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Author(s) :Jana C. Lee, Joséé F. Negróón, Sally J. McElwey, Livy Williams, Jeffrey J. Witcosky, John B. Popp, and Steven J. Seybold
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Biology of the Invasive Banded Elm Bark Beetle (Coleoptera: Scolytidae) in the Western United States

JANA C. LEE,[1,2,3] JOSÉ F. NEGRÓN,[4] SALLY J. MCELWEY,[4] LIVY WILLIAMS,[5] JEFFREY J. WITCOSKY,[6] JOHN B. POPP,[4] AND STEVEN J. SEYBOLD[2]

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ABSTRACT The banded elm bark beetle, *Scolytus schevyrewi* Semenov (Coleoptera: Scolytidae), native to Asia, was detected in the United States in 2003, and as of 2011 it is known to occur in 28 states and four Canadian provinces. *S. schevyrewi* infests the same elm (*Ulmus* spp.) hosts as the long-established invasive, the European elm bark beetle, *Scolytus multistriatus* (Marsham). Information on the basic biology of *S. schevyrewi* in its native range is sparse; thus, we conducted laboratory studies and field studies in Colorado and Nevada. Comparisons of flight and behavioral responses were made with co-occurring *S. multistriatus*. When Siberian elm, *Ulmus pumila* L., cut logs (bolts) were allowed to be colonized by wild populations in the field, *S. schevyrewi* did not differ in emergence density from 10- versus 24-cm-diameter bolts. In the laboratory, *S. schevyrewi* readily colonized bolts of American elm, *Ulmus americana* L., but not Chinese elm, *Ulmus parvifolia* Jacq.; Siberian peashrub, *Caragana arborescens* Lam.; a cherry, *Prunus fontanesiana* (Spach) C. K. Schneid.; or Russian olive, *Elaeagnus angustifolia* L. In Colorado, *S. schevyrewi* often landed on elm bolts between 12:00 p.m. and 4 p.m.; and near large elm trees, they were captured more frequently on sticky traps at 1.8 and 3.7 m aboveground than higher along the main stem. In Colorado/Nevada, *S. schevyrewi* initiated flight in April/March and ceased in October/September, whereas *S. multistriatus* initiated flight in April/May and ceased in October/September. In funnel trap flight assays of semiochemicals in Colorado or Nevada, *S. schevyrewi* had moderate responses, 3–10-fold greater than unbaited control traps, to Multilure (a commercial lure for *S. multistriatus*), 2-methyl-3-buten-2-ol (MB) + multistriatin, and MB + a plant extract that is included in a commercial formulation of Multilure. In contrast, *S. multistriatus* had a 226–259-fold greater response to Multilure than to the control. Both *Scolytus* species showed electroantennographic (EAG) responses to MB, racemic multistriatin, and (+)- and (−)-α-pinene, with the greatest sensitivity to multistriatin. *S. schevyrewi* was more responsive to (−)-α-pinene than was *S. multistriatus*.

KEY WORDS chemical ecology, electroantennography, flight behavior, host colonization, *Scolytus schevyrewi*

The banded elm bark beetle, *Scolytus schevyrewi* Semenov (Coleoptera: Scolytidae) (sensu Wood 2007), which originates from Asia, was first detected in 2003 in Colorado and Utah. As of 2011, it occurs in 28 states (Lee et al. 2009) and in southern Alberta, Manitoba, Ontario, and Saskatchewan in Canada (CFIA 2007, Langor et al. 2009). Heavy infestations of *S. schevyrewi* alone have killed drought-stressed elms in Colorado (Negrón et al. 2005, Lee et al. 2006). Also, *S. schevyrewi* may vector *Ophiostoma novo-ulmi* Brasie (Jacobi et al. 2007), one of the fungi that causes Dutch elm disease. *S. schevyrewi* colonizes the same elm hosts as the invasive European elm bark beetle, *Scolytus multistriatus* (Marsham), that has been present in the United States since 1909 (Negrón et al. 2005). These two invasive species have allopatric distributions in their native Eurasia but now have sympatric distributions in the United States (Lee et al. 2009). A seven-state survey revealed that the newly invasive *S. schevyrewi* had substantial populations in Nevada and Utah and was more abundant than *S. multistriatus* in Colorado and Wyoming (Lee et al. 2009). *S. schevyrewi* may be competitively displacing *S. multistriatus* in the western United States (Lee et al. 2010).

The arrival of *S. schevyrewi* in North America may represent an additional threat to elms in forests and urban landscapes. American elm, *Ulmus americana* L., was a commonly planted shade tree in the United

[1] Corresponding author: USDA–ARS, 3420 NW Orchard Ave., Corvallis, OR 97330 (e-mail: jana.lee@ars.usda.gov).
[2] USDA Forest Service, Pacific Southwest Research Station, 720 Olive Dr., Suite D, Davis, CA 95616.
[3] Department of Entomology, University of California Davis, One Shields Ave., Davis, CA 95616.
[4] USDA Forest Service, Rocky Mountain Research Station, 240 West Prospect Rd., Fort Collins, CO 80526.
[5] USDA–ARS, European Biological Control Laboratory, Campus International de Baillarguet, CS 90013 Montferrier-sur-Lez, 34988 Saint-Gely-du-Fesc, France.
[6] USDA Forest Service, Forest Health Management, 740 Simms St., Golden, CO 80401.

States due to its fast growth and tolerance to stress. However, Dutch elm disease (a complex of *S. multistriatus* and *Ophiostoma ulmi* (Buisman) Nannf. or *O. novo-ulmi*) killed between 50 and 75% of the elm populations that originated before 1930 in northeastern North America (Bloomfield 1979). These populations included *U. americana* as well as six other elm species (Strobel and Lanier 1981).

Little is known about the biology and potential impact of *S. schevyrewi* beyond limited studies conducted in China (Shi and Chen 1990, Wang 1992) and more recently in the United States (Negrón et al. 2005; Lee et al. 2009, 2010; Lee and Seybold 2010). In China, *S. schevyrewi* colonizes stressed elms (Shi and Chen 1990), lays 20–120 eggs per female, develops within 40–45 d, has two to three generations per year, and overwinters in the pupal stage (Wang 1992). In the United States, *S. schevyrewi* flew toward volatiles from Siberian elm, *Ulmus pumila* L., but did not respond at any greater level when females or males were allowed to colonize the host beforehand (Lee et al. 2010). Female *S. schevyrewi* have been observed to lay 1–57 eggs or 20.0 ± 0.9 (mean ± SE) eggs per gallery in small-diameter cut elm logs (bolts) in 1 wk, with some females initiating more than one gallery (Lee and Seybold 2010). *S. schevyrewi* was observed to develop within 30 d in Colorado (Negrón et al. 2005).

Understanding the biology, behavior, and chemical ecology of *S. schevyrewi* is critical for improving monitoring and management strategies. However, the behavior and chemical ecology of *S. schevyrewi* have not been studied in its native range and were only recently studied in the United States (Lee et al. 2010, Lee and Seybold 2010). *S. schevyrewi* was first detected in the United States by using flight funnel traps (Lindgren 1983) baited with either a lure of high-release α-pinene and ethanol or with a lure for *Ips typographus* (L.) (Coleoptera: Scolytidae) that consists of 2-methyl-3-buten-2-ol (MB), *cis*-verbenol, and racemic ipsdienol (Negrón et al. 2005). A subsequent test showed that *S. schevyrewi* was most frequently captured in traps baited with the "Elm bark beetle lure—European" (commonly called Multilure in the literature), a commercial pheromone-kairomone blend for *S. multistriatus.* In this test, although *S. schevyrewi* was caught less frequently in traps baited with MB, there was no significant difference in response to Multilure or MB (Negrón et al. 2005). In the same study, captures were low in the unbaited control traps, and in traps baited with 4-methyl-3-heptanol, or the *I. typographus* lure. Therefore, Multilure or MB was suggested as a bait for detection of *S. schevyrewi.* One advantage to using MB was its relative selectivity in attracting *S. schevyrewi* versus *S. multistriatus.* Thus, in areas where *S. multistriatus* occurred, MB was the recommended lure to reduce processing time while sorting samples.

