Co-Occurrence of the Invasive Banded and European Elm Bark Beetles (Coleoptera: Scolytidae) in North America

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ABSTRACT The invasive European elm bark beetle, *Scolytus multistriatus* (Marsham), was detected in Massachusetts a century ago, and it now occurs throughout the continental United States and southern Canada. The Asian banded elm bark beetle, *Scolytus schevyrewi* Semenov, was discovered in the United States in 2003, and now occurs in 28 states and the province of Alberta, Canada. Although the indigenous populations of these two species are allopatric, the invasive populations are now sympatric in North America where they co-colonize elm (*Ulmus* spp.) trees. A large-scale survey of these two *Scolytus* species was conducted with baited funnel traps, Plexiglas panel traps, and *Ulmus pumila* L. trap logs. Sites (four per locality) were monitored around Sacramento, CA; Reno, NV; Ogden, UT; Newcastle, WY; and Fort Collins, CO (2006–2007), and Manhattan, KS, and Columbia, MO (both only in 2007). Trap catches of *S. schevrewyi* relative to both *Scolytus* species captured from all three trapping methods at each survey site were 90 and 89% in Colorado, 90 and 83% in Wyoming, 60 and 68% in Utah, 43 and 68% in Nevada, and 11 and 13% in California (all in 2006 and 2007, respectively), and 3.3% in Kansas and 2.7% in Missouri (both only in 2007). Elevated abundances of *S. schevyrewi* at survey sites in Colorado and Wyoming could be the result of competitive displacement of *S. multistriatus* by *S. schevyrewi*, whose occurrence and mechanism require further study. General seasonal trends from all sites indicated peak flight in July and August for *S. schevyrewi* and two peaks (May–June and July–August) for *S. multistriatus*. Funnel traps baited with Multilure and 2-methyl-3-buten-2-ol were highly attractive to *S. multistriatus*, and mildly attractive to *S. schevyrewi*, whereas panel traps caught few beetles. The *U. pumila* trap logs were a more sensitive monitoring tool for detecting the presence of *S. schevyrewi*.

KEY WORDS competitive displacement, flight behavior, Scolytidae, *Scolytus multistriatus*, *Scolytus schevyrewi*

In the United States and Canada, >500 exotic insect species attack trees and shrubs, affecting forest and urban landscapes (Niemelä and Mattson 1996, Langor et al. 2009). The European elm bark beetle, *Scolytus multistriatus* Marsham [Coleoptera: Scolytidae, sensu Wood (2007)], originates from Europe (Fig. 1a) and was first detected in 1909 in Massachusetts (Chapman 1910). By 1970, *S. multistriatus* was found in most of the contiguous United States except for Montana, Arizona, and Florida (Barger and Hock 1971), but it has since been collected in Montana in 1973 (Claflin and Dooling 1973), in Arizona in 1976 (B. Celaya, personal communication), and in Florida in 1997 (T. H. Atkinson, personal communication) (Fig. 1a). Since the 1930s, *S. multistriatus* has been known to be a principal vector of Dutch elm disease (DED) (Readio 1935), a disease that caused 50–75% mortality of pre-1930s American elm, *Ulmus americana* L., populations in the northern and eastern United States (Bloomfield 1979). The causative agents of DED are the fungi *Ophiostoma himal-ulmi* Brasier & M.D. Mehrota, *Ophiostoma novo-ulmi* Brasier, and *Ophiostoma ulmi* (Buisman) Nannf. (Harrington et al. 2001). *S. multistriatus* vectors DED when spores of these fungi are present in the

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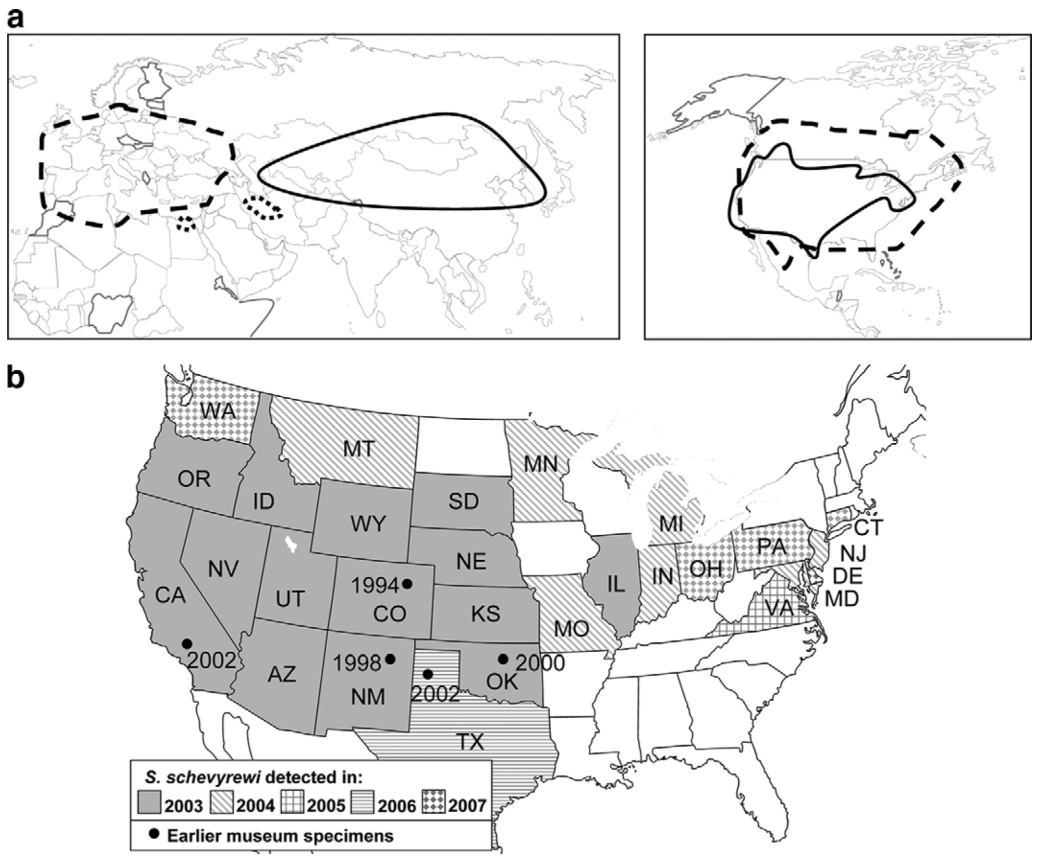

