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Pine Sawyers (Coleoptera: Cerambycidae) Attracted to α-Pinene, Monochamol, and Ipsenol in North America

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Abstract

Detection tools are needed for *Monochamus* species (Coleoptera: Cerambycidae) because they are known to introduce pine wilt disease by vectoring nematodes in Asia, Europe, and North America. In 2012–2014, we examined the effects of the semiochemicals monochamol and ipsenol on the flight responses of the sawyer beetles *Monochamus carolinensis* (Olivier), *Monochamus clamator* (LeConte), *Monochamus mutator* LeConte, *Monochamus notatus* (Drury), *Monochamus obtusus* Casey, *Monochamus scutellatus* (Say), and *Monochamus titillator* (F.) complex (Coleoptera: Cerambycidae) to traps baited with α-pinene. Experiments were set in pine forests in New Brunswick and Ontario (Canada), and Arizona, Georgia, Michigan, Montana, Oregon, South Carolina, Utah, and Washington (United States). In brief, 40 traps were placed in 10 blocks of 4 traps per block per location. Traps were baited with: 1) α-pinene; 2) α-pinene + monochamol; 3) α-pinene + ipsenol; and 4) α-pinene + monochamol + ipsenol. Monochamol increased catches of six species and one species complex of *Monochamus* with an additive effect of ipsenol for five species and one species complex. There was no evidence of synergy between monochamol and ipsenol on beetle catches. Monochamol had no effect on catches of other Cerambycidae or on any associated species of bark beetles, weevils, or bark beetle predators. We present a robust data set suggesting that the combination of α-pinene, ipsenol, and monochamol may be a useful lure for detecting *Monochamus* species.

Key words: α-pinene, monochamol, ipsenol, detection, trapping

Recent introductions of adventive species such as the Asian longhorn beetle, *Anoplophora glabripennis* (Motschulsky) (Coleoptera: Cerambycidae), have highlighted the need for better detection tools for wood borers (Allison et al. 2004, Hanks et al. 2012, Miller et al. 2013b). Some borers such as pine sawyers (*Monochamus* spp.) can carry nematodes that cause pine wilt disease, a disease that has resulted in the death of thousands of trees in Asia and now poses a threat to forests in Europe (Wingfield et al. 1982, Evans et al. 1996, Vincente et al. 2012). Eight species of *Monochamus* are native to Canada and the United States, with seven found in pine forests (Lingafelter 2007, Bezark 2015).

A popular tool in detection programs is the combination of a trap and an attractant. Pine sawyers are broadly attracted to host volatiles such as α-pinene and bark beetle pheromones such as ipsenol (Allison et al. 2004, Pajares et al. 2004, Miller et al. 2013b, and references therein). Pajares et al. (2010) identified monochamol (2-undecyloxy-ethanol) as a male-produced aggregation pheromone for *Monochamus galloprovincialis* (Olivier) (native to Europe).

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Table 1. Locations, predominant pine species, brands of antifreeze, and trapping dates for each of 11 experiments on flight responses of *Monochamus* species to multiple-funnel traps baited with α-pinene, monochamol, and ipsenol in North America

Exp.	Location	Coordinates	Predominant tree species	Brand of RV antifreeze	Type of funnel trap	Trapping dates
1	Centennial Forest, Flagstaff, Coconino Co., AZ	35.163 N, 111.762 W	*Pinus ponderosa* P. Lawson	Splash[a]	12-Unit	5 June–31 July 2013
2	Scull Shoals Experiment Forest, Greene Co., GA	33.742 N, 83.282 W	*Pinus taeda* L. and *Pinus echinata* Miller	Splash[a]	10-Unit[b]	17 May–2 July 2012
3	Scull Shoals Experiment Forest, Oglethorpe Co., GA	33.775 N, 83.246 W	*P. taeda* and *P. echinata*	Splash[a]	10-Unit[b]	24 April–24 June 2014
4	Kellogg Research Forest, Kalamazoo Co., MI	43.356 N, 85.340 W	*P. resinosa* Aiton	Prestone[c]	12-Unit[b]	25 June–13 Aug. 2013
5	Missoula, Missoula Co., MT	46.813 N, 113.939 W	*P. ponderosa*, *Pseudotsugae menziesii* (Mirbel), and *Larix occidentalis* Nuttall	Winter Ban[d]	12-Unit	3 July–22 Aug. 2013
6	Acadia Research Forest, Sunbury Co., NB	45.999 N, 66.263 W	*Pinus strobus* L., *Abies balsamea* (L), and *Picea rubens* Sargent	Prestone[c]	12-Unit	27 June–15 Aug. 2013
7	Aubrey Falls Provincial Park, Algoma Co., ON	47.022 N, 83.191 W	*Pinus banksiana* Lambert, *Picea glauca* (Moench) Voss, and *A. balsamea*	Prestone[c]	12-Unit	16 July–29 Aug. 2012
8	Deschutes National Forest, Jefferson Co., OR	44.480 N, 121.664 W	*P. ponderosae*	Winter Ban[d]	10-Unit[b]	4 July–30 Aug. 2013
9	Harbison State Forest, Richland Co., SC	34.086 N, 81.116 W	*P. taeda*	Splash[a]	10-Unit[b]	17 July–12 Sep. 2012
10	Uinta-Wasatch-Cache National Forest, Summit Co., UT	40.854 N, 110.890 W	*Pinus contorta* Douglas, *Picea engelmannii* Engelmann, and *Abies lasiocarpa* Nuttall	Quicksilver[e]	12-Unit	9 July–11 Sep. 2013
11	Wenatchee National Forest, Chelan Co., WA	47.784 N, 120.706 W	*P. ponderosae* and *P. menziesii*	Winter Ban[d]	10-Unit[b]	26 June–5 Sep. 2012

[a] Splash RV & Marine Antifreeze, Fox Packaging Inc., St. Paul, MN.

[b] Modified by widening size of funnel openings as in Miller et al. (2013a).

[c] Prestone Low Tox Antifreeze, Prestone Products Corp., Danbury, CT.

[d] Winter Ban-50, CAMCO Mfg. Inc., Greensboro, NC.

[e] Quicksilver −50°F Water System Antifreeze, Mercury Marine, Fond du Lac, WI.

Teale et al. (2011) found that male *Monochamus alternatus* Hope (native to Asia) produced monochamol, and that both sexes of *M. alternatus* were attracted to it. In New York, monochamol is produced by male *M. scutellatus*, and is attractive to both sexes of *M. scutellatus* and *M. notatus* in stands of *Pinus strobus* L. (Fierke et al. 2012). In Louisiana, Allison et al. (2012) found production of monochamol by male *M. carolinensis* and male *M. titillator*, with attraction to monochamol exhibited by both sexes of each species in stands of loblolly pine, *Pinus taeda* L. In addition, monochamol is attractive to *M. clamator*, *M. obtusus*, and *M. scutellatus* in stands of *Pinus ponderosa* Lawson & Lawson in British Columbia, Canada (Macias-Samano et al. 2012). Similarly, monochamol increased trap catches of *Monochamus urossovii* (Fischer) in Poland, *Monochamus saltuarius* (Gebler) in China, and *M. scutellatus* and *M. notatus* in New Brunswick and Ontario, Canada (Ryall et al. 2015).