Among the *Scolytus*, the pheromone system of *S. multistriatus* is the best understood (Pearce et al. 1975) and may have relevance in the search for attractive baits for *S. schevyrewi.* After feeding on elm phloem, *S. multistriatus* females release (–)-*threo*-4-methyl-3-heptanol and (–)-α-multistriatin [(1*S*,2*R*,4*S*,5*R*)-(–)-2,4-dimethyl-5-ethyl-6,8-dioxabicyclo[3.2.1]octane]; injured elm tissue releases the sesquiterpene (–)-α-cubebene. These components elicit aggregation behavior of males and females (Peacock et al. 1971) and attract various hymenopteran parasitoids (Kennedy 1984). α-Multistriatin elicited the greatest EAG response among the isomers (Grant and Lanier 1982), and the greatest flight response in the field to traps baited with the combination of (–)-α-cubebene plus (–)-limonene or (–)-*threo*-4-methyl-3-heptanol (Blight et al. 1983). Host kairomones are known to be attractive to *S. multistriatus* (Lee et al. 2010) and other bark beetles (Seybold et al. 2006) and also elicit a strong flight response from both sexes of *S. schevyrewi* (Lee et al. 2010). Volatiles released from *U. americana* include (–)-α-pinene, (–)-β-elemene, and (–)-α-cubebene (Millar et al. 1986), which are common components of commercial baits that can be tested in the field.

The primary objective of this study was to increase our knowledge of the basic biology of *S. schevyrewi*, as well as that of *S. multistriatus* in their zone of sympatry in Colorado and Nevada where relative population densities of *S. schevyrewi* are high (Lee et al. 2009). Studies focused on elucidating the 1) colonization preferences for various diameter *U. pumila* bolts and acceptance of various host species, 2) temporal and spatial patterns of flight (diurnal and seasonal; height), and 3) chemical ecology.

Materials and Methods

Host Colonization. In May 2004, a field experiment was conducted with *U. pumila* in Colorado to evaluate the colonization preferences of *S. schevyrewi* and *S. multistriatus* for 46-cm-long cut bolts of varying diameters. To assess colonization, bolts collected the previous day were placed in the field for 22 d (Table 1) and exposed in sets of three (including a small [10.2–14-cm-diameter], medium [15.2–19.1-cm-diameter], and large [20.3–24.1-cm-diameter]) bolt. Twelve replicates were conducted at Pawnee National Grasslands (Weld Co.), six in Fort Collins (Larimer Co.), and four in Lakewood (Jefferson Co.). At the end of the 22-d period, bolts were brought to the laboratory and placed in 51- by 32- by 15-cm plastic rearing containers held at room temperature. Emerging *S. schevyrewi* and *S. multistriatus* beetles were identified based on the morphology and location of the spine on abdominal sternite 2 (Negrón et al. 2005). Among bolts that were attacked, a linear regression tested the association between diameter of the bolt and number of emerging *S. schevyrewi* and *S. multistriatus* adults per unit of surface area (SAS Institute 2007).

In July 2006, host acceptance under no-choice conditions was screened by exposing *S. schevyrewi* to cut bolts (30.5 cm in length by 5–20 cm in diameter) of *U. americana;* Chinese elm, *Ulmus parvifolia* Jacq.; Siberian peashrub, *Caragana arborescens* Lam.; a cherry, *Prunus fontanesiana* (Spach) C. K. Schneid.; and Russian olive, *Elaeagnus angustifolia* L. In a literature review, these species and other plants in the genera

Table 1. Dates, baits, and locations of field studies of *S. schevyrewi* and *S. multistriatus* in Colorado (CO) and Nevada (NV) during 2004–2006

Study	Dates (no. collections)	Lure or treatments[a]	Location (no. sites or replicates)
Host colonization			
Diameter test	5–27 May 2004	*U. pumila* elm bolts, a small- (10.2–14-cm), medium- (15.2–19.1-cm), and large (20.3–24.1-cm)-diam bolt	12 replicates in Pawnee National Grasslands, CO[b]; 6 replicates in Fort Collins, CO[c]; 4 replicates in Lakewood, CO[d]
Flight patterns			
Diurnal 2005	27 June 2005	*U. pumila* and *U. americana* bolts	3 sites in Pawnee
Diurnal 2006	9 June 2006	*U. pumila* bolts	4 sites in Fort Collins
Seasonal 2004	31 Mar.–5 Nov. 2004 (30)	Multilure (Phero Tech Inc.)	12 sites in Fort Collins; 10 sites in Pawnee
Seasonal 2005	8 Mar.–14 Oct. 2005 (31)	Multilure (Phero Tech Inc.)	12 sites in Fort Collins
Seasonal 2006	20 Mar.–16 Oct. 16, 2006 (28)	Multilure (Phero Tech Inc.)	10 sites in Fort Collins; 10 sites in Pawnee
Height 2005	12 Aug.–21 Oct. 2005 (6)	1.83, 3.66, 5.49, 7.32, 9.14 m	4 trees in Fort Collins; 10 trees in Pawnee
Height 2006	1 May–16 Oct. 2006 (14)	1.83, 3.66, 5.49, 7.32, 9.14 m	7 trees in Pawnee
Flight responses to semiochemicals			
Colorado 1	22 March–2 Nov. 2004 (31)	Unbaited trap, 2-methyl-3-buten-2-ol (MB) (Phero Tech Inc.), MB (ChemTica Internacional S.A.), MB (IPM Tech. Inc.), 3-methyl-3-buten-2-ol, Multilure (Phero Tech Inc.)	7 blocks in Lakewood
Nevada 1	7 April–21 Oct. 2004 (26)	Same treatments as Colorado 1, also Multilure (ChemTica Internacional S.A.)	3 blocks in Reno, NV[e]
Colorado 2	9 May–21 July 2005 (10)	Unbaited trap, MB (Sigma-Aldrich, St. Louis, MO) release rates of 5–18, 17–60, 81–271, 810–2,710 mg/d	3 blocks in Lakewood
Nevada 2	22 April–2 Aug. 2005 (12)	Same treatments as Colorado 2	3 blocks in Reno
Colorado 3	4 Aug.–3 Oct. 2005 (12)	Unbaited trap, MB (Sigma-Aldrich) 5–18 mg/d, Siberian elm extract, Multistriatin, MB + Sib. elm extract, MB + multistriatin, Sib. elm extract + multistriatin, MB + Sib. elm extract + multistriatin	3 blocks in Lakewood
Nevada 3	2 Aug.–6 Sept. 2005 (7)	Same treatments as Colorado 3	3 blocks in Reno
Colorado 4	13 April–21 Oct. 2005 (27)	Unbaited trap, Multilure, Multilure-host, Multilure-multistriatin, MB + Multilure, Elemene	1 block each in Lakewood and Pawnee, and 2 blocks in Fort Collins
Colorado 5	20 April–20 July 2006 (12)	Unbaited trap, Multilure, MB, Plant extracts, Multistriatin, MB + Multilure, MB + Plant extracts, MB + Multistriatin	4 blocks in Lakewood

[a] Product information in Table 2.
[b] Pawnee National Grasslands, Weld Co., CO, 40.6436° N, 104.3439° W.
[c] Fort Collins, Larimer Co., CO, sites located around 40.6189° N, 105.0847° W.
[d] Denver Federal Center, Lakewood, Jefferson Co., CO, 39.72° N, 105.1161° W.
[e] Reno, Washoe Co., NV, 39.5411° N, 119.8056° W; 39.52° N, 119.7708° W; and 39.5008° N, 119.7622° W.

Caragana and *Prunus* have been suggested as hosts for *S. schevyrewi* from reports from Asia (Negrón et al. 2005). Bolts were placed individually in a plastic box (30 by 24 by 14 cm), and each species was replicated four times. Twenty-five adult *S. schevyrewi* of mixed sexes reared from field-infested elm logs (*U. americana* and *U. pumila*) were placed into each box with the host bolt, and the box was placed in an environmental chamber at 25°C. One week later, hosts were examined for evidence of gallery construction.

