miller et al. 2011) (Tables 1 and 2 and Figs. 1, 2 and 3). In addition to promoting synchrony of associate arrival at bark beetle mass attacks and the associated reductions in bark beetle brood production (e.g., Linit and Stephen 1983; Riley and Goyer 1986), kairomonal responses are likely an important factor in the hypothesized role of natural enemies in some bark beetle population cycles (e.g., Reeve 1997; Turchin et al. 1999; Reeve and Turchin 2002). Given the negative consequences resource competitors and natural enemies (e.g., Schroeder and Weslien 1994) can have on bark beetle brood production, the kairomonal responses observed in this study are likely examples of exploitation by illicit receivers (Otte 1974).

Illicit receivers have the potential to constrain signal evolution and it has been hypothesized that runaway sexual selection of signals may be limited by costs associated with increased detectability by illicit receivers. Haynes and Yeargan (1999) point out that many communication systems are cryptic, species-specific and require specialized mechanisms for detection. As a consequence, illicit receivers that exploit low amplitude signals (e.g., sex pheromones) are assumed to be specialists whereas this assumption is relaxed for species that exploit high amplitude signals (e.g., aggregation pheromones) (Haynes and Yeargan 1999). Illicit receivers of bark beetle pheromones are considered habitat specialists (bark beetle colonized trees); however, within their habitat they are often feeding generalists that are able to respond to the pheromones of many species (Payne et al. 1984; Shepherd et al. 2005).

If exploitation of a communication system by an illicit receiver persists in evolutionary time, the predictable costs experienced by the signaler must be less than the costs associated with reduced intraspecific function that would accompany signal evolution. Evolutionary theory predicts change in the communication system if the costs of exploitation exceed those associated with signal evolution and heritable variation exists in signal production and response traits. Change in the communication system may in turn select for change in the illicit receiver (i.e., co-evolution of signaler and illicit receiver). For example, disparities exist between the responses of *Ips pini* (Say) and its associated natural enemies to pheromone blends with varying component composition and enantiomeric ratios (Raffa 2001). Repeatable variation in male signal production and female pheromone preferences in *I. pini* (Teale et al. 1994; Hager and Teale 1994, 1996) is consistent with the hypothesis that *I. pini* pheromone blends and predator preferences are co-evolving (see Raffa 2001).

The consequences of quantitative and qualitative variation in southern *Ips* aggregation pheromones are not fully understood. Some studies have demonstrated that variation in enantiomeric ratios and the presence and absence of pheromone components influences southern *Ips* behavior (Smith et al. 1993; Miller and Allison 2011; Allison et al. 2012). Nothing is known about the genetics of pheromone signal and response traits in the southern *Ips*. In the absence of an improved understanding of the causes and consequences of variation in southern *Ips* aggregation pheromones it is not possible to predict either the nature or strength of selection illicit receivers impose on southern *Ips* aggregation pheromones.

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