α-Pinene is an important synergist for *M. carolinensis* and *M. titillator* in responding to monochamol (Allison et al. 2012). Catches of *M. scutellatus* in monochamol-baited traps were enhanced by the addition of α-pinene and ethanol in New Brunswick (Ryall et al. 2015). The bark beetle pheromone ipsenol is attractive to pine sawyers, typically in association with α-pinene (Miller et al. 2013b). Our goal was to assess the attractiveness of the tertiary combination of α-pinene, monochamol, and ipsenol to seven species of *Monochamus* in North America. The binary blend of ipsenol and ipsdienol increased numbers of *M. clamator* (but not *M. obtusus* or *M. scutellatus*) in traps baited with monochamol, α-pinene, and ethanol in British Columbia, Canada (Macias-Samano et al. 2012). We also noted impacts of monochamol and ipsenol on attraction of other Cerambycidae, bark beetles (Coleoptera: Curculionidae: Scolytinae), and associated predators.

Materials and Methods

In each of 11 locations, 40 multiple-funnel traps were hung at breast height in 10 blocks of 4 traps per block. The methodology was the same as that used by Miller et al. (2013b, 2015), with the following characteristics for the current study: 1) locations, tree species in forest, trapping periods, brands of alcohol-free RV antifreeze, trap type, and trapping periods as noted in Table 1; 2) lures used in study as noted in Table 2; and 3) intertrap spacing of 10-25 m and each trap >2 m from a tree. Traps within each block were baited with one of the following: 1) α-pinene; 2) α-pinene + monochamol; 3) α-pinene + ipsenol; and 4) α-pinene + ipsenol + monochamol. As noted by Miller et al. (2013b), separating *M. carolinensis* from *M. titillator* is difficult where the two species are sympatric, specifically Georgia and South Carolina in our study. Therefore, we retained *M. titillator* complex for those two locations and *M. carolinensis* in Michigan. Voucher specimens were deposited in the Entomology Collection, Museum of Natural History, University of Georgia (Athens, GA).

Table 2. Description of lures used in the study

Compound	Supplier	Release rate[a]
α-Pinene, 75% (–)	Contech Enterprises[b]	2–6 g/d at 25°C
Ipsenol, racemic (2012)	Synergy Semiochemicals[c]	0.4 mg/d at 20°C
Ipsenol, racemic (2014)	Contech Enterprises[b]	0.2 mg/d at 20°C
Monochamol	Synergy Semiochemicals[c]	0.8 mg/d at 20°C

All chemical purities >95%

[a] Determined by manufacturer.

[b] Victoria, BC Canada.

[c] Burnaby, BC Canada.

The statistical methodology used in the study was similar to that used by Miller et al. (2013b) on catch numbers, transformed by ln (Y+1) to ensure homoscedasticity and normality in the data sets (Pepper et al. 1997), and on sex ratio data expressed as the proportion of female beetles among the total of males and females of a given species. A treatment was omitted from analysis when all traps with the same bait at a location had no beetle catches. Analyses of sex ratio data were conducted only on treatments containing monochamol and/or ipsenol, as too few beetles were captured in traps baited solely with α-pinene to determine sex ratio accurately without high variances. Three separate analysis of variance (ANOVA) models were used to analyze the data. Model 1 components were 1) replicate (nested within location); 2) location; 3) treatment; and 4) location × treatment, whereas Model 2 components were 1) replicate; 2) monochamol (M); 3) ipsenol (S); and 4) M × S. The SYSTAT statistical package (SYSTAT Software Inc., Point Richmond, CA) was used for Models 1 and 2. The components for Model 3 were 1) replicate and 2) treatment, followed by the Holm–Sidak multiple comparison procedure ($\alpha = 0.05$) and conducted with the SigmaStat (ver. 3.01) statistical package (SYSTAT Software Inc.).

Results

Sufficient numbers of beetles ($N \geq 30$) to conduct analyses were obtained for seven species of pine sawyers; *Monochamus marmorator* was not captured in our study. In Michigan, trap catches of *M. carolinensis* were increased by both monochamol ($F_{1,\ 27} = 70.17$, $P < 0.001$) and ipsenol ($F_{1,\ 27} = 175.1$, $P < 0.001$). Beetle catches were greatest in traps with α-pinene + monochamol + ipsenol (Fig. 1A). Traps with α-pinene + ipsenol caught more *M. carolinensis* than those with α-pinene + monochamol; catches in both treatments were greater than those in traps with α-pinene alone. There was no significant treatment effect on proportion of females (P_F) in trap catches, which exhibited a female-biased sex ratio of about 2:1 and an overall mean P_F (±SE) = 0.68 ± 0.02 (Table 3).

There was a significant effect on catches of *M. titillator* complex across the locations/years with a significant interaction across locations/years (Table 4). In South Carolina (2012), catches were affected by ipsenol ($F_{1,\ 27} = 39.82$, $P < 0.001$) but not monochamol ($F_{1,\ 27} = 3.91$, $P = 0.058$), with no significant interaction between ipsenol and monochamol on catches of beetles ($F_{1,\ 27} = 0.126$, $P = 0.725$). In Georgia (2012), catches were affected by both ipsenol ($F_{1,\ 27} = 489.1$, $P < 0.001$) and monochamol ($F_{1,\ 27} = 88.92$, $P < 0.001$), with a significant interaction between the two ($F_{1,\ 27} = 89.45$, $P < 0.001$). The highest numbers of *M. titillator* complex (in both Georgia and South Carolina in 2012) were in traps with α-pinene + ipsenol and in traps with α-pinene + monochamol + ipsenol (Fig. 1B,C), with no difference between the two at each location in 2012. As in 2012, catches of sawyer beetles in Georgia in 2014 were affected by both ipsenol ($F_{1,\ 27} = 202.2$, $P < 0.001$) and monochamol ($F_{1,\ 27} = 136.8$, $P < 0.001$), with a significant interaction between the two factors ($F_{1,\ 27} = 29.42$, $P < 0.001$). In contrast to 2012, numbers of beetles (in Georgia in 2014) were greatest in traps with α-pinene + monochamol + ipsenol (Fig. 1D). Traps with α-pinene + ipsenol caught the same number of *M. titillator* complex as those with α-pinene + monochamol; catches in both treatment types of traps were greater than in traps with α-pinene alone. *Monochamus titillator* complex was not collected elsewhere.