Flight Patterns. Diurnal patterns of flight activity of *S. schevyrewi* and *S. multistriatus* were recorded from 9 a.m. to 6 p.m. on 27 June 2005 at three locations separated by at least 500 m at the Pawnee National Grasslands and from 10 a.m. to 8 p.m. on 9 June 2006 at four locations separated by at least 5 km in Fort Collins (Table 1). Freshly cut *U. americana* and *U. pumila* bolts (46 cm in length and ≈38 cm in diameter) were placed either on a table at a height of 1 m above the ground or directly on the ground. An observer stationed at each location captured beetles as they landed. The sexes of both species were later identified based on the degree of convexity and pubescence on the frons. The male frons is concave and more pubescent (Wood 1982). Air temperature was measured at one location, and a linear regression tested the relationship between mean temperature and the proportion of beetles caught among all sites per hour (SAS Institute 2007).

Seasonal patterns of flight activity of *S. schevyrewi* and *S. multistriatus* were monitored from March to October–November, 2004–2006, in Colorado by using 12-unit Lindgren funnel traps baited with Multilure (Phero Tech Inc., now Contech Enterprises Inc., Delta, BC, Canada). Traps were checked weekly at 12–22 trap sites each year (dates and locations in Table

Table 2. Semiochemicals used in baited funnel traps, and for electroantennographic assays of *S. schevyrewi* and *S. multistriatus* in Nevada and Colorado during 2004–2006

Use	Chemical[a]	Release rate (mg/d)	Other information	Source
Lure	β-Elemene	0.1	70–75% chemical purity, 10% of the sample was α-elemene, enantiomeric purity not determined, released from 400-μl polyethylene Eppendorf tubes, 85-mg load	Phero Tech Inc.[b]
Lure	2-Methyl-3-buten-2-ol (MB)	17–19 (20°C) 60 (32°C)	3.8-g load	Phero Tech Inc.
Lure	2-Methyl-3-buten-2-ol	60	4.8-g load	ChemTica Internacional S.A. (Heredia, Costa Rica)
Lure	2-Methyl-3-buten-2-ol	21 (24°C)	2-g load	IPM Tech, Inc. (Portland, OR, USA)
Lure EAG	2-Methyl-3-buten-2-ol	5–18, 81–271, and 810-2710 (ambient outdoor conditions)	Released from 10 400-μl polyethylene Eppendorf tubes, from a 17-ml polyethylene bottle with 0.476-cm hole on side of cap, and from 10 of the modified polyethylene bottles	Sigma-Aldrich, Eppendorf–Evergreen Scientific (Los Angeles, CA), bottle–Phero Tech Inc.
Lure	3-Methyl-3-buten-1-ol	60	4.8-g load	ChemTica Internacional S.A.
Lure	Elm bark beetle lure-European (also known as Multilure)		Host volatile blend in 400-μl polyethylene Eppendorf tube: hexanol, hexanal, δ-cadinene; second 400-μl tube: Multistriatin, 4-methyl-3-heptan-1-ol, α-copaene, α-cubebene	Phero Tech Inc.
Lure	P189-M *Scolytus multistriatus* (also known as Multilure)			ChemTica Internacional S.A.
Lure	84% (−)-Multistriatin		A mixture of four stereoisomers (≈49:27:18:3 ratio of δ-, α-, γ-, and β-multistriatin)	Phero Tech Inc.
EAG	84% (−)-Multistriatin		A mixture of four stereoisomers (≈49:27:18:3 ratio of δ-, α-, γ-, and β-multistriatin)	Phero Tech Inc.
EAG	(*R*)-(+)-α-Pinene		≥99% chemical purity, 98.5% enantiomeric purity	Sigma-Aldrich product 268070-25G
EAG	(*S*)-(−)-α-Pinene		≥99% chemical purity, 98.5% enantiomeric purity	Sigma-Aldrich product 305715-25G
EAG	Octanal (positive control)		99% chemical purity	Sigma-Aldrich

[a] Semiochemicals used in studies described in Table 1.
[b] Now Contech Enterprises Inc. (Delta, BC, Canada).

1), and baits were replaced monthly. Although standardized seasonal trapping was not conducted in Nevada as in Colorado, both species were monitored in Reno, NV (Washoe Co.) from 7 April to 21 October 2004; traps baited with Multilure were one of the treatments used in semiochemical study 1 in Nevada (Table 1), and resulting flight patterns are discussed.

Height of flight and landing behavior of beetles were examined in 2005 and 2006 in Colorado with 15.2- by 30.5-cm mesh screen traps sprayed with Tanglefoot (The Tanglefoot Company, Grand Rapids, MI). The mid-points of the traps were located at 1.83, 3.66, 5.49, 7.32, and 9.14 m (6, 12, 18, 14, and 30 feet, respectively) aboveground and along the main stem of *Ulmus* spp. trees. One test (2005) was conducted in Fort Collins with traps hung from four *U. americana* trees; a second test (2005) was conducted at the Pawnee National Grasslands with traps hung from ten *U. pumila* trees. Each week, traps were checked, *Scolytus* beetles were removed and identified, and traps were resprayed with Tanglefoot. A third test (2006) was conducted at the Pawnee National Grasslands with traps hung from seven *U. pumila* trees. Analyses were conducted separately for trees at each site and year. The effect of height on flight was examined by nonparametric Kruskal–Wallis tests (SAS Institute 2007). If the effect of height was significant, all possible pairwise comparisons were made among the heights with a Wilcoxon test. The α-level for each comparison was adjusted to control for an experiment-wise error of 0.05 [$\alpha_{new} = 1 - (1-0.05)^{1/k} = 0.0051$, k = 10 possible pairwise comparisons] (Sokal and Rohlf 1981).

Flight Responses to Semiochemicals. From 2004 to 2006, flight responses of *S. schevyrewi* and *S. multistriatus* to various semiochemical baits in Fort Collins, Lakewood, and Pawnee National Grasslands, and in Reno were compared. The traps were positioned within 10 m of infested elm trees or piles of cut elm debris. All baits were hung on the sixth funnel of a 12-unit Lindgren funnel trap. Traps were checked and emptied weekly and rerandomized in position each time. The first study was conducted in Lakewood and Reno, and it compared flight response to MB from three commercial sources, 3-methyl-3-buten-2-ol from one source, and Multilure from one or two sources (Tables 1 and 2). Seven blocks were installed

Table 3. Percentages of females, and ANOVA of *S. schevyrewi* and *S. multistriatus* captured in baited funnel traps in Colorado and Nevada during 2004–2006

Study[a]	Effect	*S. schevyrewi*				*S. multistriatus* (same df)		
		% ♀, *n*	df	*F*	*P*	% ♀, *n*	*F*	*P*
Colorado 1	Lure	55, 2,814	5, 972	7.2	**<0.001**[b]	48, 434	131	**<0.001**
	Block		6, 972	19.5	<0.001		2.2	0.041
	Wk		28, 972	8.7	<0.001		7.2	<0.001
	Lure × wk		140, 972	1.1	0.29		6.4	<0.001
Nevada 1	Lure	64, 954	6, 362	1.8	0.10	50, 16, 611	353	**<0.001**
	Block		2, 362	25.1	<0.001		1.1	0.35
	Wk		25, 362	7.3	<0.001		16.9	<0.001
	Lure × wk		150, 362	0.74	0.98		7.8	<0.001
Colorado 2	Lure	59, 294	4, 98	2.2	0.080	50, 2	Not tested[c]	
	Block		2, 98	2.9	0.057			
	Wk		9, 98	1.9	0.57			
	Lure × wk		36, 98	1.3	0.16			
Nevada 2	Lure	63, 161	4, 118	2.3	0.063	45, 66	0.67	0.61
	Block		2, 118	21.6	<0.001		2.2	<0.001
	Wk		11, 118	3.5	<0.001		14.4	0.021
	Lure × wk		44, 118	1.3	0.13		0.82	0.78
Colorado 3	Lure	45, 95	7, 186	0.61	0.75	0	Not tested[c]	
	Block		2, 186	10.6	<0.001			
	Wk		11, 186	2.9	0.0014			
	Lure × wk		77, 186	0.86	0.78			
Nevada 3	Lure	52, 346	7, 110	2.5	**0.019**	49, 308	4.7	**<0.001**
	Block		2, 110	8.8	<0.001		25.2	<0.001
	Wk		6, 110	2.8	0.014		2.0	0.073
	Lure × wk		42, 110	1.5	0.043		0.79	0.80
Colorado 4	Lure	50, 897	5, 360	5.7	**<0.001**	51, 744	10.2	**<0.001**
	Block		3, 360	21.7	<0.001		28	<0.001
	Wk		26, 360	4.3	<0.001		3.2	<0.001
	Lure × wk		128, 360	1.1	0.36		1.2	0.13
Colorado 5	Lure	50, 678	7, 309	4.3	**<0.001**	45, 22	Not tested[c]	
	Block		3, 309	19.8	<0.001			
	Wk		12, 309	7.7	<0.001			
	Lure × wk		84, 309	1.2	0.104			

