

Semiochemical-Mediated Flight Strategies of Two Invasive Elm Bark Beetles: A Potential Factor in Competitive Displacement

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ABSTRACT A seven-state survey showed that the recently detected invasive Asian banded elm bark beetle, *Scolytus schevyrewi* Semenov, was abundant in areas of Colorado and Wyoming, whereas the long-established European elm bark beetle, *S. multistriatus* (Marsham), was not as abundant. In one of a series of studies to evaluate whether *S. schevyrewi* is competitively displacing *S. multistriatus* in their North American zone of sympatry, we characterized long-range flight responses infested or uninfested to small cut logs of American, Chinese, and Siberian elm, *Ulmus americana*, *U. parvifolia*, and *U. pumila*. Trials were conducted in Colorado and Wyoming to test the flight response of *S. schevyrewi*; in California to test the response of *S. multistriatus*; and in Nevada to test the responses of both species simultaneously. Studies with *S. schevyrewi* showed that males and females aggregated toward *Ulmus* spp. host volatiles but provided no evidence of a putative aggregation pheromone during the 0- to 48- or 48- to 96-h period of infestation. In contrast, *S. multistriatus* was attracted to *U. pumila* over unbaited controls, more to *U. pumila* infested with conspecific females than without, and more during the 48- to 96- versus 0- to 48-h period of infestation. This confirmed that male and female *S. multistriatus* aggregated toward host volatiles and that females produced an aggregation pheromone. In a cross-attraction study, *S. schevyrewi* displayed neither flight preference nor interruption to *U. pumila* infested with conspecifics, heterospecifics, or a mix of both species. Response of *S. multistriatus* was too low to draw conclusions. Although *S. multistriatus* aggregates moderately to host volatiles and strongly to female-derived pheromones emitted after a few days, *S. multistriatus* may have a relative disadvantage by selecting elm hosts more slowly than *S. schevyrewi*, which aggregates very strongly to host volatiles. The differential long-range host location strategy may be one factor in a chain of behavioral events that leads to advantageous host colonization and development by *S. schevyrewi*.

KEY WORDS aggregation pheromones, kairomones, Scolytidae, *Scolytus multistriatus*, *Scolytus schevyrewi*

Competitive displacement events warrant study for their (1) applied value of understanding environmental and economic impacts; (2) evolutionary insights into speciation; and (3) ecological value as “natural experiments” to study mechanisms of competition (DeBach 1966). Such mechanisms can involve differential searching ability, resource acquisition, resource preemption, fecundity, resource degradation, direct physical agonistic interactions, reproductive interference, intraguild predation, and susceptibility to natural enemies (reviewed by Reitz and Trumble 2002). The displacement of one invasive species by another represents 55% of the documented cases of competi-

tive displacement (Reitz and Trumble 2002). In a well-studied case of two invasive cerambycid beetles, *Phoracantha recurva* Newman was observed to replace *P. semipunctata* F. in eucalyptus trees in southern California in the 1990s (Bybee et al. 2004). From experiments, replacement was likely mediated by the preference of an egg parasitoid to oviposit on *P. semipunctata* eggs and its lower survival rate developing on *P. recurva* eggs (Luhring et al. 2004). However, many cases of displacement have provided anecdotal evidence of competition but lack empirical documentation or understanding of the mechanisms involved (Simberloff et al. 1997). The North American invasion of the Asian banded elm bark beetle, *Scolytus schevyrewi* Semenov [(Coleoptera: Scolytidae) *sensu* Wood (2007)], provides a timely opportunity to examine newly formed interspecific interactions with the long-established European elm bark beetle, *S. multistriatus* (Marsham). These two bark beetle species, which are allopatric in Eurasia, are now sympatric in North America and both colonize the phloem of

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Table 1. Life history attributes for *S. schevyrewi* and *S. multistriatus*

Attribute	<i>S. schevyrewi</i> (new invasive)	<i>S. multistriatus</i> (established invasive)
Eggs per female	20–120 eggs in China ^a	9–86 eggs in laboratory ^b
Developmental time	30 d in Colorado ^c 40–45 d in China ^a	35–40 d in eastern United States ^d <60 d in Colorado ^e
Overwintering stage	Pupae in China ^a	Larvae in eastern United States ^d and Colorado ^e
Initial seasonal flight		
California ^f	3–9 Apr. 2007	3–9 Apr. 2007 (in same traps)
Nevada ^g	7–23 Apr. 2004 22–27 Apr. 2005	7–23 Apr. 2004 4–26 May 2005
Colorado ^h	5–11 Apr. 2007 22 Mar.–5 Apr. 2004 (Jefferson Co.) 14–22 Apr. 2004 (Larimer Co.) 31 Mar.–7 Apr. 2004 (Weld Co.) 31 Mar.–7 Apr. 2005 (Larimer Co.) 14–19 Apr. 2005 (multiple counties) 20–27 Apr. 2006 (Jefferson Co.) 31 Mar.–7 Apr. 2006 (Larimer Co.) 21–28 Apr. 2006 (Weld Co.)	5–11 Apr. 2007 12–19 Apr. 2004 14–22 Apr. 2004 21–28 Apr. 2004 4–12 May 2005 5–11 May 2005 18–25 May 2006 28 Apr.–4 May 2006 19–26 May 2006
Generations per year	2–3 in China ^a	2, partial third generation in California ⁱ

^a Wang (1992); ^bCannon (1985); ^cNegrón et al. (2005); ^dBaker (1972); ^eCranshaw et al. (1993); ^fLee et al. (2009); ^gLee et al. (unpublished data); ^hNegrón et al. (unpublished data); and ⁱBrown (1965).

American and Siberian elm, *Ulmus americana* L. and *U. pumila* L. (Ulmaceae) (Negrón et al. 2005).