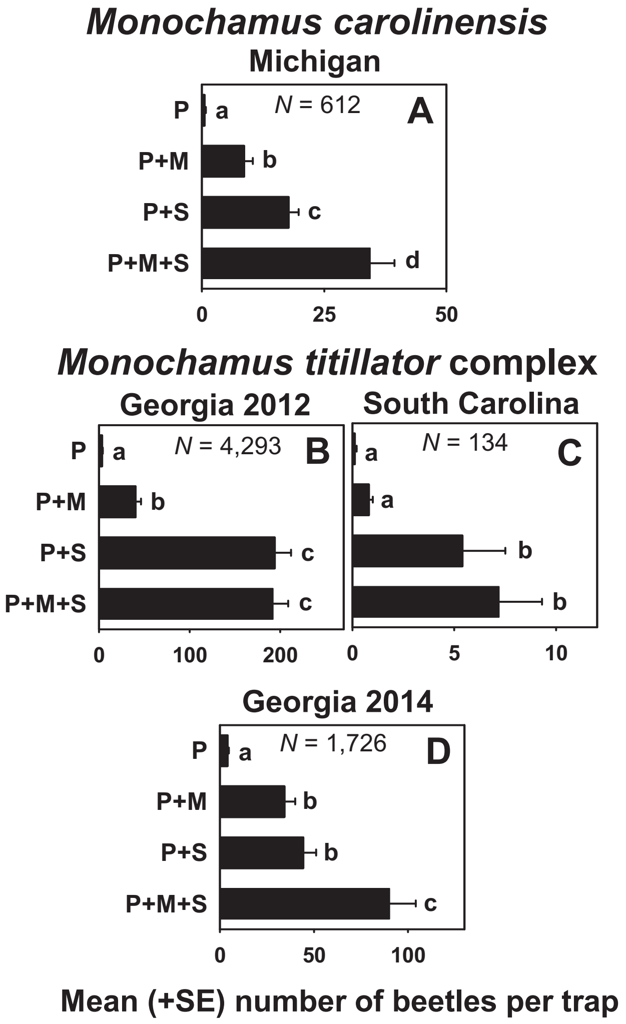

Fig. 1. Mean (+ SE) number of *Monochamus carolinensis* (A) and *M. titillator* complex (B–D) captured in multiple-funnel traps baited with α-pinene (P), α-pinene + ipsenol (P + S), α-pinene + monochamol (P + M), and α-pinene + ipsenol + monochamol (P + S + M) in Georgia (B, D), Michigan (A), and South Carolina (C). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). N = Total trap catch of beetles per location.

Trap catches of *M. titillator* complex tended to be female-biased in South Carolina with an overall sex ratio between 3:2 and 3:1, overall mean P_F (±SE) = 0.63 ± 0.08 (Table 3). There was no significant effect of treatment on P_F of *M. titillator* complex in South Carolina trap catches (Table 3). The sex ratio of *M. titillator* complex in trap catches in Georgia was affected by treatments in both 2012 and 2014 (Table 3), with catches in traps with α-pinene + monochamol more female-biased (with a sex ratio of 3:1 and

Table 3. Proportion of trap catches of *Monochamus* species consisting of female beetles (P_F) in experiments on flight responses to multiple-funnel traps baited with α-pinene + monochamol (P + M), α-pinene + ipsenol (P + S), and α-pinene + monochamol + ipsenol (P + M + S) in North America

Species	Location	Mean P_F (± SE) per trap			ANOVA		
		P + M	P + S	P + M + S	df	*F*	*P*
M. carolinensis	MI	0.72 ± 0.04	0.67 ± 0.04	0.62 ± 0.04	2,18	2.516	0.109
M. clamator	AZ	0.62 ± 0.02b	0.32 ± 0.03a	0.58 ± 0.01b	2,18	48.32	<0.001
	MT	0.73 ± 0.06	0.58 ± 0.06	0.72 ± 0.06	2,17	3.554	0.051
	OR	0.70 ± 0.02b	0.53 ± 0.03a	0.71 ± 0.02b	2,18	34.27	<0.001
	WA	0.82 ± 0.08	0.59 ± 0.10	0.78 ± 0.08	2,16	1.806	0.196
M. mutator	ON	0.50 ± 0.03	0.48 ± 0.03	0.57 ± 0.03	2,18	3.064	0.072
M. notatus	ON	0.46 ± 0.13	0.64 ± 0.13	0.61 ± 0.12	2,12	0.526	0.604
M. obtusus	OR	0.66 ± 0.02b	0.58 ± 0.03a	0.62 ± 0.01ab	2,18	3.868	0.040
	MT	0.69 ± 0.09	0.76 ± 0.12	0.73 ± 0.09	2,15	0.108	0.898
	WA	0.67 ± 0.02b	0.46 ± 0.04a	0.60 ± 0.01b	2,18	19.66	<0.001
M. scutellatus	MI	0.76 ± 0.10	0.73 ± 0.14	0.79 ± 0.12	2,14	0.064	0.939
	MT	0.63 ± 0.09	0.44 ± 0.09	0.63 ± 0.07	2,14	2.407	0.118
	NB	0.63 ± 0.09	0.30 ± 0.14	0.71 ± 0.09	2,14	3.727	0.050
	ON	0.51 ± 0.02	0.51 ± 0.04	0.59 ± 0.03	2,18	1.807	0.193
	UT	0.64 ± 0.04	0.48 ± 0.07	0.62 ± 0.04	2,18	3.557	0.050
M. titillator complex	GA 2012	0.74 ± 0.02b	0.49 ± 0.02a	0.54 ± 0.04a	2,18	58.156	<0.001
	SC	0.75 ± 0.14	0.66 ± 0.11	0.60 ± 0.11	2,12	0.375	0.695
	GA 2014	0.64 ± 0.04b	0.43 ± 0.03a	0.54 ± 0.02a	2,18	10.312	0.001

At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test).

Table 4. ANOVA table for effects of treatment (T), location (L), treatment and location interaction (T × L), and replicate nested within location (R{L}) on catches of *M. clamator*, *M. obtusus*, *M. scutellatus*, and *M. titillator* complex in North America

Factor	*M. clamator*			*M. obtusus*			*M. scutellatus*			*M. titillator* complex		
	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*	df	*F*	*P*
T	3	679.6	<0.001	3	216.8	<0.001	3	37.58	<0.001	3	49.56	<0.001
L	3	339.2	<0.001	2	319.2	<0.001	4	51.93	<0.001	2	96.15	<0.001
T × L	9	2.53	0.011	6	9.13	<0.001	12	0.72	<0.001	6	3.76	<0.001
R{L}	36	2.26	0.001	27	1.30	0.186	45	0.47	<0.001	27	0.46	0.016
Error	108			81			135			81		

2:1, respectively) than those in traps with α-pinene + ipsenol and the tertiary blend (sex ratio about 1:1). There was no difference in P_F for the latter two treatments in both years, with overall mean (±SE) $P_F = 0.51 \pm 0.01$ and 0.48 ± 0.02 for 2012 and 2014, respectively.