[a] Studies described in Table 1.
[b] *P* values for the effect of lure <0.05 are in bold.
[c] Number of beetles captured was low and not tested in statistical analysis.

in Lakewood, and three blocks in Reno. Baits were replaced every 6–7 wk. Traps within a block were spaced ≈20 m apart. The second study (also in Lakewood and Reno) compared flight response to various release rates of MB by using a similar experimental protocol to that in study 1 (Tables 1 and 2). A third study (also in Lakewood and Reno) compared flight responses to multistriatin, MB, and extracts from *U. pumila* (referred to as Siberian elm extract) either alone or in two-part or three-part combinations (Tables 1 and 2). Extracts were prepared by trapping volatiles from freshly cut uninfested *U. pumila* bolts on 15 g of Porapak Q (50/80 mesh size, Supelco, Bellefonte, PA) with an air flow of 4 liters/min for 8 d (Seybold et al. 1995). The Porapak was extracted with ≈350 ml pentane; concentrated to 10 ml by Kuderna-Danish distillation; and 750 μl of the extract was transferred into 1.5-ml Eppendorf tubes (Phero Tech Inc.). A fourth study (in Lakewood, Pawnee, and Fort Collins) compared the flight responses to Multilure alone or in combination with MB, Multilure separated into components, and to the *Ulmus* spp. volatile elemene (Tables 1 and 2). One 400-μl polyethylene Eppendorf tube contained host volatiles, and a second 400-μl Eppendorf tube contained multistriatin as well as some additional host components (Table 2). A fifth study (in Lakewood) compared the flight responses to Multilure or each of its release tubes individually and also to the combination of Multilure, or each of the release tubes, with MB (Tables 1 and 2).

For statistical analyses, trap catches of both sexes of a given species were pooled because the sexes responded similarly in all experiments. The sex ratio of responding insects was frequently 1:1 except for Nevada 1, NV 2, and Colorado 2, which captured more females than males (Table 3). The number of *S. schevyrewi* or *S. multistriatus* captured was divided by the number of days that had elapsed between trap collections, and $\log_{10}(x + 1)$ transformed to homogenize variances. An analysis of variance (ANOVA) (PROC GLM, SAS Institute 2009) tested the effects of lure (treatment), block, time, and lure × time interaction on trap catch. If the effect of treatment was significant ($\alpha = 0.05$), then treatment means over the sampling period were compared by using Ryan's Q multiple comparison technique, which has more power ($1 - \beta$) while reducing the probability of experiment-wise type I error (Day and Quinn 1989). For data presentation, trap catches were standardized on a 7-d basis.

EAG Assays. Both *S. schevyrewi* and *S. multistriatus* were tested for their antennal responses to the plant

volatiles (*R*)-(+)-α-pinene, (*S*)-(−)-α-pinene, and MB, as well as to the insect-produced volatile 84%-(−)-multistriatin (Table 2). The selection of these stimuli was based on previous research on field flight responses and host volatile content (Millar et al. 1986, Negrón et al. 2005). Beetles were reared in Davis, CA (Browne 1972), from infested *U. pumila* logs collected in June 2007 from a green waste pile in Reno. Emerging adults were sorted, separated by sex, and held at ≈6°C before shipping to the USDA–ARS Exotic and Invasive Weeds Research Unit (also located in Reno). These insects were transferred to Plexiglas cages (26 by 26 by 20 cm) with moistened lab matting and held at 8 ± 1°C, 75–90% RH, and photoperiod of 14:10 (L:D) h until 1 h before EAG trials when the beetles acclimatized to ≈22°C.

The four compounds included in this study (Table 2) were tested individually as olfactory stimuli. Serial dilutions [10^{-1}, 10^{-2}, 10^{-3}, and 10^{-4} (vol:vol)] of each compound were made with paraffin oil (Merck, Darmstadt, Germany) and stored at 4°C. Stimulus applicators were prepared by pipetting 25 μl of a test solution onto a V-shaped strip (6 cm by 0.5 cm and folded lengthwise) of Whatman no. 1 filter paper (Whatman International Ltd., Maidstone, Kent, United Kingdom), after which the filter paper was placed inside a 14.5-cm-long glass Pasteur pipette. Fresh stimulus applicators were prepared after 2 h of use. Three controls were used: 1) an empty pipette, 2) a pipette containing 25 μl of paraffin oil only on filter paper, and 3) an octanal standard consisting of a pipette containing 25 μl of 10^{-1} (vol:vol) octanal in paraffin oil on filter paper. Octanal served as a positive control because 1) it provided a relatively strong response to facilitate normalization of treatment responses, and 2) the electrical potential of antennae exposed to octanal recovered quickly to baseline levels.

The electroantennography apparatus (Syntech Ltd., Hilversum, The Netherlands) was linked to a desktop computer (with IDAC-02 data acquisition interface board) on which recording, storing, and quantifying of EAG responses were performed. The recording and indifferent electrodes were silver wires enclosed in drawn glass capillary tubes filled with phosphate-buffered saline (4 g of NaCl, 0.57 g of Na_2HPO_4, 0.1 g of KH_2PO_4, and 0.1 g of KCl in 500 ml of distilled water, pH 7.4). Antennal preparations were made by cutting off the head with a scalpel and mounting it on the indifferent electrode. Care was taken not to damage the antennae or mouthparts. Both antennae remained intact and the recording electrode was placed on the tip of one antenna. The left antenna was selected if a number from the random number table ended with 0–4; the right antenna was selected if the number ended with 5–9. The antennal preparation was bathed continuously by a stream of charcoal-filtered and humidified air at a flow rate of 1 liter/min. Air temperature and relative humidity were measured ≈15 cm from the antennal preparation (overall ranges for all trials: 21–23°C, 24–36% RH).

EAG recording began 6 min after the antennal preparation was set up. At this time, the following test protocol was used for each recording trial. First, the controls were tested in the following order (1, 2, 3, 2), after which the four chemical treatments were tested in random order. For each chemical, order of delivery of the four doses was random. Delivery of controls (2, 3, 2) was made after each four-dose series of a chemical. After the final chemical treatment for each recording trial, controls were presented in the following order (2, 3, 2, 1). Presentation of controls throughout the recording trial permitted standardization of antennal responses, and correction for antennal fatigue. Test compounds and controls were applied (0.5-s pulse) at 30-s intervals separated by a purge of filtered-humidified air via an aluminum tube ≈3 mm from the antenna. EAGs were measured as maximum amplitude of depolarization (millivolts). Each chemical was tested on 23 *S. schevyrewi* and 18 *S. multistriatus* individuals of each sex.

Maximum EAG responses were normalized relative to the response to the paraffin oil only control, and expressed as proportional responses relative to the octanal standard. These data were then square root-transformed [$0.5(\sqrt{x} + \sqrt{x+1})$] (Zar 1996), and regression analysis was used to assess the influence of species, sex, and chemical treatment on EAG amplitude (PROC REG and PROC MIXED, SAS Institute 2003). Due to heteroscedasticity over concentrations, a weighted regression (reciprocal of the variance) was calculated.