Scolytus multistriatus was first detected a century ago in North America (Chapman 1910) and now occurs in most of the continental United States (Lee et al. 2009). It has been a principal vector of Dutch elm disease (Radio 1935) and the most serious bark beetle affecting elm trees (Ohmart 1989). *S. schevyrewi* was initially detected in 2003 in the United States (Negrón et al. 2005) and is now known to occur in 28 U.S. states (Lee et al. 2009) and in southern Alberta, Manitoba, Ontario, and Saskatchewan in Canada (CFIA 2007, Langor et al. 2009). *S. schevyrewi* colonizes stressed elms (Shi and Chen 1990), causes tree mortality (Negrón et al. 2005), and may vector one of the fungal species that causes Dutch elm disease, *Ophiostoma novo-ulmi* (Jacobi et al. 2007). Despite their co-occurrence and the potential for confusion, the two bark beetle species are readily separated by external morphological characters, even by the non-specialist (Negrón et al. 2005). A seven-state survey for both beetles was conducted around Sacramento, CA; Reno, NV; Ogden, UT; Newcastle, WY; Fort Collins and Denver, CO, in 2006–2007, and in Manhattan, KS, and Columbia, MO, in 2007 (Lee et al. 2009). Abundance of *S. schevyrewi* relative to total *Scolytus* captured was 90 and 89% in Colorado in 2006 and 2007, respectively. Relative abundance in both years was 90 and 83% in Wyoming, 60 and 68% in Utah, 43 and 68% in Nevada, 11 and 13% in California, 3.3 in Kansas (2007), and 2.7% in Missouri (2007).

We have hypothesized that the high incidence of *S. schevyrewi* and low incidence of *S. multistriatus* in some areas of the United States may be the result of *S. schevyrewi* competitively displacing *S. multistriatus* (Lee et al. 2009, Lee and Seybold 2010). A reduction in *S. multistriatus* population density seems to have occurred in Colorado since *S. multistriatus* was recovered in the thousands from elm logs in the 1970s in Fort Collins and Denver (Hostetler and Brewer 1976). In

2003, *S. multistriatus* was recovered as only 1 and 13% of *Scolytus* spp. emerging from elm logs in Fort Collins and flying into baited funnel traps in Denver, respectively (Negrón et al. 2005). In 2006 and 2007 in Fort Collins and Denver, *S. multistriatus* accounted for 10–11% of *Scolytus* spp. detected in surveys with baited funnel traps, unbaited Plexiglas traps, and trap logs (Lee et al. 2009). Similar declining trends of *S. multistriatus* and increasing trends of *S. schevyrewi* have been observed in Reno, NV. In 2003, *S. multistriatus* represented 88.6% of emerging *Scolytus* beetles from elm logs (Negrón et al. 2005), and then at 57% in 2006, and 32% in 2007 from the three trapping methods (Lee et al. 2009). Changes in *S. multistriatus* population densities may also be caused by environmental changes, differential rates of parasitism or predation, or other causes. Thus, longer-term surveys would validate the competitive displacement of *S. multistriatus* by *S. schevyrewi*.

Evaluation of the potential for competitive displacement of *S. multistriatus* involves an examination of long- and short-range behavioral events that occur during bark beetle host colonization (Wood 1982, Graves et al. 2008), as well as any differential aspects of development that occur at points in the life cycle after the establishment phase of host colonization (Light et al. 1983). Investigation of semiochemical-mediated host location strategies may elucidate advantageous long-range flight behaviors in *S. schevyrewi* in the earliest phases of host colonization. Later, following host location, potential components in the mechanism of competitive displacement may include differential host acceptance, oviposition, and larval development when the two species are on or below the bark surface (Lee and Seybold 2010). Differences in fecundity, generation time, and emergence period could also provide *S. schevyrewi* with an advantage or disadvantage compared with *S. multistriatus* (Table 1), but these parameters have yet to be substantiated under controlled conditions. Differences in genera-

tion time and emergence period might be inferred from comparisons of seasonal flight activity of the two species, but measurement of this activity might also be influenced by the abundance of the two species in a given area. From limited and preliminary flight trap catch data recorded in March, April, and May, *S. schevyrewi* seems to fly earlier than *S. multistriatus* (Table 1, one of three studies in Nevada; seven of eight studies in Colorado). However, in one case in California and two cases in Nevada, the initial flight of both species was concurrent (Table 1).

In this study, we investigated the long-range aspects of host colonization behavior that may impart a competitive advantage for *S. schevyrewi*. Our first objective was to compare the relative flight attraction of *S. schevyrewi* and *S. multistriatus* to *U. americana* and to *U. pumila*. Given that *S. schevyrewi* and *U. pumila* share the same native range in Asia (Michalski 1973, Moore 2003), *S. schevyrewi* may be better adapted than *S. multistriatus* to locate and colonize *U. pumila*. The incidence of *S. schevyrewi* in the United States has been associated anecdotally with markedly higher levels of *U. pumila* mortality in the western Great Plains (Negrón et al. 2005, Lee et al. 2006). Our second objective was to compare the responses of both beetle species to host elm (i.e., kairomone) volatiles and beetle-produced (i.e., pheromone) volatiles, and the timing of potential pheromone production. The pheromone biology of *S. multistriatus* has been studied in the United States the 1970s (Lanier et al. 1976), but information is lacking on the pheromone biology of *S. schevyrewi*. A species that aggregates strongly to pheromones relative to kairomones may have an advantage but is also limited by the timing of the initiation of pheromone production, which might delay aggregation. Our third objective was to determine how each species responded to heterospecific cues because a differential response might lead one species to locate hosts more rapidly. A species that is cross-attracted to volatiles associated with hosts attacked by heterospecifics might find more reproductive opportunities (Birch et al. 1980). Similarly, a species that avoids hosts with heterospecifics, even though conspecifics are also present, would miss opportunities to mate with available conspecifics and have fewer resources to use locally (Birch and Wood 1975). Although an interruptive (allomonal) response to heterospecifics may be adaptive to avoid competition (Birch and Wood 1975, Byers and Wood 1980, Byers 1993), the evolution of this response will be important to understand the host colonization behavior and ultimately the success of each beetle species.