Fig. 1. (a) Approximate native distribution of *S. multistriatus* (dotted delineation) and *S. schevyrewi* (solid delineation) in Europe and Asia, respectively, and their adventive distributions in North America. (b) States in the United States that have detected *S. schevyrewi* since 2003 and sites (dots) where specimens predating 2003 were identified. Distributions based on Michalski (1973), Commonwealth Institute of Entomology (1975), Wood and Bright (1992), Bright and Skidmore (1997, 2002), Negrón et al. (2005), Lee et al. (2007), Government of Canada (2008), Langor et al. (2009), National Agricultural Pest Information System website (http://pest.ceris.purdue.edu/pestlist.php), and personal communications from T. H. Atkinson (Florida), B. Celaya (Arizona), J. Cena (Washington), A. Eitam (Ohio), R. Hiskes (Connecticut), D. Martin (Virginia), and E. G. Riley (Texas).

beetle's galleries in the phloem. New adults emerge from pupal chambers carrying fungal spores. When they feed on branches of living elms, the fungus enters the tree and develops in the vascular tissues (Collins et al. 1936).

The banded elm bark beetle, *Scolytus schevyrewi* Semenov, originates from Mongolia and Northern Asia (references in Fig. 1a) and was first detected in flight traps in April 2003 in Aurora, CO, and in Ogden, UT (Negrón et al. 2005). Like *S. multistriatus*, adult *S. schevyrewi* colonize elms by boring into branches and trunks of stressed or moribund trees to feed and develop in the inner and outer bark (Wang 1992). By the end of 2003, *S. schevyrewi* was detected in 14 states, by the end of 2004 in seven more states, and from 2005 to 2007 in seven more states (Fig. 1b). Detection has not necessarily reflected presence throughout an entire state. For example, *S. schevyrewi* was caught in 2003 on the eastern edge of Oregon, and as of December 2008, it has been caught in the northern but not the central and southern portions of the state (Oregon Department of Agriculture, unpublished data). Likewise, in central and northern California it has not been reported from the coastal urban areas or from the northern Central Valley (R. L. Penrose et al., unpublished data). The nearly simultaneous detection of *S. schevyrewi* in 14 states in 2003 strongly implies that the beetle likely arrived earlier but remained undetected. This was confirmed when an examination of museum collections later revealed previously collected specimens of *S. schevyrewi*, including the earliest collection in 1994 from Denver, CO (Negrón et al. 2005), and the first collection from Texas (Randall Co.) in 2002 (E. G. Riley, personal communication). The mode of entry of *S. schevyrewi* into North America is unknown, but many invasive bark beetles have been found in barked wood packaging materials associated with imports inspected at U.S. ports (Haack 2001, Lee et al. 2007). Between 1985 and 2000, 92 interceptions of *Scolytus* beetles have occurred at U.S. ports of entry, 14 specimens were identified to species (Haack 2006), and none were found to be *S. schevyrewi* (R. A. Haack, personal communication).

The mere presence of *S. schevyrewi* or any other exotic species is not necessarily detrimental if it does not cause harm to the economy, environment, or human health. Rather, exotic species become "invasive" by progressing through the phases: 1) arrival; 2) establishment—organism survives and reproduces; and 3) spread (Venette and Carey 1998, Liebhold and Tobin 2008). *S. schevyrewi* has arrived and is established in more than half of the land area of the continental United States and seems to have spread in areas such as Colorado and Wyoming (Negrón et al. 2005, Lee et al. 2006). As invasive populations of *S. schevyrewi* spread, the impacts on urban and unmanaged landscapes are a major concern. Infestations of *S. schevyrewi* alone can kill water-stressed elms, as observed in China (Wang 1992) and Colorado (Negrón et al. 2005). In addition, *S. schevyrewi* is a suspected vector of DED because beetles collected from diseased trees were found to carry spores of *O. novo-ulmi* (Jacobi et al. 2007) although vectoring efficiency is still being investigated.