Results and Discussion

Host Colonization. When variously sized *U. pumila* bolts were exposed in the field where *S. schevyrewi* was known to occur, 16.1 ± 2.7 (mean ± SE) *S. schevyrewi* per dm^2 emerged from small diameter bolts, 13.7 ± 3.6 from medium-diameter bolts, and 11.8 ± 3.4 from large-diameter bolts. The diameter of the bolt did not significantly regress with the number of emerging *S. schevyrewi* adults per dm^2 ($F_{1,34} = 0.52$; $P = 0.47$). Thus, host diameter in the range from 10.2 to 24.1 cm had little influence on the colonization and development of *S. schevyrewi. Scolytus schevyrewi* is able to successfully complete development in branches smaller than 10 cm in diameter (J.F.N., personal observation). It is unknown whether *S. schevyrewi* would prefer branches smaller than 10 cm or the minimum size branch that would be sufficient to support development. A previous study with bolts in the range of 3–13 cm in diameter showed that *S. multistriatus* attacked smaller diameter bolts less frequently and that beetle mortality on smaller diameter bolts was also higher (Hajek and Dahlsten 1985). In our study, emergence rates of *S. multistriatus* were too low, 0.17–0.5 beetles per dm^2, to assess how host diameter might influence their colonization. These low emergence rates probably occurred because *S. schevyrewi* larvae have a superior competitive ability compared with *S. multistriatus* when developing on the same host (Lee and Seybold 2010).

In a no-choice laboratory host acceptance study, *S. schevyrewi* successfully excavated galleries in *U. amer-*

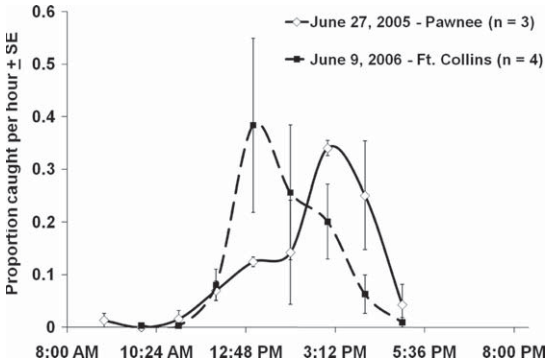

Fig. 1. Mean diurnal landing rate of *S. schevyrewi* on *U. pumila* bolts in Colorado.

icana bolts within a week. We observed no colonization of *U. parvifolia* (Chinese elm), *C. arborescens*, *P. fontanesiana*, or *E. angustifolia*. Previously, *S. schevyrewi* has been recorded on an unspecified Chinese elm, *Caragena* spp. *Prunus* spp., and *E. angustifolia* (Michalski 1973; Bright and Skidmore 1997, 2002); however, it was unclear whether the adults were actually colonizing or had developed in the host, or were simply collected while on the host surface. Although the congener *S. multistriatus* colonizes *U. parvifolia* in the field, the survival rate is low (Švhira and Volney 1983, Švihra 1998). Neither *S. schevyrewi* nor *S. multistriatus* were attracted to small cut bolts of *U. parvifolia* in a flight assay in California (Lee et al. 2010).

Flight Patterns. For diurnal flight patterns, *S. schevyrewi* was observed to fly toward *Ulmus* bolts primarily between noon and 4 p.m. (Fig. 1). Both sexes exhibited similar diurnal patterns, their flights were pooled and compared with air temperatures. In 2005, the air temperature from 9 a.m. to 5 p.m. ranged from 26.3 to 33.2°C and did not significantly regress with the proportion in flight ($F_{1,7} = 2.3$; $P = 0.17$). In 2006, as temperature increased from 24.0 to 29.1°C, flight activity also increased ($F_{1,8} = 9.7$; $P = 0.021$) ($y = -1.5 + 0.06x$, $r^2 = 0.55$). Only one *S. multistriatus* was caught at the bolts, precluding any conclusions about the diurnal flight pattern of this species.

For seasonal flight patterns, both sexes within a species were combined in the results because their ratios were often near 1:1 (Table 3), and their responses were similar. Early season flight of *S. schevyrewi* in Colorado was first observed between 31 March and 7 April in 2004, 2005, and 2006 in the funnel traps baited with Multilure (Fig. 2a–c) when maximum air temperatures were 12–19°C as recorded from a weather station located at one of the experimental sites. The Colorado semiochemical test 1 detected flight by *S. schevyrewi* slightly earlier between 22 March and 5 April 2004. In Nevada, flight of *S. schevyrewi* was first observed between 7 and 23 April, 2004 in Nevada semiochemical test 1 (data not shown). In other studies, early season flight was observed between 5 and 11 April 2007 in Nevada and between 3 and 9 April 2007 in California (Lee et al. 2009).

Peak flight of *S. schevyrewi* in Colorado was observed from June to September with the two highest captures during mid-July and mid-August and averages as high as 40 beetles per trap per week in 2006 (Fig. 2c). Peak flights also were observed in the same Colorado locations from June to August in 2006–2007 (Lee et al. 2009). In Nevada, peak flight occurred approximately July 2004 in Nevada semiochemical test 1 (data not shown) and approximately July–August 2007 (Lee et al. 2009). Late-season flight of *S. schevyrewi* was last observed in Colorado between 24 September and 1 October in 2004, 7 and 14 October 2005, and 29 September and 16 October 2006 (Fig. 2). Other records from Colorado have shown *S. schevyrewi* to fly as late as 21 and 28 October 2003 (Negrón et al. 2005). In Nevada, late-season flight was last observed between 14 and 21 October 2004 during Nevada semiochemical test 1 (data not shown). Based on these trapping data and other studies, *S. schevyrewi* is expected to initiate flight activity by March–April in Colorado and Nevada, have peak activity from July to August, and decrease activity in October.

Early season flight of *S. multistriatus* in Colorado was first observed between 12 and 19 April 2004 in Colorado semiochemical test 1 and between 4 and 12 May 2005 and 28 April and 4 May 2006 in the seasonality monitoring traps (Fig. 2c; Table 3) when maximum temperatures were 15–19°C at one Fort Collins site. Flight in Nevada was first observed between 7 and 23 April 2004 during semiochemical test 1 (data not shown) and between 3 and 9 April 2007 (Lee et al. 2009). In other U.S. states, *S. multistriatus* has been recorded in flight traps ≈10 March 1960 in San Fernando, CA (Brown 1965); between 3 and 9 April 2007 in Sacramento, CA (Lee et al. 2009); and in mid-April in 1978–1980 in Georgia (Hanula and Berisford 1984).

Peak flights of *S. multistriatus* in Colorado were observed in May and August, with mean responses as high as 75 beetles per trap per wk (Fig. 2c) and in August in 2003 in a previous study (Negrón et al. 2005). Some of the same locations were monitored in 2006–2007, and very few *S. multistriatus* were captured in traps to compare peak flight periods (Lee et al. 2009). Peak flight in Nevada was observed twice—approximately May and July in 2004 in semiochemical test 1 (data not shown) and May and July–August in 2006–2007 (Lee et al. 2009). In Georgia, peak flight occurred in May and July in 1978–1980 (Hanula and Berisford 1984). Late season flight of *S. multistriatus* in Colorado was observed between 17 and 24 September 2004, 7 and 14 October 2005, and 29 September and 16 October 2006 (Fig. 2a–c). Other records in Colorado have shown *S. multistriatus* to fly between 14 and 21 October 2003 (Negrón et al. 2005). In Nevada, late flight was observed between 14 and 21 October 2004 during semiochemical test 1. Based on these trapping data and other studies throughout its range, *S. multistriatus* is expected to initiate flight by April–May, have peak activity in May and July–August, and decrease activity by September–October.