Materials and Methods

The flight responses of *S. schevyrewi* and *S. multistriatus* to *Ulmus* spp. were evaluated in five experiments in the western United States. In all experiments, freshly cut pieces of *Ulmus* branches and stems were obtained from private property and municipal tree removals (Table 2) and were stored at 8°C until they were cut into smaller test logs (bolts hereafter). Also,

large infested *U. pumila* logs were collected from field sites known to have high populations of *Scolytus* spp. (Table 2). These logs were placed into large rearing boxes (Browne 1972), and newly emerged (within 1 wk) adult *S. schevyrewi* or *S. multistriatus* were used in each experiment.

In experiment 1, the flight response of *S. schevyrewi* was tested in Colorado and Wyoming where this species is abundant (Lee et al. 2009) (treatments, dates, and locations in Table 2). The objectives were to compare the host preference of *S. schevyrewi* for *U. americana* or *U. pumila* and determine the flight response to pheromonal and/or kairomonal cues by comparing elm hosts with and without female *S. schevyrewi*. Freshly cut bolts (≈ 11 cm long by 9 cm diameter) were placed into separate mesh fabric bags 16 h before placement in the field and kept indoors at ambient room temperature. For one half of the bolts, 25 female *S. schevyrewi* were released onto the bolt so that they could bore into the elm, feed, and possibly produce pheromones. After 16 h, the four types of bolts (treatments) were each hung next to the midpoint of a separate 12-unit Lindgren funnel trap (Lindgren 1983) and traps were spaced at least 20 m apart; an unbaited trap served as a control. Treatments were set up in four blocks, collections were made daily, and bolts were removed each time that the traps were emptied. Replacement bolts were placed on the same traps and the traps were rerandomized in position during each replication over time. Old bolts were debarked, and the number of females that had constructed galleries was recorded. Similar protocols were used in experiments 2–5 (below), except that the amount of time that beetles were allowed to infest bolts before placement in the field, and the trapping intervals varied (Table 2). All experiments tested the flight response of these *Scolytus* spp. with cut bolts because both species have been frequently observed to locate and develop in cut stem sections, broken limbs, or dying elms in the field. Experiments with living elms might yield different results because of induced plant responses that may impact plant volatile and beetle pheromone production. These more complex phenomena were not examined in our experiments.

In experiment 2, the flight response of *S. multistriatus* was tested in California, where this species is relatively abundant. The objectives were to compare the host preference of *S. multistriatus* for *U. americana*, *U. parvifolia*, and *U. pumila*, and to determine the attraction to pheromone and/or kairomonal host cues by comparing the flight responses to elm hosts with and without female *S. multistriatus*. Bolts were prepared as in experiment 1, but with female *S. multistriatus* infesting *U. americana* and *U. pumila*. Newly emerged females collected from the rearing box were presumably unmated and used because elms infested by virgin female *S. multistriatus* are known to be highly attractive to conspecifics in the field (Peacock et al. 1971). Most emerging female *S. multistriatus* and *S. schevyrewi* were considered to be unmated because they could make nuptial chambers, but did not excavate egg galleries when placed onto new elms without

Table 2. Field experiments of the flight behavior of *S. schevyrewi* and *S. multistriatus* in California (CA), Colorado (CO), Nevada (NV), and Wyoming (WY)

Experiment	Treatments	Trapping dates	Locations
1	Unbaited <i>U. americana</i> ^a <i>U. pumila</i> <i>U. americana</i> , 25 ♀ <i>S. schevyrewi</i> 16–40 h (4.6 ± 0.5 beetles that constructed galleries in test logs established by post-exp dissection of logs) <i>U. pumila</i> , 25 ♀ <i>S. schevyrewi</i> 16–40 h (14.9 ± 0.9)	11–21 July 2006 8 collections 1-d trapping intervals	Larimer Co., WY, Cheyenne East High School, 41°08'57"N, 104°46'37"W Larimer Co., CO, Colorado State University Experimental Station, 40°39'28"N, 104°59'49"W Larimer Co., CO, elm lot in Fort Collins, 40°33'54"N, 105°04'43"W Jefferson Co., CO, Lakewood Federal Center, 39°43'12"N, 105°06'58"W
2	Unbaited <i>U. americana</i> ^b <i>U. pumila</i> <i>U. americana</i> , 25 ♀ <i>S. multistriatus</i> 16–64 h (17.9 ± 0.7) <i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i> 16–64 h (19.8 ± 0.5) <i>U. parvifolia</i>	16 Aug. to 8 Sep. 2006 Eight collections 2-d intervals	Yolo Co., CA, Woodland residence, 38°40'20"N, 121°45'35"W Yolo Co., CA, Davis laboratory, 38°32'21"N, 121°44'21"W Yolo Co., CA, UC Davis tree disposal yard, 38°32'01"N 121°48'42"W Sacramento Co., CA, Bing Maloney Golf Course, 38°30'08"N, 121°29'36"W
3	Unbaited <i>U. pumila</i> ^c <i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i> 0–48 h (13.6 ± 0.7) <i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i> 48–96 h (16.8 ± 0.6)	6 June to 3 Aug. 2007 11 collections unbalanced 2-d intervals	Same as experiment 2
4	Unbaited <i>U. pumila</i> ^d <i>U. pumila</i> , 25 ♀ <i>S. schevyrewi</i> 0–48 h (15.4 ± 1.3) <i>U. pumila</i> , 25 ♀ <i>S. schevyrewi</i> 48–96 h (18.0 ± 0.9) <i>U. pumila</i> , 13 ♂ <i>S. schevyrewi</i> 0–48 h, 13 ♂ <i>S. schevyrewi</i> 48–96 h (17.1 ± 0.8)	5–19 July 2007 7 collections 2 d intervals	Larimer Co., WY, Cheyenne East High School (2 blocks), 41°08'57"N, 104°46'37"W Larimer Co., CO, Colorado State Forest Service nursery, 40°35'15" N, 105°08'36"W Larimer Co., CO, elm lot in Fort Collins, 40°33'54"N, 105°04'43"W
5	Unbaited <i>U. pumila</i> ^e , 25 ♀ <i>S. multistriatus</i> 24–96 h (14.5 ± 0.8) <i>U. pumila</i> , 25 ♀ <i>S. schevyrewi</i> 24–96 h (17.4 ± 0.9) <i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i> (14.2 ± 0.9), 25 ♀ <i>S. schevyrewi</i> 24–96 h (17.3 ± 0.9)	25 July–18 Aug. 2007 Eight collections 3-d intervals	Washoe Co., NV, Equestrian Center, 39°32'28"N 119°48'20"W Washoe Co., NV, Idlewild Park, 39°31'18"N 119°49'59"W Washoe Co., NV, City tree yard, 39°31'12"N 119°46'15"W Washoe Co., NV, Brookside Golf Course, 39°30'03"N 119°45'44"W