The impact and spread of *S. schevyrewi* in the United States will depend on its ecological interactions, particularly those with *S. multistriatus*, which shares the same niche in the inner and outer bark of elms. Infested elm logs collected in 2003 in Fort Collins, CO, revealed that 99% of emerging adult scolytids were *S. schevyrewi* (Negrón et al. 2005), whereas *S. multistriatus* was readily found in city elm groves in the past (Hostetler and Brewer 1976). The numerical dominance of *S. schevyrewi* suggests that it may be competitively displacing *S. multistriatus*, i.e., the "elimination in a given habitat, of one species by another where one possesses the identical ecological niche to the other" (DeBach 1966). Analogously, *S. multistriatus* is thought to have displaced the native elm bark beetle, *Hylurgopinus rufipes* (Eichhoff), in areas where *S. multistriatus* could overwinter (Lanier 1983). *S. multistriatus* was considered to be more aggressive and has a second generation each year, compared with the native beetle with one generation per year. Displacement of a native insect species by an exotic is undesirable and represents 33% of the documented cases of competitive displacement (Reitz and Trumble 2002). If it is occurring, displacement of *S. multistriatus* by *S. schevyrewi* would represent the displacement of a previously established exotic by another exotic, like 55% of documented cases. For elm bark beetles, the second displacement event will potentially also be undesirable because *S. schevyrewi* is causing additional damage to already embattled elm populations, particularly to Siberian elm, *Ulmus pumila* L. (Lee et al. 2007).

Unfortunately, many cases of displacement have been accompanied by anecdotal evidence of competition without empirical documentation (Simberloff et al. 1997). The current invasion of *S. schevyrewi* provides a timely opportunity to begin obtaining evidence of displacement lacking from most post hoc studies, particularly because this invasion may be at different stages at different locations in the United States. Documenting the extent to which *S. schevyrewi* has replaced *S. multistriatus* across their respective adventive ranges is a key first step in exploring the mechanism of displacement, i.e., whether displacement in this case may be mediated by differential abilities to locate hosts during flight (J.C.L. et al., unpublished data), to accept hosts at close range, to lay eggs, and the competitive ability of larvae (J.C.L. and S.J.S., unpublished data). In this study, our objective was to quantify the relative abundance of *S. schevyrewi* and *S. multistriatus* along a wide-scale geographic transect that included California, Nevada, Utah, Wyoming, Colorado, Kansas, and Missouri.

Materials and Methods

In 2006, elm bark beetles were monitored from May/June to September at four sites each around Sacramento, CA; Reno, NV; Ogden, UT; Newcastle, WY; and Fort Collins, CO; in 2007, monitoring continued in the same areas with the addition of Manhattan, KS, and Columbia, MO (Table 1). Four sites within each state were within a circle that was 2.4–98 km in diameter, and sites were selected for proximity to standing elm trees or cut elm stem wood or branches, and where anthropogenic disturbance of traps would be less likely. For brevity in the results and figures, we refer to the sites by their state names, although the captures from a city or several cities of each state do not necessarily reflect abundances throughout the entire state. To assess populations, three types of traps were used simultaneously because each trap may have a bias toward catching one species over another. First, a 12-unit Lindgren funnel trap (Lindgren 1983) was baited with Multilure released at 0.3 mg/d (Pherotech International Inc. [now Contech Inc., Delta, BC, Canada]), and 2-methyl-3-buten-2-ol (Aldrich Chemical Co., Milwaukee, WI) released at 5–18 mg/d from 10 heat-sealed 400-μl polyethylene Eppendorf tubes (Evergreen Scientific, Los Angeles, CA). Baits were replaced after 2 mo. This baited flight trap was expected to elicit a higher response from *S. multistriatus* because Multilure contains the pheromone blend for this species. Multilure and methylbutenol were also known to be mildly attractive to *S. schevyrewi* (Negrón et al. 2005, Lee et al. 2007).

Next, a 30- by 30- by 50-cm clear Plexiglas Schmitz panel trap (Schmitz 1984) was installed at each site under an elm tree or next to elm debris. This trap consisted of two Plexiglas panels slit halfway in the center and fitted together perpendicularly at the slits, appearing as a '+' sign from the top view. The bottom of each of the four trapping vanes was connected to an inverted 3.8-liter milk jug, which was in turn connected to a collection cup. This passive trap was considered to be the least biased, because it would trap any insect flying in the vicinity of the bole of elms or responding to volatiles from cut logs. Funnel and panel traps were spaced at least 15 m apart and emptied weekly.