Generally, both *S. schevyrewi* and *S. multistriatus* seem to overlap in flight activity from March–May to

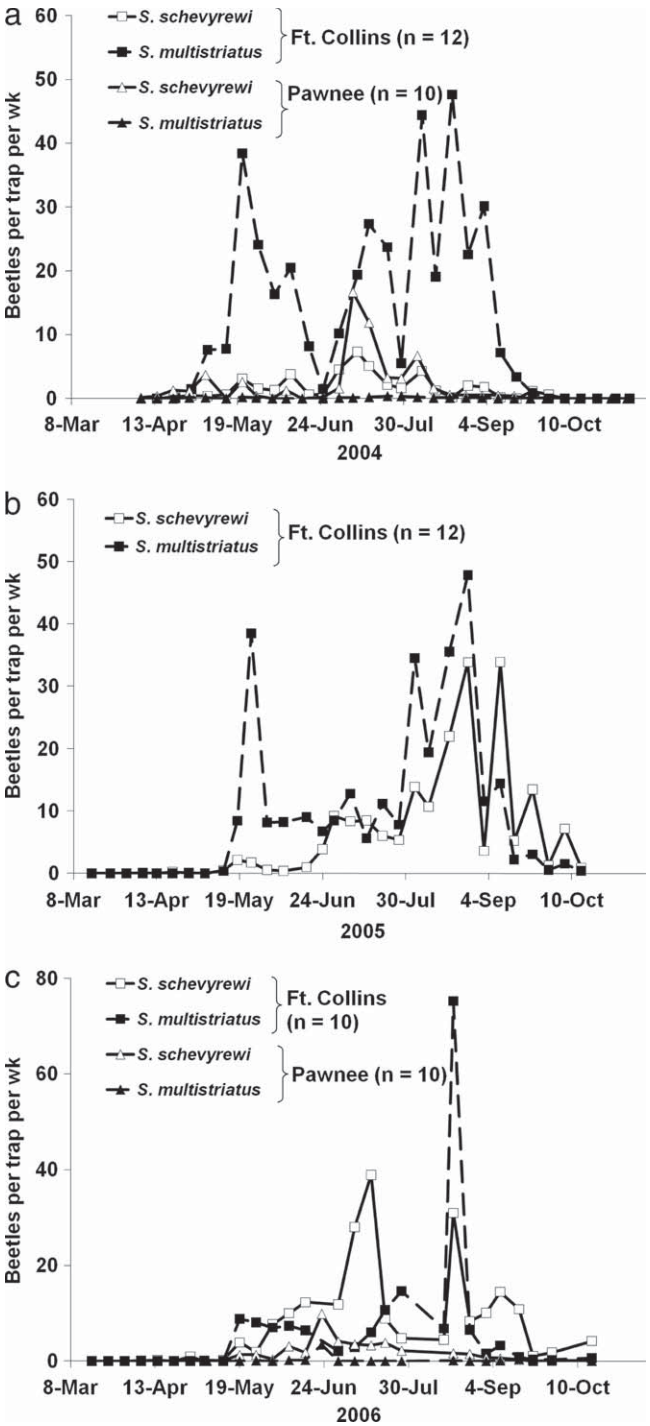

Fig. 2. Mean weekly captures of *S. schevyrewi* and *S. multistriatus* in funnel traps baited with Multilure in Colorado in 2004 (a), 2005 (b), and 2006 (c).

October. Based on limited trapping data, *S. schevyrewi* was sometimes observed to fly earlier in the season than *S. multistriatus*, but this also may have been influenced by lower population densities of *S. multistriatus* occurring in some locations (Lee et al. 2010).

For height of flight in Fort Collins, *S. schevyrewi* and *S. multistriatus* captures varied significantly by height, and more beetles were captured at 1.83 and 3.66 m aboveground than at 7.32 and 9.14 m aboveground (Fig. 3). Captures of *S. multistriatus* also were greater

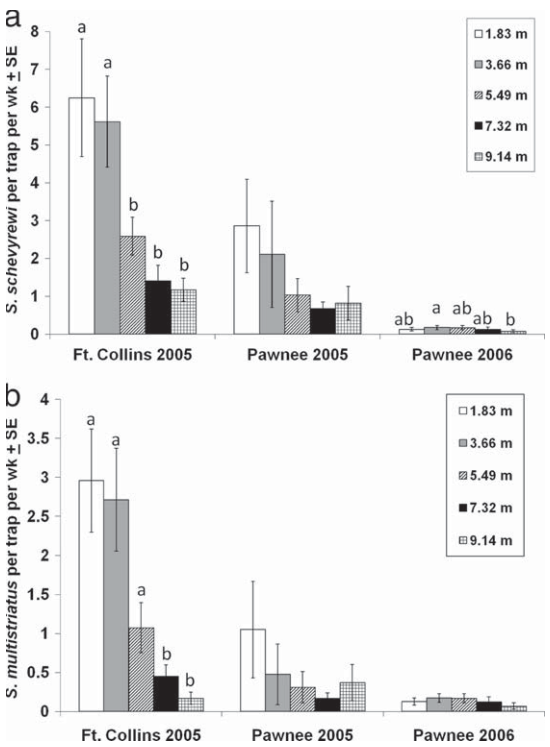

Fig. 3. Mean captures of *S. schevyrewi* (a) and *S. multistriatus* (b) at various heights along the main stem of *Ulmus* trees in Fort Collins (2005; $n = 4$) and Pawnee (2005; $n = 10$ and 2006; $n = 7$). For *S. schevyrewi*: Fort Collins (2005): $\chi^2 = 22.2$, df = 4, $P = 0.002$; Pawnee (2005): $\chi^2 = 3.1$, df = 4, $P = 0.54$; and Pawnee (2006): $\chi^2 = 11.8$, df = 4, $P = 0.0031$. For *S. multistriatus*: Fort Collins (2005): $\chi^2 = 14.7$, df = 1, $P < 0.001$; Pawnee (2005): $\chi^2 = 0.58$, df = 4, $P = 0.97$; and Pawnee (2006): $\chi^2 = 4.6$, df = 4, $P = 0.33$. Letters denote significant difference by Wilcoxon tests with pairwise adjusted α of 0.0051.

at 5.49 m than in traps placed at greater heights. No differences were detected for either species at Pawnee but a decreasing trend was observed with increasing trap height. By 2006, populations of both species had declined markedly, consistent with the semiochemical trap caches. Although the feeding habits of *S. schevyrewi* are mostly unknown, *S. multistriatus* is known to feed on the crotches of elm twigs and would be expected in the higher canopy level of the tree. The tendency to capture more *S. multistriatus* at the lower heights may be influenced by the concentrated source of host material, i.e., the large-diameter bole of the tree. Beetles flying into the upper canopy have a larger area of branches to select and were less likely trapped in the sticky mesh screen, which was placed along the stem.

Flight Responses to Semiochemicals. Significant differences in flight response of *S. schevyrewi* to various lures were found in three out of five tests in Colorado and one out of three tests in Nevada (Table 3). The lures or combinations that attracted the most beetles were as follows: Multilure in Colorado test 1 (Fig. 4a); MB + multistriatin in Nevada test 3 (Fig. 4c); the plant extract vial of Multilure in Colorado test 4 (Fig. 4d); and MB and the plant extract vial of Multilure (although it was only different from MB and the unbaited trap) in Colorado test 5 (Fig. 4e). The lure tests did not identify a compound or blend that was highly attractive to *S. schevyrewi* as mean trap catches were no >2.5–7 beetles per trap per wk. The best lures only increased captures of *S. schevyrewi* by 3.2-fold, 10.8-fold, and 3.9-fold more than the unbaited control traps (Fig. 4a–e), or were not significantly different from the unbaited control (Fig. 4c). The modest response by *S. schevyrewi* to commercial lures was likewise observed by Negrón et al. (2005), where captures of *S. schevyrewi* to either Multilure and MB were ≈16.5 and 10.5 beetles per trap per wk and only two- to three-fold greater than the unbaited control. In general, when differences were observed, *S. schevyrewi* favored plant extracts or combinations with Multilure, which also contains plant extracts. Moreover, a strong response has been observed to traps baited with freshly cut *U. pumila* bolts enclosed in mesh bags in Nevada and Colorado with catches as high as 100+ *S. schevyrewi* per trap per 2 d and 100-fold greater than the unbaited control (Lee et al. 2010). In these studies, *S. schevyrewi* responded similarly to bolts that were uninfested; infested with conspecific females or males; or infested with *S. multistriatus* females. This suggests that *S. schevyrewi* may not produce an aggregation pheromone during the 0–96 h postinfestation period; rather, there is a strong aggregation response to host volatiles. However, *S. schevyrewi* did not respond strongly to the Siberian elm extract in the current study. The difference in responses to the extract versus freshly cut bolts may be explained if the attractive compounds are highly volatile and were not retained in sufficient quantities during the 8-d aeration procedure or were not released in sufficient quantities from the extract presented in our release devices.