^a Uninfested *U. pumila* and *U. americana* collected on 19 and 27 June 2006, respectively, from Washoe Co., NV, and stored at 8°C for 30 d; *S. schevyrewi* emerging within 1 wk before the experiment was reared from infested *U. pumila* collected in June 2006 from Jefferson Co., CO.

^b Uninfested *U. parvifolia* collected in Aug. 2006 from Sacramento Co., CA, whereas the other two infested elm bolts were collected as described in experiment 1 but were stored at 8°C for 60 d; *S. multistriatus* was reared from infested *U. pumila* collected in Aug. 2006 in Yolo Co., CA.

^c Uninfested *U. pumila* collected on 8 Mar. 2007 from Washoe Co., NV, and stored at 8°C for 90–120 d; *S. multistriatus* was reared from a laboratory colony started from infested *U. pumila* collected on 20 Sept. 2006 in Washoe Co., NV.

^d Uninfested *U. pumila* collected on 29 Mar. 2007 from El Paso Co., CO, and stored at 8°C for 120 d; *S. schevyrewi* was reared from infested *U. pumila* collected in June 2007 in Jefferson Co., CO.

^e Uninfested *U. pumila* collected as described in experiment 3 but stored at 8°C for 120–150 d; *S. multistriatus* was reared from infested *U. pumila* collected in June 2007 in Yolo Co., CA; *S. schevyrewi* was reared from infested *U. pumila* collected on 5 June 2007 in Washoe Co., NV.

conspecific males (unpublished data). Chinese elm, *U. parvifolia*, was also tested because it is a frequently planted elm in California landscapes and sometimes attacked by *S. multistriatus* (Švihra 1998). However, because of the limited amount of *U. parvifolia* available and the difficulty of getting *S. multistriatus* to bore into this host (unpublished data), *U. parvifolia* was only tested alone and not as a beetle-infested bolt.

In experiment 3, the flight response of *S. multistriatus* was tested again in California. The objective was to determine how the timing of infestation would affect flight response of *S. multistriatus*. A wider interval of

infestation was tested because pheromone production among unmated female *S. multistriatus* was known to increase by the third day under laboratory conditions (Peacock et al. 1973). Two days before placement in the field, freshly cut *U. pumila* bolts were placed in mesh bags. One third of the bolts were uninfested controls, a second third of the bolts initially received females, and the final third of the bolts received females as they were placed in the field, such that bolts exposed in the field contained females releasing volatiles during the 48- or 0- to 48-h period of infestation, respectively.

Table 3. ANOVA results for field experiments of the flight responses of *S. schevyrewi* and *S. multistriatus* in California, Colorado, Nevada, and Wyoming in 2006–2007

Experiment	Species	Effect	df	Males		Females	
				F	P	F	P
1	<i>S. schevyrewi</i>	Block	3, 117	12.6	<0.001	17	<0.001
		Treatment	4, 117	41.0	<0.001	48	<0.001
		Replication over time	7, 117	7.6	<0.001	10	<0.001
		Treatment × replication	28, 117	1.2	0.28	1.4	0.12
2	<i>S. schevyrewi</i>	Block	3, 129	4.85	0.003	Both sexes pooled	
		Treatment	5, 129	6.52	<0.001		
		Replication	7, 129	0.70	0.672		
		Treatment × replication	35, 129	0.81	0.76		
	<i>S. multistriatus</i>	Block	3, 129	8.1	<0.001	10.8	<0.001
		Treatment	5, 129	7.3	<0.001	10.2	<0.001
		Replication	7, 129	1.0	0.41	0.9	0.51
		Treatment × replication	35, 129	0.86	0.69	0.80	0.77
3	<i>S. schevyrewi</i>	Block	3, 97	8.08	<0.001	Both sexes pooled	
		Treatment	3, 97	2.35	0.077		
		Replication	12, 97	3.20	<0.001		
		Treatment × replication	36, 97	1.12	0.326		
	<i>S. multistriatus</i>	Block	3, 97	42.5	<0.001	40.5	<0.001
		Treatment	3, 97	11.7	<0.001	12.1	<0.001
		Replication	12, 97	3.75	<0.001	5.12	<0.001
		Treatment × replication	36, 97	0.73	0.86	0.68	0.91
4	<i>S. schevyrewi</i>	Block	3, 102	2.42	0.07	4.28	0.007
		Treatment	4, 102	60.8	<0.001	62.9	<0.001
		Replication	6, 102	2.00	0.073	2.99	0.01
		Treatment × replication	24, 102	1.22	0.24	1.16	0.30
5	<i>S. schevyrewi</i>	Block	3, 93	22.0	<0.001	16.5	<0.001
		Treatment	3, 93	69.1	<0.001	66.3	<0.001
		Replication	7, 93	7.8	<0.001	6.47	<0.001
		Treatment × replication	21, 93	1.43	0.13	1.61	0.063
	<i>S. multistriatus</i>	Block	3, 93	9.79	<0.001	Both sexes pooled	
		Treatment	3, 93	12.4	<0.001		
		Replication	7, 93	1.93	0.073		
		Treatment × replication	21, 93	1.57	0.074		