Treatment and location had significant effects on numbers of *M. scutellatus* captured in traps across six locations in North America, with a significant interaction between location and treatments (Table 4). At five locations, numbers of *M. scutellatus* were highest in traps with α-pinene + monochamol and in traps baited with the tertiary blend, with no significant difference between these two treatments (Fig. 2B–F). At the sixth location (Michigan), there were fewer *M. scutellatus* in traps with α-pinene + monochamol + ipsenol than in traps with α-pinene + monochamol (Fig. 2A). Numbers of beetles in traps with α-pinene + ipsenol were greater than those baited solely with α-pinene in Montana, Ontario, and Utah (Fig. 2B,D,E), but not in Michigan, New Brunswick, and Washington (Fig. 2A,C,F). There was a significant effect of treatment on the proportion of females in catches (P_F) of *M. scutellatus* in New Brunswick and Utah, with catches seemingly more female-biased in traps with α-pinene + monochamol and the tertiary blend of α-pinene + monochamol + ipsenol than in traps with α-pinene + ipsenol, although the Holm–Sidak test was unable to separate mean P_F (Table 3). There was no significant treatment effect on the sex ratio of captured beetles in Michigan, Montana, and Ontario, with overall sex ratios ranging from 3:1 in Michigan to 1:1 in Ontario.

In the western United States, trap treatments had a significant effect on catches of *M. clamator* across four states and *M. obtusus* across three states (Table 4). For both species, traps with the tertiary blend of α-pinene + monochamol + ipsenol outperformed the other three treatments in all locations (Fig. 3). Numbers of *M. clamator* and *M. obtusus* were greater in traps with α-pinene + monochamol than in traps baited with α-pinene + ipsenol, with catches in both greater than those in traps baited solely with α-pinene. Only two *M. clamator* were captured in Utah. *Monochamus obtusus* was not collected elsewhere.

Catches of *M. clamator* and *M. obtusus* in traps baited with monochamol tended to be female-biased, with ratios ranging from 3:2 to 4:1 (Table 3). In Arizona and Oregon, but not Montana or Washington, P_F of *M. clamator* was significantly greater in traps with α-pinene + monochamol and in traps with α-pinene + monochamol + ipsenol than in traps with α-pinene + ipsenol. The same was true for *M. obtusus* in Oregon and Washington, but not Montana.

Monochamus mutator was captured only in Ontario, whereas *M. notatus* was captured in Ontario and New Brunswick. Both monochamol ($F_{1,\ 27} = 71.21$, $P < 0.001$) and ipsenol ($F_{1,\ 27} = 63.52$,

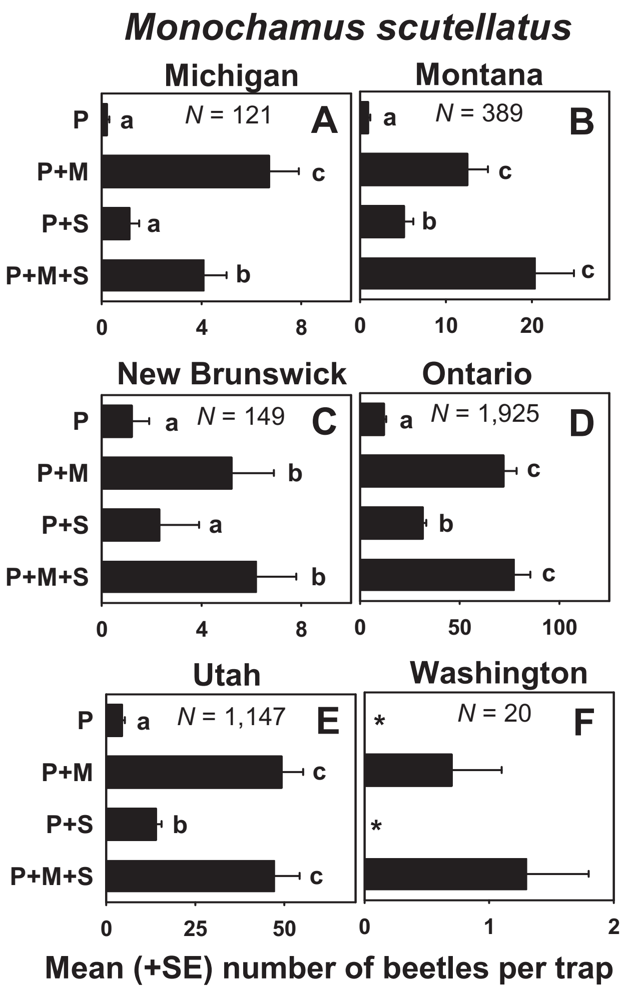

Fig. 2. Mean (+ SE) number of *Monochamus scutellatus* captured in multiple-funnel traps baited with α-pinene (P), α-pinene + ipsenol (P + S), α-pinene + monochamol (P + M), and α-pinene + ipsenol + monochamol (P + S + M) in Michigan (A), Montana (B), New Brunswick (C), Ontario (D), Utah (E), and Washington (F). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatment with an asterisk had 0 catches. N = Total trap catch of beetles per location.

$P < 0.001$) had a significant effect on catches of *M. mutator*. Traps with the tertiary blend outperformed traps with the other three treatments (Fig. 4A). Traps with either of the binary blends caught the same mean number of *M. mutator*, with both catching more than traps baited solely with α-pinene. For *M. notatus* in New Brunswick, data for traps baited solely with α-pinene were not included because mean catch and variance were both zero (Fig. 4B). There was no significant effect of treatment across the three remaining treatments ($F_{1,\ 18} = 2.707$, $P < 0.094$). In Ontario, there was a significant effect of monochamol ($F_{1,\ 27} = 13.88$, $P < 0.001$) but not ipsenol ($F_{1,\ 27} = 1.659$, $P < 0.209$) on catches of *M. notatus*. Traps with the tertiary blend caught more beetles than those baited solely with α-pinene; catches in traps with binary blends were intermediate between the two (Fig. 4C). In Ontario, there was no treatment effect on sex ratio of beetle catches for *M. mutator* with overall mean (±SE) $P_F = 0.52 \pm 0.02$ or for *M. notatus* with overall mean (±SE) $P_F = 0.52 \pm 0.08$ (Table 3) and a sex ratio of 1:1 in both cases.