The third trap was a cut Siberian elm, *U. pumila*, log with $\approx$14.1-dm^2 surface area and wax-sealed ends to reduce desiccation. One trap log was laid at each site three times each summer during May/June, July, and

Table 1. Description and location of trapping sites for determining the relative abundance of *S. multistriatus* and *S. schevyrewi* in the western United States

State	Description	Location	Latitude and longitude	Dates for flight traps and when trap logs were exposed in field
California	Private residence, single *U. pumila*	Woodland, Yolo Co.	38° 39′ 53″ N, 121° 46′ 18″ W	Flight: May 26–Oct. 4, 2006; April 3–Sept. 12, 2007
	Shaded area, distant *U. pumila* and *U. americana*	Davis, Yolo Co.	38° 32′ 24″ N, 121° 44′ 24″ W	Trap logs: June 7–22, July 6–21, Aug. 9–23, 2006; May 15–June 1, July 5–20, July 31–Aug. 15, 2007
	Green waste pile with cut *Ulmus* spp.	Davis, Yolo Co.	38° 32′ 12″ N 121° 48′ 22″ W	
	Green waste pile, Bing Maloney Golf Course, *U. parvifolia*	Sacramento, Sacramento Co.	38° 30′ 10″ N, 121° 29′ 41″ W	
Nevada	Equestrian Center, *U. pumila*	Reno, Washoe Co.	39° 32′ 26″ N 119° 48′ 23″ W	Flight: May 24–Oct. 3, 2006; April 5–Sept. 9, 2007
	Green waste pile, cut *Ulmus* spp.	Reno, Washoe Co.	39° 31′ 13″ N 119° 46′ 19″ W	Trap logs: June 7–20, July 4–18, Aug. 11–25, 2006; May 17–31, July 6–20; Aug. 1–15, 2007
	Golf course, *U. pumila*	Reno, Washoe Co.	39° 30′ 05″ N 119° 45′ 50″ W	
	Office complex, *U. pumila* (2006 only)	Carson City, Carson Co.	39° 07′ 32″ N 119° 46′ 12″ W	
	Private residence, *U. pumila* (2007 only)	Minden, Douglas Co.	38° 58′ 3″ N 119° 41′ 31″ W	
Utah	Golf course, *U. pumila*	Ogden, Weber Co.	41° 17′ 11″ N, 111° 59′ 15″ W	Flight: June 9–Sept. 11, 2006; May 18–Sept. 11, 2007
	Campgrounds, *U. americana* and *U. pumila*	Huntsville, Weber Co.	41° 15′ 01″ N, 111° 47′ 10″ W	Trap logs: June 9–23, July 5–21, Aug. 11–25, 2006; May 18–June 1, July 6–20, Aug. 3–17, 2007
	Nature Center, *U. pumila*	Ogden, Weber Co.	41° 14′ 42″ N, 111° 59′ 41″ W	
	Train depot, *U. pumila*	Clearfield, Davis Co.	41° 06′ 19″ N, 112° 02′ 19″ W	
Wyoming	City shop, *U. pumila*	Newcastle, Weston Co.	43° 51′ 31″ N, 104° 12′ 15″ W	Flight: June 15–Sept. 13, 2006; May 21–Sept. 9, 2007
	Private residence, *U. pumila*	Newcastle, Weston Co.	43° 51′ 21″ N, 104° 13′ 09″ W	Trap logs: June 15–29, July 7–20, Aug. 14–28, 2006; May 21–June 6, July 5–19; Aug. 2–15, 2007
	Private residence, *U. pumila*	Newcastle, Weston Co.	43° 51′ 09″ N, 104° 11′ 52″ W	
	Green waste pile, cut *Ulmus* spp.	Newcastle, Weston Co.	43° 50′ 27″ N, 104° 12′ 59″ W	
Colorado	Nursery, *U. pumila* (2007 only)	Ft. Collins, Larimer Co.	40° 35′ 14″ N, 105° 08′ 42″ W	Flight: June 12–Sept. 15, 2006; May 16–Sept. 7, 2007
	School, *U. americana* and *U. pumila* (2006 only)	Ft. Collins, Larimer Co.	40° 34′ 23″ N, 105° 04′ 03″ W	Trap logs: June 13–28, July 10–26, Aug. 9–23, 2006; May 17–June 1, July 5–17, Aug. 1–15, 2007
	Research Station, *U. pumila*	Ft. Collins, Larimer Co.	40° 34′ 06″ N, 105° 05′ 09″ W	
	Office complex, *U. pumila*	Lakewood, Jefferson Co.	39° 43′ 13″ N, 105° 06′ 44″ W	
	Office complex, single *U. pumila*	Lakewood, Jefferson Co.	39° 43′ 28″ N, 105° 07′ 11″ W	
Kansas	Private residence, *U. americana* and *U. pumila*	Near Randolph, Riley Co.	39° 29′ 59″ N, 96° 45′ 22″ W	Flight: May 23–Sept. 3, 2007 Trap logs: May 24–June 6, July 3–18, Aug. 8–22, 2007
	Private residence, *U. pumila*	Near Louiseville, Pottawatomie Co.	39° 13′ 40″ N, 96° 21′ 32″ W	
	Private residence, *U. pumila*	Manhattan, Riley Co.	39° 09′ 42″ N, 96° 32′ 12″ W	
	Private residence, *U. americana*	Near Tri-County Road and Quaker Road, Morris Co.	38° 52′ 24″ N, 96° 35′ 51″ W	
Missouri	Office complex, *Ulmus* spp.	Columbia, Boone Co.	38° 56′ 08″ N, 92° 19′ 19″ W	Flight: May 22–Sept. 5, 2007 Trap logs: May 22–June 5, 2007, July 3–17; July 31–Aug. 14, 2007
	Park, *Ulmus* spp.	South of Columbia, Boone Co.	38° 55′ 44″ N, 92° 18′ 40″ W	
	Office complex, *Ulmus* spp.	Columbia, Boone Co.	38° 55′ 30″ N, 92° 18′ 15″ W	
	Park, *Ulmus* spp.	South of Columbia, Boone Co.	38° 48′ 45″ N, 92° 15′ 21″ W	