For *S. multistriatus*, 94.0 ± 16.5 (mean ± SE) and 108.4 ± 26.7 beetles were captured per trap per wk in Multilure-baited traps in Nevada test 1 (Table 3), and these responses were 226- and 259-fold greater than to the unbaited control. Although lure type significantly affected captures of *S. multistriatus* in Colorado tests 1 and 4 (Table 3), the mean captures were <3 beetles per trap per wk, which were too low to draw conclusions. In Nevada test 3, 6.8 ± 2.0 *S. multistriatus* were captured per trap per wk in response to the Siberian elm extract + multistriatin, which was approximately four-fold more than to the unbaited control, MB alone, Siberian elm extract alone, or MB + Siberian elm extract. As expected, high responses occurred toward traps baited with Multilure or multistriatin + Siberian elm extract because of the combination of host kairomone and pheromone volatiles. The pheromonal response has been well-documented for *S. multistriatus*. For example, traps with both pheromone and host volatiles have consistently caught high numbers of *S. multistriatus* in Colorado (Boutz et al. 1985), Michigan (Lanier et al. 1976), and New York (Lanier and Jones 1985).

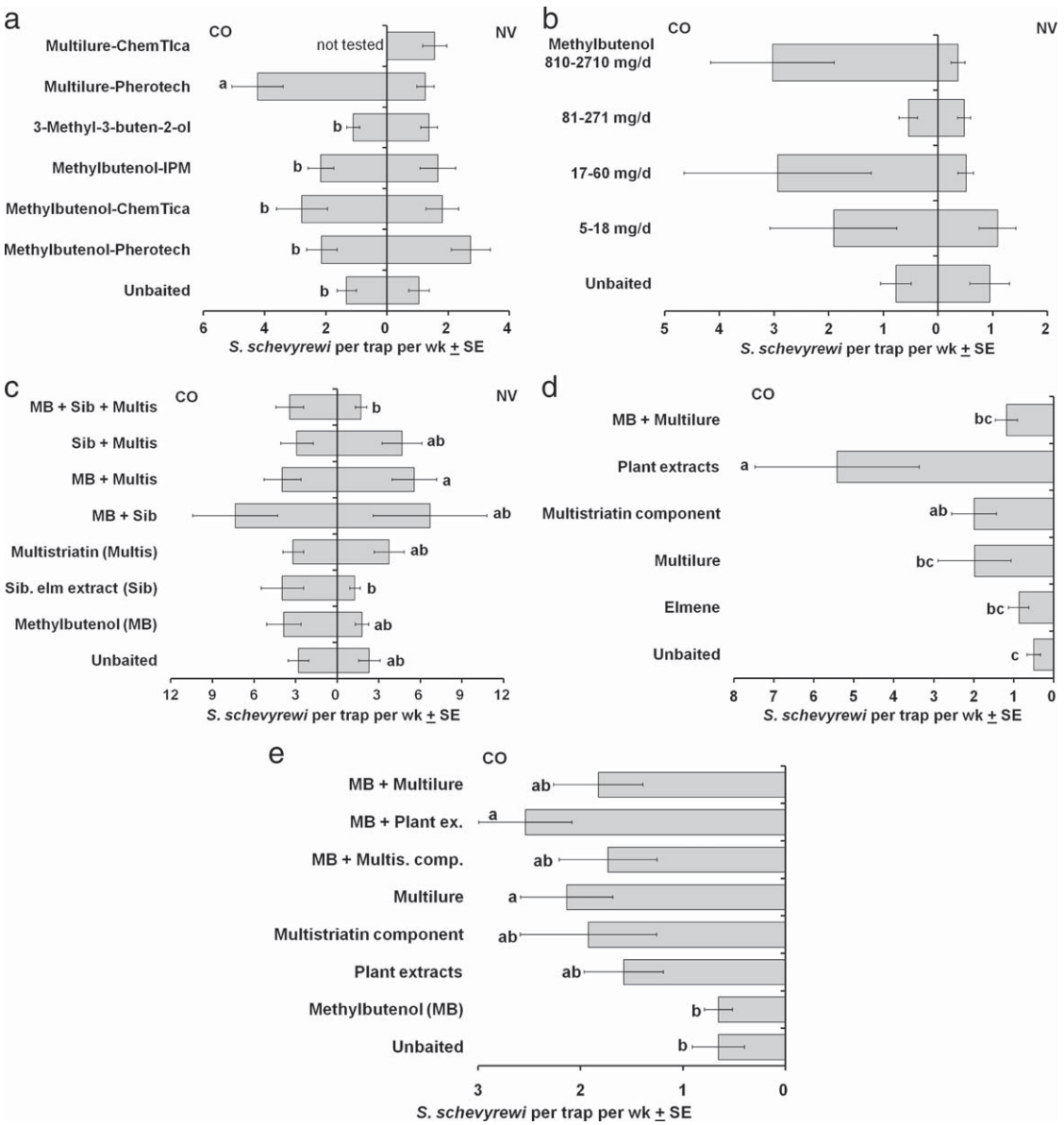

Fig. 4. Mean captures of *S. schevyrewi* in baited funnel traps in Colorado and Nevada semiochemical test 1 ($n = 7$ and 3, respectively) (a), test 2 ($n = 3$ and 3) (b), test 3 ($n = 3$ and 3) (c), Colorado test 4 ($n = 4$) (d), and Colorado test 5 ($n = 4$) (e) (refer to Table 1 for descriptions). Letters on bars denote significant difference by Ryan's Q multiple comparison on $\log_{10}(x + 1)$-transformed data; back-transformed data are presented. The adjusted mean of MB + multistriatin was greater than MB + Siberian elm extract (c), and multistriatin was greater than Multilure (d).

In the flight studies with *S. schevyrewi*, there was a measurable trap catch to the unbaited traps in nearly every experiment (Fig. 4). There has been a trend in the literature of bark beetle chemical ecology not to include negative controls such as unbaited traps in flight studies. The rationale for conducting these incomplete experiments is that the negative controls often result in 0 trap catch values and corresponding 0 variances, and this creates difficulties in the statistical analyses (Reeve and Strom 2004). In this *Scolytus* system, and probably in other bark beetle systems, it might be warranted to always include a negative control in the experiment.

EAG Assays. Regression analysis of antennal response as a function of species, sex, and volatile treatment indicated a linear response between antennal receptiveness (y) and volatile concentration ($\log_{10}$x) (Fig. 5). Contrasts of slopes between sexes were not significant ($P > 0.05$) for either species, so sexes were pooled for further analyses. The EAG saturation concentration, the concentration of volatile molecules beyond which there is no further increase in EAG