Ipsenol significantly increased mean catches of *Acanthocinus nodosus* (F.), *Acanthocinus obliquus* (LeConte), *Acanthocinus*

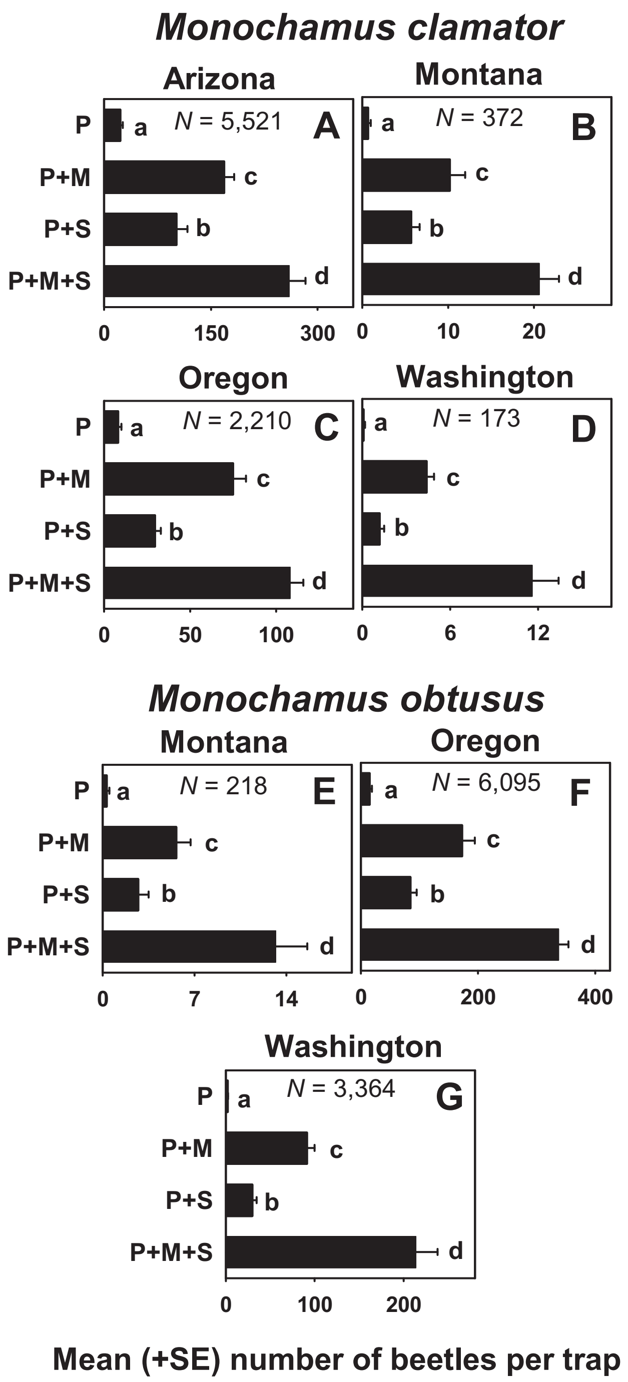

Fig. 3. Mean (+ SE) number of *Monochamus clamator* (A–D) and *M. obtusus* (E–G) captured in multiple-funnel traps baited with α-pinene (P), α-pinene + ipsenol (P + S), α-pinene + monochamol (P + M), and α-pinene + ipsenol + monochamol (P + S + M) in Arizona (A), Montana (B, E), Oregon (C, F), and Washington (D, G). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). N = Total trap catch of beetles per location.

obsoletus (Olivier), *Acanthocinus princeps* (Walker), and *Rhagium inquisitor* (L.) in traps baited with α-pinene (Fig. 5). These results are consistent with those of Miller et al. (2015) for *A. nodosus*, *A. obsoletus*, and *R. inquisitor*. However, the addition of monochamol to traps baited with α-pinene or α-pinene + ipsenol did not enhance catches of *R. inquisitor* or any *Acanthocinus* species. In fact, traps with α-pinene + monochamol caught significantly fewer *A. princeps*

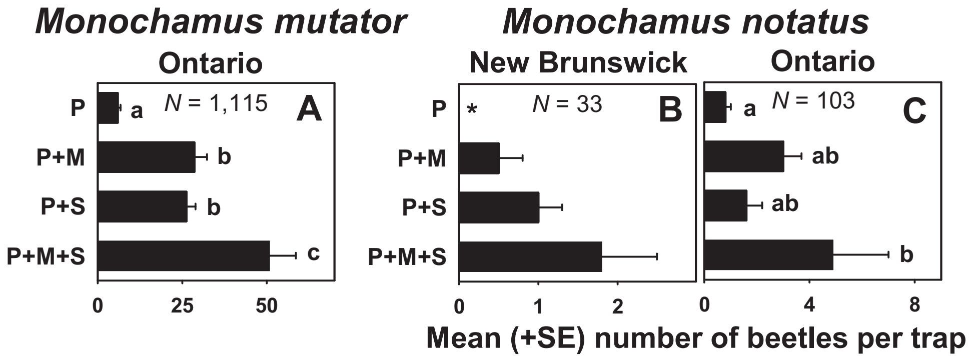

Fig. 4. Mean (+ SE) number of *Monochamus mutator* (A) and *M. notatus* (B–C) captured in multiple-funnel traps baited with α-pinene (P), α-pinene + ipsenol (P + S), α-pinene + monochamol (P + M), and α-pinene + ipsenol + monochamol (P + S + M) in New Brunswick (B) and Ontario (A, C). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatment with an asterisk had 0 catches. N = Total trap catch of beetles per location.

in Oregon than did traps with α-pinene alone (Fig. 5J). Neither ipsenol nor monochamol had any effect on catches of 17 other species of Cerambycidae captured in Arizona, Georgia, Michigan, Montana, Oregon, Utah, and Washington (Table 5).