[1] Freshly cut *Ulmus pumila* trap logs were collected from: 1) Carson City, NV in Mar. 2006 and stored at 4°C until placement in the field in June 2006; 2) Reno, NV on June 19, 2006 for placement in the field in July and Aug. 2006; and 3) Reno, NV on Mar. 8, 2007 for placement in May, July, and Aug. 2007.

August and retrieved ≈2 wk later (Table 1). Insects were then reared from the logs at the USDA Forest Service Chemical Ecology of Forest Insects Laboratory in Davis, CA, at ambient conditions. Each log was placed in an individually aerated and sealed plastic 18.9-liter paint bucket (Lee et al. 2008). Emerging adults were collected from a glass collection jar at the bottom of each bucket every week for 2 mo because *S. schevyrewi* can develop from egg to adult within 30–45 d (Wang 1992, Negrón et al. 2005), and *S. multistriatus* within 35–60 d (Drooz 1985, Cranshaw et al. 1993). After the 2-mo rearing period, logs were stored at 4°C until they could be debarked to collect any remaining adults; some adults recolonized the logs after emergence and needed to be accounted for in the assessment. Some parental beetles in good condition may have been counted as progeny because parents could not be separated definitively from progeny beetles. However, this overestimation would have occurred among all trap logs. The trap log served as a measure of the expected recruitment rate of progeny of both species when host material was available in the field. The trap log would likely recruit more progeny of the earlier colonizing species if it has the competitive advantage of equaling or preceding the other species in development.

Despite their co-occurrence and the potential for confusion, the two bark beetle species were readily separated by external morphological characters (Negrón et al. 2005). These characters are diagnostic, even when evaluated by the nonspecialist (LaBonte et al. 2007). For data analysis, we used the number of beetles per species collected from funnel and panel traps on a weekly basis, and the total number of beetles per species reared from each trap log. To compare the relative abundance of the two species, the percentage of *S. schevyrewi* adults [*S. schevyrewi*/(*S. multistriatus* + *S. schevyrewi*)] collected per flight trap or per log was converted to a proportion and arcsine$\sqrt{x}$ transformed to normalize variances. Trap catches without *Scolytus* spp. were excluded from the analyses. To compare total abundance among flight traps, the number of *S. schevyrewi* or *S. multistriatus* captured per trap was standardized on a daily basis (number of beetles/sampling days between collection intervals) and then $\log_{10}(x + 1)$ transformed. Among trap logs, the total abundance of each species collected per log was analyzed. The percentage and total *S. schevyrewi* and *S. multistriatus* captured/reared out were analyzed with a repeated measures analysis ($\alpha = 0.05$) with the variables state, time, and state × time in PROC MIXED (SAS Institute 2001). If the effect of state was significant, means from each state across time were compared by Ryan's Q multiple comparison, which has high power and controls for experimentwise type I error (Day and Quinn 1989). Because flight trapping durations varied from state to state, only samples during 21 June–13 September 2006 and 29 May–7 September 2007 were incorporated in the statistical analyses because all states were simultaneously monitored at these times. Voucher specimens from each location have been deposited at the Oregon State University Arthropod Collection, Corvallis, OR (accession 00229), University of California Davis Bohart Museum of Entomology, and the California Academy of Sciences, San Francisco, CA.

Results and Discussion

Geographic Trends. This 2-yr monitoring survey revealed that higher percentages of *S. schevyrewi* than *S. multistriatus* were found in sites in Colorado (CO), Wyoming (WY), Nevada (NV), and Utah (UT) (Fig. 2). Relatively fewer *S. schevyrewi* than *S. multistriatus* were recovered in California (CA), Kansas (KS), and Missouri (MO) (Figs. 2 and 3). Funnel, panel, and log

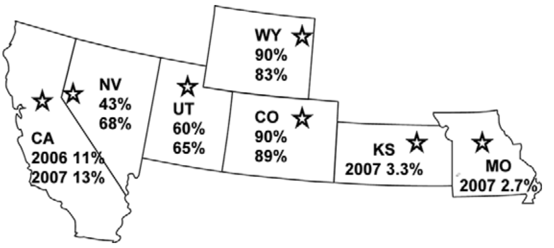

Fig. 2. Trapping sites (stars) and overall percentages of *S. schevyrewi* at sites in 2006–2007 in California (CA), Nevada (NV), Utah (UT), Wyoming (WY), and Colorado (CO), and in 2007 in Kansas (KS) and Missouri (MO).