In experiment 4, the flight response of *S. schevyrewi* was tested again in Colorado and Wyoming. The objective was to compare the response of *S. schevyrewi* to test bolts of *U. pumila* infested by conspecifics for 0–48 and 48–96 h. An additional treatment of male-infested bolts was included because the pheromone and mating habits of *S. schevyrewi* are not well understood. For the treatment with the male-infested bolt, 13 male *S. schevyrewi* were released onto the bolt during the initial preparation, and another 13 males were released onto the same bolt as it was placed outside. Because elm bolts were a limited resource at the time, this treatment was prepared to release volatiles specific to males during the 0- to 48-h, as well as the 48- to 96-h period of infestation.

In experiment 5, the flight responses of *S. schevyrewi* and *S. multistriatus* were tested in Reno, NV, where in 2006 both species had been found to co-occur in relatively similar abundances (Lee et al. 2009). The objective was to simultaneously compare both *S. schevyrewi* and *S. multistriatus* attraction or interruption to bolts infested with con- and heterospecifics. Each treatment received two *U. pumila* bolts kept in separate mesh bags: (1) uninfested bolt, bolt with 25 female *S. schevyrewi*; (2) uninfested bolt, bolt with 25 female *S. multistriatus*; (3) bolt with 25 female *S. schevyrewi* and bolt with 25 female *S. multistriatus*; or (4) unbaited control. Females were released onto the bolts 24 h before placement in the field for 3 d and

hence exposed at 24–96 h of infestation. Bolts infested by both *Scolytus* species were stored separately until placement in the field in case the species would interact and change their volatile production in each other's presence. Hypothetically, if one species avoided hosts infested by heterospecifics, the numbers of beetles captured in the conspecific treatment would be higher than those captured in the mixed species treatment.

To compare flight responses to the treatments, the number of male and female *S. schevyrewi* and *S. multistriatus* captured per trap was transformed by $\log_{10}(x + 1)$ to homogenize variances. For each sex and species, an analysis of variance (ANOVA) was used to test for the significance of block, treatment, replication over time (rep), and treatment × rep on trap catches in PROC GLM (SAS Institute 2001). If the effect of treatment was significant at the level of $\alpha = 0.05$, treatment means over the sampling period were compared by using Ryan's Q multiple comparison, which has more power ($1 - \beta$) while reducing the probability of experimentwise type I error (Day and Quinn 1989). No *S. multistriatus* were captured in experiments 1 and 4 in Colorado and Wyoming. Because less than two beetles were captured per trap per interval in some experiments, both sexes of *S. schevyrewi* were combined for analyses in experiments 2 and 3 and combined for *S. multistriatus* in experiment 5. Voucher specimens have been deposited at the Or-

Table 4. Comparison of fold-increases of trap catches of *S. schevyrewi* and *S. multistriatus* relative to the unbaited control from five experiments in the western United States

Experiment	Treatment	Fold-increase relative to the unbaited control treatment			
		<i>Scolytus schevyrewi</i>		<i>Scolytus multistriatus</i>	
		Male	Female	Male	Female
1	<i>U. americana</i>	6.7	3.6	Not caught in experiment	
	<i>U. pumila</i>	26.1	14.6		
	<i>U. americana</i> , 25 ♀ <i>S. schevyrewi</i> 16–40 h ^a	8.7	3.8		
	<i>U. pumila</i> , 25 ♀ <i>S. schevyrewi</i> 16–40 h	25.3	11.9		
2	<i>U. americana</i>	NS		NS	NS
	<i>U. pumila</i>	80.0 (both sexes combined) ^b		25.0	12.8
	<i>U. americana</i> , 25 ♀ <i>S. multistriatus</i> 16–64 h	NS		NS	NS
	<i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i> 16–64 h	60.0		57.5	31.2
	<i>U. parvifolia</i>	NS		NS	NS
3	<i>U. pumila</i>	NS (both sexes combined)		7.4	7.4
	<i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i> 0–48 h	NS		10.4	12.4
	<i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i> 48–96 h	NS		20.7	27.4
4	<i>U. pumila</i>	97.4	110.3	Not caught in experiment	
	<i>U. pumila</i> , 25 ♀ <i>S. schevyrewi</i> 0–48 h	90.8	86.3		
	<i>U. pumila</i> , 25 ♀ <i>S. schevyrewi</i> 48–96 h	94.9	89.3		
	<i>U. pumila</i> , 13 ♂ <i>S. schevyrewi</i> 0–48 h, 13 ♂ <i>S. schevyrewi</i> 48–96 h	71.0	79.6		
	<i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i> 24–96 h	32.2	36.5	92 (both sexes combined)	
5	<i>U. pumila</i> , 25 ♀ <i>S. schevyrewi</i> 24–96 h	25.6	25.4	67	
	<i>U. pumila</i> , 25 ♀ <i>S. multistriatus</i>	30.9	34.2	51	
	25 ♀ <i>S. schevyrewi</i> 24–96 h				

^a This is the no. of beetles initially included in the treatment; the actual no. of beetles later found to have constructed galleries in the test logs is provided in the treatment column of Table 2.