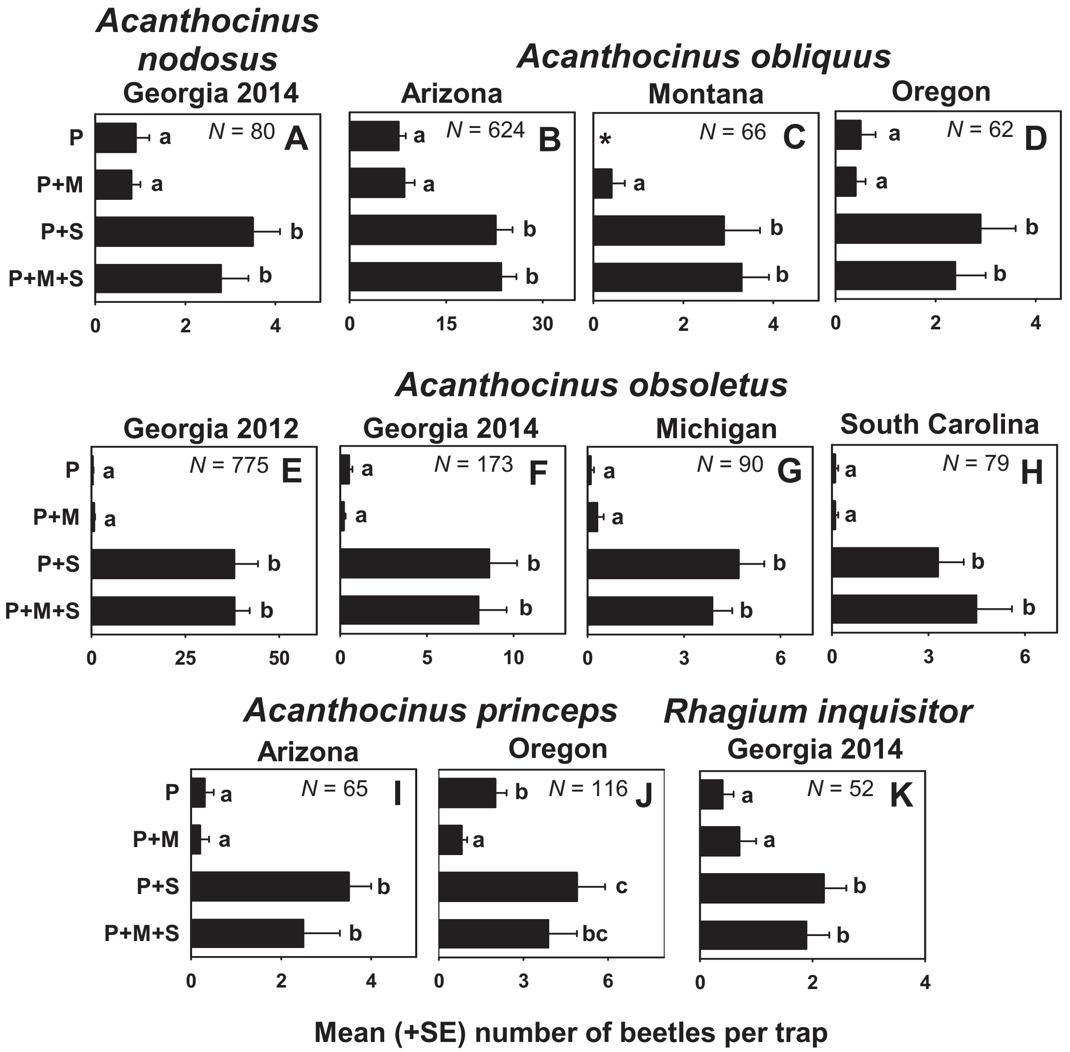

Fig. 5. Mean (+SE) number of *Acanthocinus nodosus* (A), *A. obliquus* (B–D), *A. obsoletus* (E–H), *A. princeps* (I–J), and *Rhagium inquisitor* (K) captured in multiple-funnel traps baited with α-pinene (P), α-pinene + ipsenol (P + S), α-pinene + monochamol (P + M), and α-pinene + ipsenol + monochamol (P + S + M) in Arizona (B, I), Georgia (A, E, F, K), Michigan (G), Montana (C), Oregon (D, J), and South Carolina (H). At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test). Treatment with an asterisk had 0 catches. N = Total trap catch of beetles per location.

Table 5. Catches of Cerambycidae (Coleoptera) species in traps baited with α-pinene that were not affected by monochamol or ipsenol in North America

Species	Location	*N*	ANOVA		Mean (±SE) number per trap
			$F_{(3,27)}$	*P*	
Acmaeops proteus (Kirby)	AZ	207	0.258	0.855	5.2 ± 0.5
	OR	129	1.014	0.402	3.2 ± 0.3
	UT	309	0.688	0.567	7.7 ± 0.6
Arhopalus asperatus (LeConte)	OR	35	0.889	0.459	0.9 ± 0.2
Arhopalus rusticus (LeConte)	OR	101	0.468	0.707	2.5 ± 0.3
Asemum striatum L	GA 2014	56	2.886	0.054	1.4 ± 0.2
Brachyleptura spp.	MI	44	0.674	0.575	1.1 ± 0.2
Cosmosalia chrysocoma (Kirby)	OR	37	0.180	0.909	0.9 ± 0.2
Megasemum aspersum (LeConte)	AZ	1,331	0.745	0.535	33.3 ± 2.2
	MT	1,059	0.464	0.986	26.5 ± 4.7
	OR	72	0.134	0.939	1.8 ± 0.2
	WA	110	0.842	0.483	2.8 ± 0.3
Neoclytus modestus Fall	MT	101	0.336	0.779	2.5 ± 0.3
Phymatodes dimidiatus (Kirby)	MT	69	0.206	0.891	1.7 ± 0.2
Prionus californicus Motschulsky	AZ	39	0.525	0.669	1.0 ± 0.2
Stictoleptura canadensis (Olivier)	MT	47	0.448	0.721	1.2 ± 0.2
Tetropium velutinum (LeConte)	MT	71	2.564	0.076	1.8 ± 0.3
Tragosoma depsarium (L.)	UT	511	0.350	0.789	12.8 ± 1.9
Xestoleptura crassipes (Leconte)	OR	1,915	1.076	0.376	47.9 ± 1.7
Xylotrechus albonotatus Casey	UT	61	1.038	0.392	1.5 ± 0.2
Xylotrechus longitarsis Casey	MT	639	0.337	0.799	16.0 ± 1.3
	OR	50	0.423	0.738	1.3 ± 0.2
	WA	85	1.231	0.318	2.1 ± 0.2
Xylotrechus sagittatus (Germar)	GA 2012	115	1.570	0.220	2.9 ± 0.4
	GA 2014	590	0.207	0.890	14.7 ± 0.4
	MI	82	1.668	0.197	2.1 ± 0.3
	SC	30	0.169	0.916	0.8 ± 0.2

N = Total number of beetles captured.

Table 6. Catches of root weevils and bark beetles (Curculionidae) in traps baited with α-pinene (P), α-pinene + monochamol (P + M), α-pinene + ipsenol (P + S), and α-pinene + monochamol + ipsenol (P + M + S) in North America

Species	Location	*N*	Mean (±SE) number of beetles per trap				ANOVA	
			P	P + M	P + S	P + M + S	$F_{(3,27)}$	*P*
Molytinae								
Hylobius pales	GA 2012	130	1.4 ± 0.3a	2.0 ± 0.4a	4.7 ± 0.7b	4.9 ± 0.8b	7.889	<0.001
	GA 2014	294	7.1 ± 1.4	5.9 ± 1.7	7.5 ± 1.1	8.9 ± 1.7	1.059	0.383
	SC	40	1.3 ± 0.4	0.8 ± 0.4	1.3 ± 0.3	0.6 ± 0.2	1.402	0.264
Pachylobius picivorus	GA 2012	129	1.3 ± 0.2a	1.6 ± 0.5a	5.1 ± 1.1b	4.9 ± 0.8b	14.18	<0.001
	GA 2014	197	4.5 ± 1.1ab	3.1 ± 0.7a	5.1 ± 0.8ab	7.0 ± 1.5b	0.017	0.017
Scolytinae								
Ips grandicollis	MI	5,437	25.8 ± 2.4a	21.8 ± 1.9a	245.6 ± 16.3b	250.5 ± 19.4b	457.4	<0.001
	GA 2012	4,091	16.4 ± 1.7a	20.5 ± 2.2a	179.2 ± 11.0b	193.0 ± 13.2b	252.4	<0.001
	GA 2014	10,995	40.0 ± 4.9a	47.9 ± 4.8a	479.8 ± 35.7b	531.8 ± 31.9b	440.9	<0.001
	SC	1,862	10.6 ± 1.6a	12.9 ± 1.8a	79.3 ± 9.0b	83.4 ± 7.7b	104.3	<0.001
Orthotomicus latidens	AZ	1,121	2.5 ± 1.4a	1.0 ± 0.5a	54.8 ± 8.3b	53.8 ± 4.7b	110.1	<0.001

N = Total number of beetles captured.