trap catches were often affected by the state × wk or state × mo interactions (Table 2), but general trends over time are discussed. Relative abundance in funnel traps in 2006–2007 had the following trend: CO ≥ WY > UT > NV > CA = KS = MO (Table 2; Fig. 3a and b). Relative abundance in panel traps had similar trends: in 2006 CO = WY > UT = NV > CA (Fig. 3c) and in 2007 CO = WY > NV > UT > CA = KS = MO (Fig. 3d). Recruitment of beetles from trap logs showed slightly different trends in relative abundance than the flight traps. Nevada ranked generally higher among most states in recruiting a higher percentage of *S. schevyrewi* from logs: in 2006 WY ≥ CO = NV ≥ UT > CA (Fig. 2e); and in 2007 CO = NV ≥ UT ≥ WY > CA ≥ KS ≥ MO (Fig. 3f).

These results suggest that *S. schevyrewi* may be at different stages of invasion across the western United States with the highest abundances in Colorado and Wyoming. Interestingly, a reduction in *S. multistriatus* population density seems to have occurred in Colorado because *S. multistriatus* was recovered abundantly in elm bolts in 1973 in Fort Collins, CO, and in 1974 in Denver, CO (Hostetler and Brewer 1976). Now the high incidence of *S. schevyrewi* in Fort Collins and Lakewood (near Denver), CO, may be the result of competitive displacement, but additional monitoring over time in Colorado and other states is needed to determine whether displacement is occurring. A similar pattern was found with the invasive eucalyptus longhorned borers (Coleoptera: Cerambycidae) in southern California where *Phoracantha semipunctata* F., discovered in 1984 (Scriven et al. 1986), was likely displaced by *Phoracantha recurva* Newman, discovered in 1995 (Hanks et al. 1997). *P. recurva* made up 1.4% of *Phoracantha* spp. emerging from naturally infested eucalyptus in 1996, 74% in 1997, and >95% in 1998 (Hanks et al. 1997, Bybee et al. 2004). The advantage for *P. recurva* seems to lie with the susceptibility of *P. semipunctata* to an egg parasitoid (Luhring et al. 2004). This displacement led to establishment of a second invasive species that was less likely to be naturally regulated than the first invasive species.

Total numbers of *S. schevyrewi* and *S. multistriatus* collected per day in funnel and panel traps showed similar trends as the relative abundance of the two species, but with less separation among states. Total captures of *S. schevyrewi* followed this trend: in funnel