^b Unbaited trap catch of 0 was substituted with 0.01 to facilitate calculation of this increase.
NS, not significant.

egon State University Arthropod Collection (accession 00231), University of California Davis Bohart Museum, and the California Academy of Sciences, San Francisco, CA.

Results and Discussion

Both sexes for each species generally responded similarly in all five experiments (Tables 3 and 4; Figs.

1–5), indicating that there were no long-range sex-specific flight responses by *S. schevyrewi* and *S. multistriatus* and that both kairomonal and pheromonal stimuli elicited aggregation responses.

***Scolytus schevyrewi* Host Location Strategy.** *Scolytus schevyrewi* showed a very strong aggregation response to host *U. pumila* odors compared with the unbaited control and no discrimination between uninfested and conspecific-infested elms in experiments

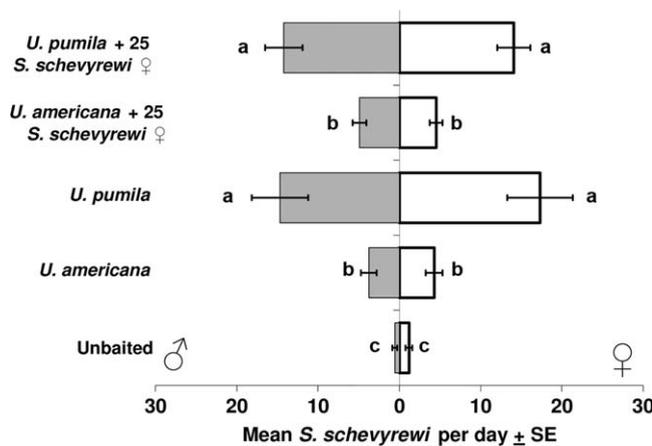


Fig. 1. Mean (\pm SE) numbers of male and female *S. schevyrewi* captured per trap in July 2006 in Colorado and Wyoming in experiment 1. Letters next to histogram bars within a sex denote significant differences [Ryan's Q multiple comparison on $\log_{10}(x + 1)$ transformed data]. Back-transformed data are presented.

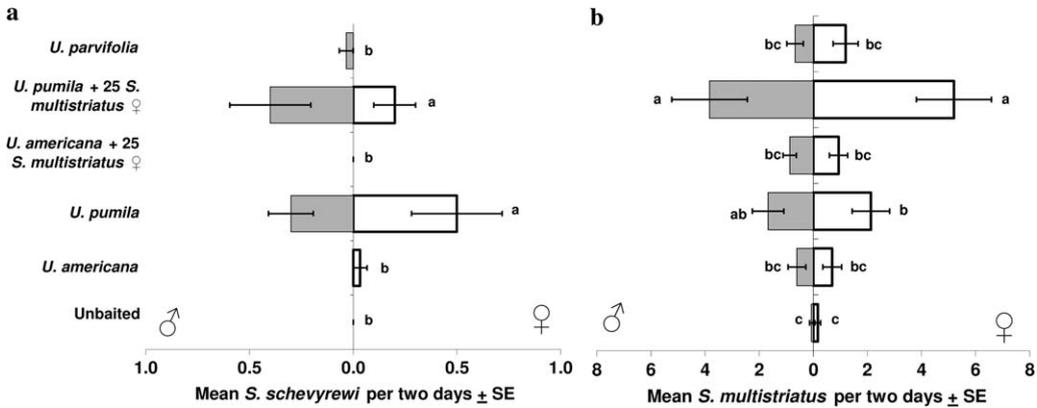


Fig. 2. Mean (\pm SE) numbers of male and female (a) *S. schevyrewi* and (b) *S. multistriatus* captured per trap in August-Sept. 2006 in California in experiment 2. Letters next to histogram bars denote significant differences [Ryan's Q multiple comparison on $\log_{10}(x + 1)$ transformed data] among treatments in (a) with both sexes combined for analysis because of low sample size or (b) within a sex. Back-transformed data are presented.

1 and 4 (Table 3; Figs. 1 and 4). This suggests that neither male nor female *S. schevyrewi* produce a pheromone or pheromone component that enhances attraction to the host, at least during the early stages of infestation. It does not exclude the possibility that each sex may contribute one or more pheromone components that are not attractive alone but may function synergistically. This should be examined in the future. The fir engraver, *Scolytus ventralis* LeConte, is also reported to only be attracted to host compounds and not to produce an aggregation pheromone (Macías-Sámano et al. 1998a, b).

Also, *S. schevyrewi* did not exhibit a clear preference or show any signs of interruption in response to elms colonized by conspecifics, heterospecifics, or the mixture of both species (Fig. 5a). A few *S. schevyrewi* were also captured in experiments 2 and 3 in California with *S. multistriatus*-infested bolts, but *S. schevyrewi* did not seem to differentiate between uninfested and heterospecific-infested elms in these experiments either (Figs. 2a and 3a). Although trap catches of *S. schevyrewi* were too low to confidently test its response in California, these trends are consistent with

observations in Nevada where responses were substantially higher (Fig. 5a). Future studies might attempt to test the effect of mixing heterospecifics in the same host log, which was a treatment that we did not include in our study. For other bark beetles, attraction/interruption has been well documented among *Ips* spp. for maintaining reproductive isolation between sibling species (Fox et al. 1991) or maintaining resource exclusion between more distantly related taxa (Birch and Wood 1975, Byers and Wood 1980, Byers 1993). For example, two relatively distantly related sympatric species, *I. pini* and *I. paraconfusus*, are both mutually interrupted in flight by hosts infested with both species compared with hosts with their own species (Birch and Wood 1975). Laboratory studies later confirmed that interspecific competition was detrimental to the reproductive success of both species so their mutual avoidance of each other's pheromones may have enabled them to avoid co-colonization and interspecific competition (Light et al. 1983). Because *S. schevyrewi* and *S. multistriatus* have allopatric distributions in Eurasia (Lee et al. 2009) and their zone of sympatry has only recently formed in the United