At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test).

Catches of Curculionidae species were largely unaffected by monochamol. However, the addition of ipsenol to traps significantly increased mean catches of the pitch-eating weevil *Pachylobius picivorus* (Germar) (Curculionidae: Molytinae), *Ips grandicollis* Eichhoff (Curculionidae: Scolytinae), and *Orthotomicus latidens* (LeConte), as well as the reproduction weevil *Hylobius pales* Herbst in one of three site-years (Table 6).

Trap catches of 10 different species of bark beetle predators were significantly affected by treatments, increasing substantially with the addition of ipsenol (Table 7). Adding ipsenol to traps baited with α-pinene or α-pinene + monochamol significantly increased mean catches of *Enoclerus nigrifrons* (Say), *Enoclerus nigripes* (Say), *Platysoma* spp. (Coleoptera: Histeridae), *Temnoscheila chlorodia* Mannerheim (Coleoptera: Trogossitidae), *Temnoscheila*

Table 7. Catches of bark beetle predators and associates in traps baited with α-pinene (P), α-pinene + monochamol (P + M), α-pinene + ipsenol (P + S), and α-pinene + monochamol + ipsenol (P + M + S) in North America

Species	Location	*N*	Mean (±SE) number of beetles per trap				ANOVA	
			P	P + M	P + S	P + M + S	$F_{(3,27)}$	*P*
Cleridae								
Enoclerus lecontei	AZ	5,513	35.5 ± 7.0a	27.5 ± 5.4a	239.1 ± 39.6b	249.2 ± 33.1b	97.62	<0.001
	MT	290	8.3 ± 2.9	7.0 ± 1.4	7.6 ± 1.4	6.1 ± 1.3	0.379	0.769
	OR	3,317	74.3 ± 9.3a	59.4 ± 6.5a	113.0 ± 14.3b	85.0 ± 8.6ab	7.083	0.001
	WA	462	5.3 ± 1.7a	6.6 ± 1.2a	18.6 ± 3.3b	15.7 ± 2.0b	10.88	<0.001
Enoclerus nigrifrons	MI	223	1.8 ± 0.5a	1.7 ± 0.5a	9.7 ± 1.2b	9.1 ± 1.7b	21.01	<0.001
Enoclerus nigripes	GA 2014	230	0.7 ± 0.3a	1.7 ± 0.6a	10.9 ± 1.4b	9.7 ± 1.6b	29.50	<0.001
Enoclerus sphegeus	AZ	674	12.7 ± 2.5b	5.8 ± 1.8a	24.0 ± 3.2c	24.9 ± 3.4c	12.58	<0.001
	MT	1,642	21.5 ± 3.5a	20.2 ± 2.3a	64.1 ± 13.0b	58.4 ± 7.9b	9.810	<0.001
	OR	2,559	55.0 ± 9.4a	54.2 ± 6.1a	79.1 ± 13.3b	67.6 ± 5.3ab	3.797	0.022
	UT	96	1.0 ± 0.2a	1.0 ± 0.4a	3.7 ± 0.9b	3.9 ± 1.0b	7.167	<0.001
	WA	56	0.9 ± 0.3	1.4 ± 0.6	2.3 ± 0.6	1.0 ± 0.3	1.619	0.208
Thanasimus dubius	GA 2012	46	0.4 ± 0.2a	0.3 ± 0.2a	2.5 ± 0.7b	1.4 ± 0.5ab	8.412	<0.001
	GA 2014	1,193	20.5 ± 3.2a	21.8 ± 3.7a	34.6 ± 4.0b	42.4 ± 7.1b	11.80	<0.001
	MI	707	7.5 ± 1.3a	8.2 ± 1.9a	25.9 ± 2.9b	29.1 ± 3.8b	39.57	<0.001
	SC	166	1.3 ± 0.7a	0.1 ± 0.1a	7.3 ± 1.1b	7.9 ± 1.8b	41.13	<0.001
Thanasimus undatulus	MT	743	15.4 ± 2.8	16.9 ± 2.8	22.1 ± 5.5	19.9 ± 3.7	1.456	0.249
	NB	342	10.0 ± 3.0	7.4 ± 1.8	9.0 ± 2.1	7.8 ± 2.2	0.839	0.485
	UT	684	10.1 ± 1.3a	9.6 ± 1.3a	25.3 ± 2.9b	23.4 ± 3.4b	32.56	<0.001
Histeridae								
Platysoma spp.	GA 2012	479	0.4 ± 0.2a	0.8 ± 0.4a	24.4 ± 2.5b	22.2 ± 1.7b	117.3	<0.001
	GA 2014	1,437	1.4 ± 0.4a	1.3 ± 0.4a	73.4 ± 5.7b	67.6 ± 3.1b	211.6	<0.001
	SC	755	1.1 ± 0.3a	1.3 ± 0.5a	37.4 ± 4.8b	35.7 ± 5.4b	102.7	<0.001
Trogossitidae								
Temnoscheila chlorodia	AZ	651	2.2 ± 0.6a	2.4 ± 0.6a	33.2 ± 4.2b	27.3 ± 3.3b	57.92	<0.001
	MT	637	2.5 ± 0.7a	3.1 ± 0.6a	29.8 ± 3.8b	28.3 ± 4.3b	38.88	<0.001
	OR	6,586	71.9 ± 6.8a	63.8 ± 6.1a	251.2 ± 15.2b	271.8 ± 19.2b	157.9	<0.001
	WA	1,078	8.8 ± 1.8a	7.5 ± 1.5a	47.5 ± 5.1b	44.0 ± 4.5b	58.18	<0.001
Temnoscheila virescens	GA 2012	1,532	10.9 ± 2.1a	11.0 ± 3.2a	69.5 ± 9.2b	61.8 ± 7.1b	31.96	<0.001
	GA 2014	1,688	26.2 ± 5.4a	24.1 ± 3.8a	60.2 ± 11.3b	58.3 ± 10.5b	28.02	<0.001
	SC	125	0.1 ± 0.1a	0.1 ± 0.1a	6.7 ± 2.2b	5.8 ± 1.3b	35.98	<0.001
Zopheridae								
Lasconotus spp.	GA 2012	6,066	84.0 ± 15.5a	73.0 ± 9.0a	192.9 ± 31.7b	256.7 ± 38.6b	18.06	<0.001
	SC	1,326	7.5 ± 2.0a	6.6 ± 1.5a	66.8 ± 6.8b	51.7 ± 5.5b	67.21	<0.001
	UT	183	1.4 ± 0.4a	2.0 ± 0.7a	5.6 ± 1.5b	9.2 ± 0.3b	17.14	<0.001

N = Total number of beetles captured.