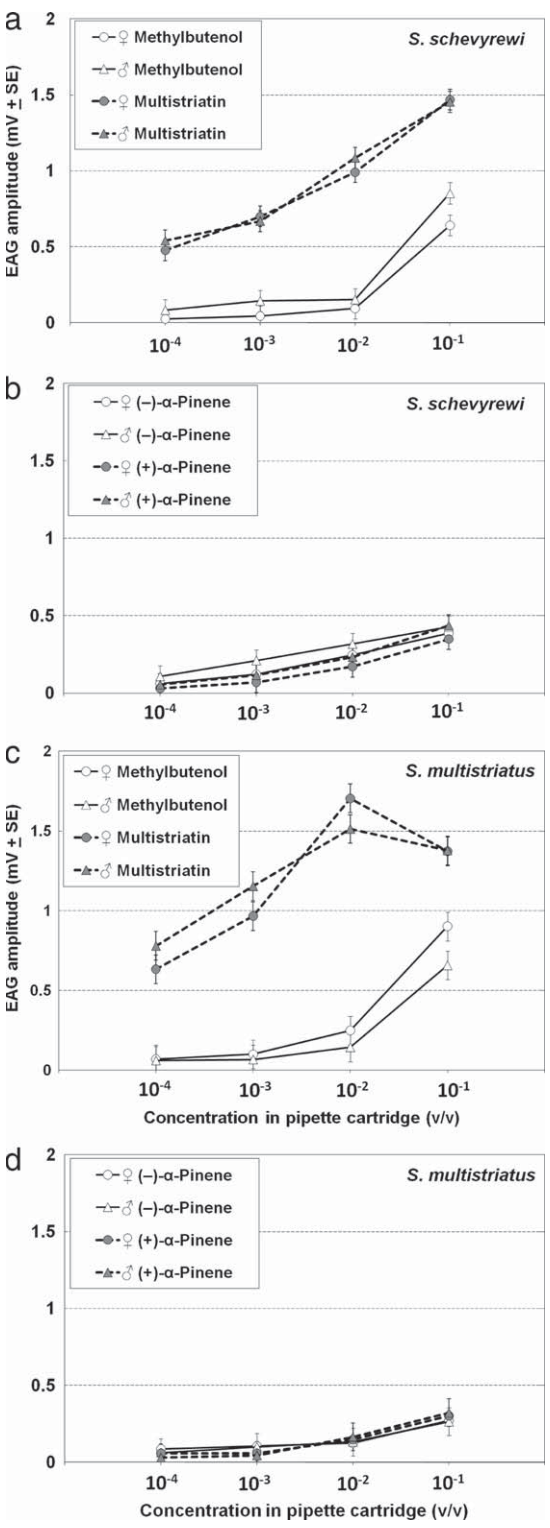

Fig. 5. EAG concentration-response curves of female and male *S. schevyrewi* to 2-methyl-3-buten-2-ol and multistriatin as individual stimuli (a), (–)- and (+)-α-pinene (b), and female and male *S. multistriatus* to the same volatiles (c and d). EAG amplitudes are control-adjusted and presented as proportional responses to the standard, 10^{-1} (vol:vol) octanal. Compounds were tested on 23 adult *S. schevyrewi* and 18 adult *S. multistriatus* of each sex.

amplitude (Boeckh 1969), was reached for α-multistriatin at 10^{-1} (vol:vol) for both species. For this reason, the 10^{-1} concentration of multistriatin was omitted from further analyses. For (*S*)-(–)-α-pinene, the slope for *S. schevyrewi* was greater than for *S. multistriatus* ($F_{1,271} = 12.26; P < 0.001$) (Table 4). This greater response slope for *S. schevyrewi* may be related to the (–)-α-pinene emissions by elms (Millar et al. 1986) and to the stronger response by *S. schevyrewi* to host kairomones in field tests than by *S. multistriatus.* For example, flight toward uninfested cut bolts was 15–110-fold greater than toward unbaited controls for *S. schevyrewi*, and 7.4–25-fold greater for *S. multistriatus* (Lee et al. 2010). Single degree of freedom contrasts between treatments were consistent for both species (Table 5). For each species, these contrasts were significant ($P < 0.05$) for MB versus (*S*)-(–)-α-pinene, MB versus (*R*)-(+)-α-pinene, (*S*)-(–)-α-pinene versus multistriatin, and multistriatin versus (*R*)-(+)-α-pinene (Table 5). For both species the response threshold for multistriatin was lower than for the other compounds (Fig. 5). *S. multistriatus* seemed to have a lower threshold than *S. schevyrewi* to multistriatin, but the difference was not significant (Table 4). EAG responses were consistent with field tests; both *Scolytus* species responded to multistriatin or Multilure-baited traps, although *S. multistriatus* was much more sensitive (Fig. 4).

In summary, this research suggests that previous reports of *S. schevyrewi* on non-*Ulmus* spp. plants may represent beetles collected from the plant surface, but were not developmental records. Even *U. parvifolia* seemed to be a less suitable host than *U. americana.* Thus, we should only regard *Ulmus* spp. as hosts for *S. schevyrewi.*

This research also provides insight into potential management guidelines. *S. schevyrewi* is active in flight between 12:00 p.m. and 4 p.m.. Therefore, branch pruning and tree removals during this time will result in volatile release that may increase the likelihood of infestation of the pruned trees or of nearby trees, or both. Seasonal flight of both *S. schevyrewi* and *S. multistriatus* is generally initiated between late March and mid-April, with *S. schevyrewi* sometimes preceding *S. multistriatus* by a few weeks (Lee et al. 2009, 2010; this study). It would be advisable to conduct branch pruning or tree removal activity for elms between the seasonal cessation of flight in late October and this early season period.

This work also suggests that no operational improvements to the lure of MB or Multilure are recommended at this time even though these lures are only moderately attractive. It should be noted that we tested a blend of optical isomers of multistriatin, of which the δ-isomer predominated. Future studies with *S. schevyrewi* might involve exploring the flight response to the individual isomers as was done by Blight

Table 4. Regression equations and contrasts of slopes (*S. schevyrewi* versus *S. multistriatus*) describing the effects of volatiles on antennal responses

Volatile treatment	*S. schevyrewi*		*S. multistriatus*		ddf	F^b	*P*
	Equation[a]	r^2	Equation[a]	r^2			
(*R*)-(+)-α-Pinene	0.958 + 0.081(x)	0.5065	0.893 + 0.070(x)	0.4200	247	1.91	0.1682
(*S*)-(−)-α-Pinene	0.992 + 0.081(x)	0.4135	0.832 + 0.040(x)	0.1887	271	12.26	<0.001
2-Methyl-3-buten-2-ol	1.039 + 0.110(x)	0.3079	1.035 + 0.102(x)	0.3697	240	0.05	0.8283
Multistriatin[c]	1.514 + 0.150(x)	0.3531	1.780 + 0.190(x)	0.2090	279	1.46	0.2273

[a] Antennal response = a + b($\log_{10}$ concentration).
[b] Numerator df = 1.
[c] Multistriatin regression calculated for concentrations between 10^{-4} and 10^{-2}.

et al. (1983) with *S. multistriatus.* Nonetheless, the flight response of *S. schevyrewi* to lures containing plant extracts in this study and the greater antennal response of *S. schevyrewi* (versus *S. multistriatus*) to (−)-α-pinene are consistent with our understanding of host selection behavior of *S. schevyrewi*, which seems to be driven by host volatiles, particularly those from *U. pumila* (Lee et al. 2010). Strong attraction to host rather than pheromonal volatiles also has been suggested for the fir engraver, *Scolytus ventralis* LeConte (Macías-Sámano et al. 1998). Further electrophysiological studies with gas chromatography-EAG may identify compounds, in *U. pumila* that are perceived by *S. schevyrewi.* These compounds should be incorporated into laboratory and field studies to identify more attractive volatiles than the current products available for monitoring *S. schevyrewi.*

Acknowledgments

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Table 5. *F* values and significance levels for contrasts of slopes between volatile treatments on antennal responses of *S. schevyrewi* and *S. multistriatus*

Volatile contrast	*S. schevyrewi*		*S. multistriatus*	
	F^a	*P*	F^b	*P*
2-Methyl-3-buten-2-ol vs (*S*)-(−)-α-pinene	12.39	<0.001	23.73	<0.001
2-Methyl-3-buten-2-ol vs multistriatin	0.05	0.8264	2.40	0.1218
2-Methyl-3-buten-2-ol vs (*R*)-(+)-α-pinene	9.25	0.0025	11.63	0.0007
(*S*)-(−)-α-Pinene vs multistriatin	16.00	<0.001	30.56	<0.001
(*S*)-(−)-α-Pinene vs (*R*)-(+)-α-pinene	0.14	0.7058	1.90	0.1688
Multistriatin vs (*R*)-(+)-α-pinene	11.99	<0.001	18.78	<0.001

[a] df = 1, 436.
[b] df = 1, 601.

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