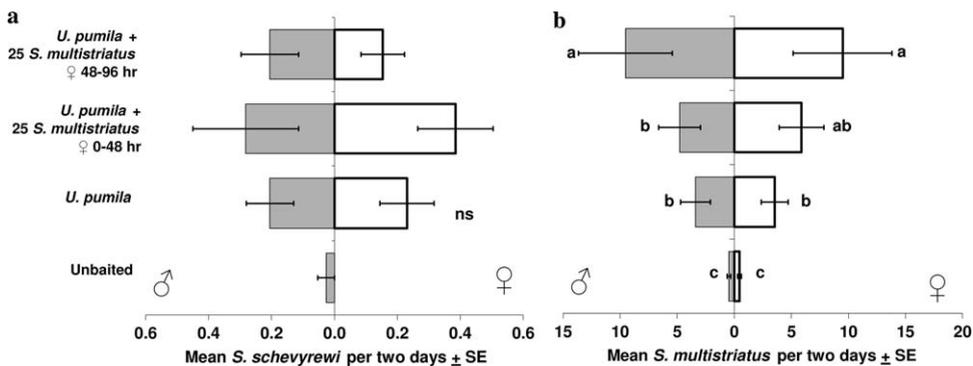


Fig. 3. Mean (\pm SE) numbers of male and female (a) *S. schevyrewi* and (b) *S. multistriatus* captured per trap in June-July 2007 in California in experiment 3. (b) Letters next to histogram bars within a sex denote significant differences [Ryan's Q multiple comparison on $\log_{10}(x + 1)$ transformed data]. Back-transformed data are presented.

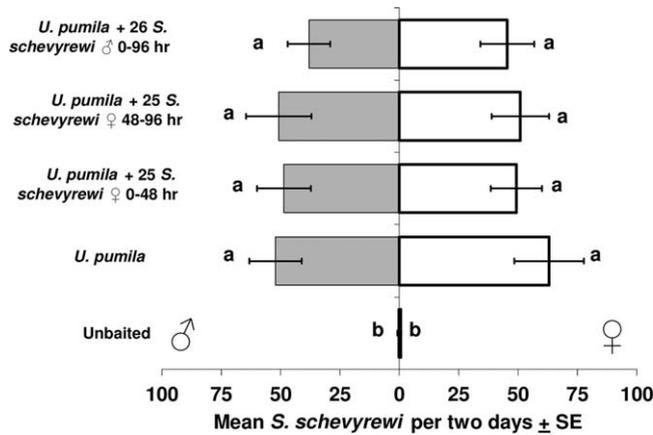


Fig. 4. Mean (\pm SE) numbers of male and female *S. schevyrewi* captured per trap in July 2007 in Colorado and Wyoming in experiment 4. Letters next to histogram bars within a sex denote significant differences [Ryan's Q multiple comparison on $\log_{10}(x + 1)$ transformed data]. Back-transformed data are presented.

States, enough time may not have elapsed for the evolutionary development of any long-range behavioral recognition.

***Scolytus multistriatus* Host Location Strategy.** *Scolytus multistriatus* exhibited moderate aggregation toward host kairomones and greater aggregation toward pheromones. In experiments 2 and 3, *S. multistriatus* preferred host volatiles over the unbaited control trap (Table 3; Figs. 2b and 3b). Volatiles associated with females infesting *U. pumila* were more attractive than all other treatments. Similarly, *S. multistriatus* has been observed to have greater attraction toward *Ulmus* sp. bolts infested with conspecific females than uninfested bolts in Wisconsin (Meyer and Norris 1967) and New York (Peacock et al. 1971). In experiment 3, the attraction of male *S. multistriatus* to female-infested elm bolts 48–96 h after female introduction was greater than to similarly infested bolts 0–48 h after introduction when both treatments were presented simultaneously in the field (Fig. 3b). This result is consistent with a laboratory study where frass produced by unmated females elicited greater responses

from males on the third and fourth day of infestation (≈ 38 and $\approx 59\%$, respectively) than during the first 2 d ($\approx 16\%$) (Peacock et al. 1973).

Behavioral responses of *S. multistriatus* toward hosts infested by heterospecifics could not be elucidated (Fig. 5b). Experiment 5 was conducted in Reno, NV, where both species were expected to be abundant, but a lower than expected abundance of *S. multistriatus* was observed. There was a $\approx 75\%$ drop in abundance from 2006 to 2007 during late July to mid-August in baited funnel traps placed at this general location (Lee et al. 2009). Captures of *S. multistriatus* in experiment 5 were less than two beetles per trap, making it difficult to evaluate responses toward hosts infested by con-, heterospecifics, or a mix of both, except that responses were greater toward any infested bolt than the unbaited control (Fig. 5a).