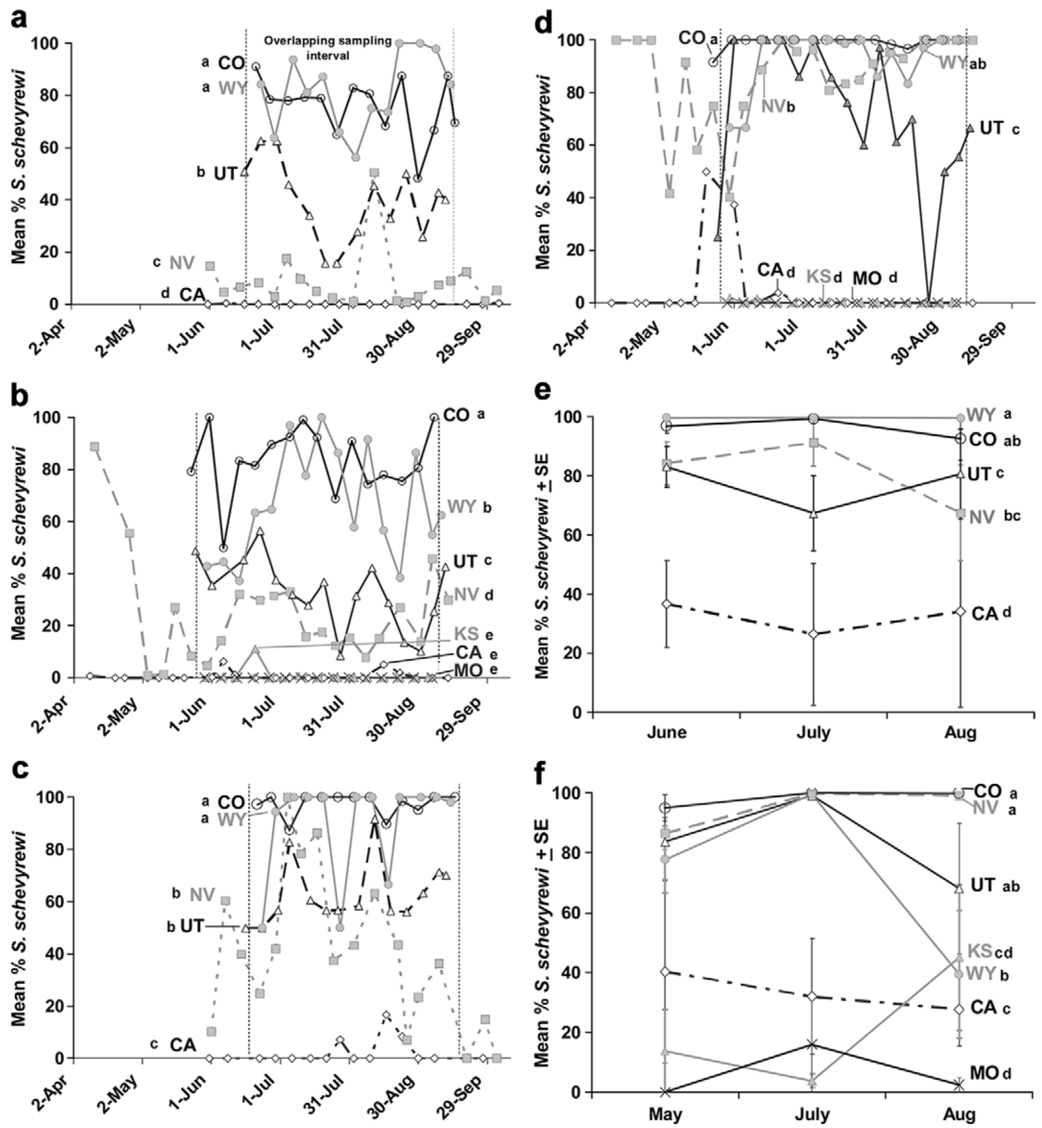

Fig. 3. Mean percentage of *S. schevyrewi* (relative to both *S. schevyrewi* and *S. multistriatus*) in funnel traps in 2006 (a) and 2007 (b), in panel traps in 2006 (c) and 2007 (d), and recovered from trap logs in 2006 (e) and 2007 (f). Vertical dotted lines in a–d indicate the beginning and ending of the sampling periods when all sites were analyzed statistically. Letters denote significant differences ($P < 0.05$) by Ryan's Q on arcsine$\sqrt{x}$-transformed data; untransformed data are shown.

traps in 2006 WY = CO = UT > NV > CA (Fig. 4a); in funnel traps in 2007 CO = NV > UT > WY > CA = KS = MO (Fig. 4b); in panel traps in 2006 WY > NV = UT = CO > CA (Fig. 4c); and in panel traps in 2007 CO = WY = UT = NV > KS = CA = MO (Fig. 4d). Total captures fluctuated year to year; Wyoming and Nevada varied with funnel traps, and Colorado varied with panel traps. However, total numbers of *S. schevyrewi* in funnel and panel traps were generally low, <10 beetles per day, with a peak in flight during July and August (Fig. 4a–d) similar to a 2003 survey in Lakewood, CO, where the peak captures occurred from 15 July to 12 August 2003 (Negrón et al. 2005).

Total captures of *S. multistriatus* followed this trend: in funnel traps in 2006 NV > CA > UT > CO = WY (Fig. 5a), in funnel traps in 2007 NV > KS > UT > CA = MO > CO = WY (Fig. 5b), in panel traps in 2006 CA > NV = UT > CO = WY (Fig. 5c), and in panel traps in 2007 KS > MO > CA > UT = NV = WY = CO (Fig. 5d). Funnel trap captures of *S. multistriatus* showed a peak in May–June and a secondary peak in July–August, and were as high as 150/d in late July 2006 in NV (Fig. 5a and b). In 2007, panel traps in KS caught >50 *S. multistriatus* per day in early June (Fig. 5d). In Lakewood, CO, peak flight activity of *S. multistriatus* was observed in mid-August (Negrón et al. 2005). In a 3-yr survey in Georgia, *S. multistriatus* flight

Table 2. Repeated measures analysis (ANOVA) of the percentage of adult *S. schevyrewi* and total counts of adult *S. schevyrewi* and *S. multistriatus* captured in flight traps or emerging from trap logs