At each location, means followed by the same letter are not significantly different at $P = 0.05$ (Holm–Sidak test).

virescens F., and *Lasconotus* spp. (Coleoptera: Zopheridae) in all site-years analyzed (Table 7). The responses of some clerid species were less consistent. Ipsenol significantly increased mean catches of *Enoclerus lecontei* Wolcott, *Enoclerus sphegeus*, and *Thanasimus dubius* F. in most sites analyzed, but increased catches of *Thanasimus undatulus* (Say) in only one of three sites (Utah; Table 7). Monochamol did not affect catches of any predator species except for *E. sphegeus* F. (Coleoptera: Cleridae) in one of five sites (Arizona), where the mean catch in traps with α-pinene + monochamol was lower than that in traps with α-pinene alone (Table 7).

Discussion

We present robust and widespread evidence of an additive, positive response to monochamol and ipsenol by a majority of *Monochamus* species across North America. In our study, monochamol increased catches of six species and one species complex of *Monochamus* in traps baited with α-pinene (Figs. 1–4). Our results are consistent with those of: (a) Fierke et al. (2012) and Ryall et al. (2015) for *M. notatus* and *M. scutellatus* in New Brunswick, New York, and Ontario; (b) Allison et al. (2012) for *M. carolinensis* and *M. titillator* in Louisiana; (c) Macias-Samano et al. (2012) for *M. clamator*, *M. obtusus*, and *M. scutellatus* in British Columbia; and (d) Ryall et al. (2015) for *M. mutator* in Ontario. We provide data that corroborate previous results in New Brunswick and Ontario, and add new data for locations in Georgia, Michigan, Montana, Oregon, Utah, and Washington with various forest stand compositions (Table 1). Similarly, we found that ipsenol increased catches of five species and one species complex of *Monochamus* in traps baited with α-pinene across North America (Figs. 1–4). Our results with ipsenol are consistent with those of Billings and Cameron (1984), Allison et al. (2001, 2003, 2013), de Groot and Nott (2004), Miller and Asaro (2005), and Miller et al. (2011, 2013b) for *M. carolinensis*, *M. clamator*, *M. mutator*, *M. obtusus*, *M. scutellatus*, and *M. titillator* complex.

The addition of ipsenol to traps baited with monochamol and α-pinene resulted in the highest trap catches of five species and one species complex of *Monochamus* in North America (Figs. 1,3, 4). Our results are new for *M. carolinensis*, *M. mutator*, *M. notatus*, *M. obtusus*, and *M. titillator* complex, whereas those with *M. clamator* (Fig. 3A–D) are consistent with Macias-Samano et al. (2012). In contrast to our additive results with *M. obtusus* (Fig. 3E–G), Macias-Samano et al. (2012) did not find an additive effect of ipsenol with monochamol, possibly owing to the inclusion of ethanol and ipsdienol in their study.

In contrast to the other *Monochamus* species, *M. scutellatus* did not exhibit an additive response in our study. Adding ipsenol to traps baited with monochamol did not increase trap catches (Fig. 2A–F). Our data are consistent with those of Macias-Samano et al. (2012), showing a lack of additive responses between monochamol and the binary blend of ipsenol and ipsdienol for *M. scutellatus*. It is possible that response by *M. scutellatus* to monochamol supersedes any responses to bark beetle compounds such as ipsenol and ipsdienol. Alternatively, another bark beetle compound such as *cis*-verbenol or methylbutenol might be more active.

Identifying a universal bark beetle kairomone for *M. scutellatus* will be a challenge owing to the transcontinental geographic range of *M. scutellatus*, and its broad host associations. In the northeast, *M. scutellatus* competes with *M. notatus* for large-diameter eastern white pine, *Pinus strobus* L. (Hughes and Hughes 1987). In the west, *M. scutellatus* is abundant in Douglas-fir, *Pseudotsuga menziesii* (Mirb.), and true firs (*Abies* spp.), whereas in boreal forests from eastern Canada to Alaska, *M. scutellatus* is most abundant in spruce (Cerezke 1975, Wilson 1975, Edmonds and Eglitis 1989). The complex of bark beetles associated with these different ecosystems varies considerably and will likely reflect variation in active semiochemicals for *M. scutellatus*. Some variation in semiochemical responses by *M. scutellatus* to ipsenol was evident in our study. When added to traps baited with α-pinene, ipsenol increased catches of *M. scutellatus* in Montana, Ontario, and Utah, but not Michigan, New Brunswick, and Washington (Fig. 2). Ipsenol decreased catches of *M. scutellatus* in traps baited with α-pinene and monochamol in Michigan, but not the other five locations.

We found an inconsistent result with *M. titillator* complex in Georgia and South Carolina. There was an additive effect of ipsenol and monochamol on trap catches of *M. titillator* complex in Georgia in 2014 but not in Georgia and South Carolina in 2012. In 2012, we used ipsenol lures with a release rate that was twice that of ipsenol lures used in 2014. It is possible that a saturation effect occurred with higher release rates of ipsenol in 2012, possibly related to an optimal ratio with monochamol or a higher importance associated with ipsenol close to oviposition sites.

It seems surprising that none of the common bark beetle predators was attracted to monochamol, whereas they were clearly attracted by ipsenol (Table 7). It is unlikely that adults of these predators prey on adult *Monochamus* spp., given the large size and mandibles of pine sawyers, but larvae of these predators also attack eggs and larvae of bark and wood-boring insects. Attraction to ipsenol is understandable, as it indicates availability of prey larvae, including those of *Monochamus* species. The lack of attraction to monochamol suggests that monochamol may not be released at oviposition sites or that the potential benefit of feeding on *Monochamus* larvae is not sufficient for selection to favor response by predators to monochamol. Perhaps selection has favored predators that respond positively to a combination that includes ipsenol because it is likely associated with a greater potential suite of prey rewards, i.e., adults, eggs, and larvae of bark beetles as well as eggs and young larvae of *Monochamus*. Further research is required to determine optimal release rates and ratios of ipsenol and monochamol for operational trapping programs.

One clear benefit of monochamol is the lack of effects on other species of bark and wood borers and predators. Managers of detection programs for adventive species of insects are always trying to optimize their programs to reduce costs. A single multipurpose lure combination for bark and wood-boring species could reduce costs of detection programs for adventive species (Hanks et al. 2012). Our results, and those of Hanks et al. (2012), suggest that monochamol could be added to existing blends to increase the likelihood of detecting *Monochamus* species without reducing catches of other species. Monochamol had no effect on other species of longhorn beetles, bark beetles, reproduction weevils, and various species of bark beetle predators and associates. In addition, ipsenol could be added to target *Acanthocinus* species, although catches of several species of bark beetles would also increase, thereby increasing handling time to process samples for identifications. Clearly, such additions to existing blends in detection programs would need to be vetted before they could become operational. The challenge for managers is to use optimal blends that maximize the likelihood of capturing target species but minimize the catches of other species that might flood traps. The time and cost of handling trap catches increase when sorting through thousands of beetles of common species while looking for the rare individuals.

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