Host Preference. In experiments 1 and 2, both *S. schevyrewi* and *S. multistriatus* were attracted more to infested *U. pumila* than to uninfested/infested *U. americana* (Figs. 1 and 2). No previous study has compared flight responses of either *Scolytus* species to *U.*

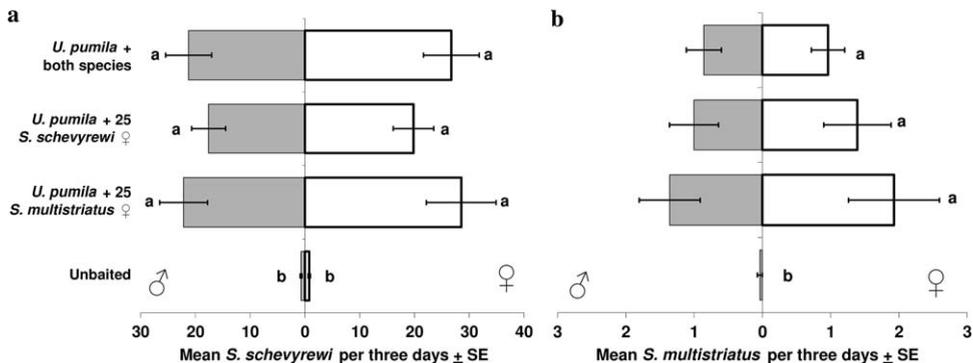


Fig. 5. Mean (\pm SE) numbers of male and female (a) *S. schevyrewi* and (b) *S. multistriatus* captured per trap in July–August 2007 in Nevada in response to *U. pumila* infested by con- and heterospecifics or both. Letters next to histogram bars denote significant differences [Ryan's Q multiple comparison on $\log_{10}(x + 1)$ transformed data] among treatments in (a) within a sex or (b) with both sexes combined for analysis because of low sample size. Back-transformed data are presented.

americana and *U. pumila*, but substantial numbers of *S. multistriatus* have been observed to fly to *U. americana* logs (Peacock et al. 1971, Barger and Cannon 1987), and high population densities of *S. schevyrewi* have been observed in *U. americana* (Negrón et al. 2005). In our study, we suspect that the lower responses of both beetles toward *U. americana* bolts were caused by the relatively low quality of the host material rather than to low innate preference. In experiments 1 and 2, the *U. americana* bolts were only available from weakened trees on a residential street, whereas *U. pumila* bolts were from a healthy standing tree. Bolts from weakened trees were considered suitable for experimentation because most bark beetles attack trees under stress. However, on debarking the bolts to count the number of beetles that tunneled inside, the phloem of *U. americana* was noticeably drier than that of *U. pumila*, and in experiment 1, a mean of less than five *S. schevyrewi* tunneled into the *U. americana* bolts (Table 2). Nevertheless, *S. schevyrewi* were still more responsive to low-quality *U. americana* bolts than to the unbaited control (Fig. 1). Further studies that use *Ulmus* spp. grown under the same conditions would more accurately test host preference.

Flight of *S. multistriatus* toward uninfested *U. parvifolia* was low and not different from the control (Fig. 2b). This low preference for *U. parvifolia* is consistent with other studies. In California, *S. multistriatus* showed a greater flight response to *U. pumila* than *U. parvifolia* bolts (Švihra and Koehler 1981). Although *S. multistriatus* has been reported to infest *U. parvifolia* (Brown 1965), many females provided with this host in the laboratory died before ovipositing and survival of progeny was low (Švihra and Volney 1983, Švihra 1998).

Two Behavioral Strategies and Competitive Displacement. *Scolytus schevyrewi* and *S. multistriatus* had different long-range responses to host stimuli when evaluated relative to the unbaited negative control trap (Table 4). In experiment 1, *S. schevyrewi* did not distinguish between the treatment with volatiles only from host *U. pumila* and from both host and conspecific females, which were 20.3- and 18.6-fold greater, respectively, than the unbaited control (mean across both sexes; Table 4). In experiment 4, the relative responses of *S. schevyrewi* to uninfested *U. pumila* versus *U. pumila* infested with conspecific females for 48–96 h were similar to each other (\approx 100- and 92-fold, respectively) and were much higher than those recorded in experiment 3 for *S. multistriatus* (Table 4). *S. multistriatus* responded moderately to host volatiles but at a higher rate to female-produced pheromones emitted after a few days. For example, in experiment 3, the responses of *S. multistriatus* to uninfested *U. pumila* versus *U. pumila* infested with conspecific females for 48–96 h showed 7-fold and 24-fold increases relative to the unbaited control, respectively (Table 4). Taken together, if both *Scolytus* species are present in the same location, it seems that a greater proportion of the population of *S. schevyrewi* may be expected to aggregate toward suitable uninfested hosts, whereas a lower proportion of the population of *S. multistriatus*

may aggregate toward uninfested hosts. Thus, *S. schevyrewi* appeared to respond strongly and immediately to host kairomones regardless of infestation status, whereas *S. multistriatus* may not respond to uninfested elm hosts as quickly. Although its female-produced aggregation pheromone may be attractive, the timing of the initiation of pheromone production may further delay aggregation in *S. multistriatus*.

The high incidence of *S. schevyrewi* and very low incidence of *S. multistriatus* in some areas of the United States may be the result of *S. schevyrewi* competitively displacing *S. multistriatus*. Current information gathered on these two species is consistent with the occurrence of competitive displacement: (1) the observed relative abundances of the two species in the field (Lee et al. 2009); (2) both species co-colonize the same elm hosts in the field (Negrón et al. 2005, Lee et al. 2006); (3) *S. schevyrewi* is a better competitor when larvae of both species are developing in the same host (Lee and Seybold 2010); and (4) *S. schevyrewi* seems to have a stronger kairomonal response to its host that elicits more rapid aggregation than does the pheromone produced in a delayed fashion by female *S. multistriatus*. The capability of high population densities of *S. schevyrewi* to kill drought-stressed trees (Negrón et al. 2005) coupled with its capacity to vector Dutch elm disease (Jacobi et al. 2007) suggest that this insect may threaten *Ulmus* trees that are relatively abundant shade trees in many urban landscapes of the United States (McPherson 1998; McPherson et al. 2004).

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