Trap type, variable [transformation]	Yr	Variable								
		State			Wk or mo			State × wk or state × mo		
		F	df	*P*	*F*	df	*P*	*F*	df	*P*
Funnel trap										
Percentage of *S. schevyrewi* [arcsine$\sqrt{}$proportion]	2006	20.3	4, 15	<0.001	1.97	12, 173	0.0295	1.37	48, 173	0.0766
	2007	21.0	6, 21	<0.001	1.90	14, 246	0.0226	1.75	83, 246	<0.001
Total count of *S. schevyrewi* $[\log_{10}(x + 1)]$	2006	3.06	4, 15	0.0497	2.10	12, 181	0.0188	1.78	48, 181	0.0037
	2007	5.22	6, 21	0.0020	3.03	14, 280	<0.001	1.77	83, 280	<0.001
Total count of *S. multistriatus* $[\log_{10}(x + 1)]$	2006	26.7	4, 15	<0.001	2.03	12, 181	0.0238	1.84	48, 181	0.0022
	2007	6.58	6, 21	<0.001	5.72	14, 280	<0.001	3.03	83, 280	<0.001
Panel trap										
Percentage of *S. schevyrewi* [arcsine$\sqrt{}$proportion]	2006	25.9	4, 15	<0.001	1.21	12, 113	0.282	0.85	46, 113	0.726
	2007	154.8	6, 21	<0.001	0.94	14, 173	0.518	1.54	83, 173	0.009
Total count of *S. schevyrewi* $[\log_{10}(x + 1)]$	2006	0.95	4, 15	0.463	1.46	12, 177	0.145	1.42	48, 177	0.053
	2007	6.63	6, 21	<0.001	3.58	14, 280	<0.001	1.36	83, 280	0.0342
Total count of *S. multistriatus* $[\log_{10}(x + 1)]$	2006	2.08	4, 15	0.134	1.98	12, 177	0.0285	0.92	48, 177	0.622
	2007	4.66	6, 21	0.0037	3.21	14, 280	<0.001	3.70	83, 280	<0.001
Trap logs										
Percentage of *S. schevyrewi* [arcsine$\sqrt{}$proportion]	2006	5.47	4, 15	0.0064	5.40	2, 24	0.0116	2.07	8, 24	0.0799
	2007	14.2	6, 21	<0.001	3.27	2, 33	0.0505	3.07	12, 33	0.0053
Total count of *S. schevyrewi* $[\log_{10}(x + 1)]$	2006	4.93	4, 15	0.0098	17.9	2, 30	<0.001	6.41	8, 30	<0.001
	2007	10.1	6, 21	<0.001	12.1	2, 42	<0.001	2.52	12, 42	0.0136
Total count of *S. multistriatus* $[\log_{10}(x + 1)]$	2006	8.11	4, 15	0.0011	7.10	2, 30	0.003	2.62	8, 30	0.0265
	2007	5.03	6, 21	0.0024	15.1	2, 42	<0.001	3.97	12, 42	<0.001

Only flight trap catches from June 21 to Sept. 13, 2006 and from May 29 to Sept. 6, 2007 were included in the statistical analysis because all states were monitored simultaneously at these times.

peaked in late April/May, mid-July, and late August/early September (Hanula and Berisford 1984).

Among trap logs, total recruitment of *S. schevyrewi* from cut elm was greatest in Nevada and Colorado during both years, and in Utah in 2007, sometimes reaching >1,000 within the 2-mo rearing period, or 71 beetles per dm^2 (Fig. 4e and f). Recruitment of *S. multistriatus* was highest in CA during both years, and in MO in 2007 (Fig. 5e and f), with >1,000 beetles emerging per log in these cases. Recruitment of progeny for both species was always greatest among logs exposed in the field in August (Figs. 4e and f and 5e and f). August may be the period when the highest number of reproducing adults is present, or when conditions are best for reproduction and development. Interestingly, flight of *S. multistriatus* toward funnel traps peaked noticeably in late July 2006 in Nevada (Fig. 5a) and remained steady in California through most of the summer, whereas logs exposed in mid-August in both places resulted in the highest level of recruitment (Fig. 5e). This suggests that captures from the flight traps and trap logs may reflect activity of different portions of a population.

Comparison of Trapping Methods. As expected, funnel traps containing an attractant generally collected more *Scolytus* beetles than passive panel traps. For example, in 2006, no *Scolytus* spp. were collected from eight of 261 funnel trap samples compared with 65 of 257 panel trap samples. In 2007, no *Scolytus* spp. were collected from 34 of 405 funnel trap samples compared with 108 of 405 panel trap samples. Also expected was that funnel traps baited with the pheromone for *S. multistriatus* were more sensitive in capturing *S. multistriatus* (as many as 150 per d) than *S. schevyrewi* (no >10 per d) (Figs. 4a and b and 5a and b). Also, trap logs of *U. pumila* were much more sensitive in detecting *S. schevyrewi* throughout its adventive range, even in instances when funnel and panel traps failed to detect the beetle. For example, no *S. schevyrewi* were captured in funnel and panel traps in MO; a few were captured in flight traps in California and Kansas (Fig. 4a–d); but trap logs recruited at least a few *S. schevyrewi* in Missouri, and up to 300–400 in California and Kansas (Fig. 4e and f). Unlike flight traps, recruitment of new adults from trap logs depends on the flight and close-range responses of each species to the log, the abilities of each species to colonize and mate on the log surface, and the developmental capacities of their larval progeny beneath the bark of the log. The relative sensitivity of the trap logs as a detection tool for *S. schevyrewi* may be because of greater intrinsic suitability of *U. pumila* as a host for *S. schevyrewi* than *S. multistriatus*. *U. pumila*, like *S. schevyrewi*, originates from central Asia (Moore 2003). Nevertheless, studies suggest that *U. pumila* is also a highly suitable host for *S. multistriatus*; >90 progeny were produced per dm^2 when *S. multistriatus* were placed onto a cut *U. pumila* log (J.C.L. and S.J.S., unpublished data), and >200 progeny emerged per dm^2 when *U. pumila* logs were exposed to *S. multistriatus* populations in the field (Švihra and Volney 1983). Alternatively, the recruitment bias of *U. pumila* trap logs for *S. schevyrewi* may have occurred because *S. schevyrewi* is a better competitor in colonizing elm hosts than *S. multistriatus*.

Implications. The arrival of *S. schevyrewi*, a second invasive elm bark beetle in North America, represents a rekindled threat to native and ornamental elm pop-

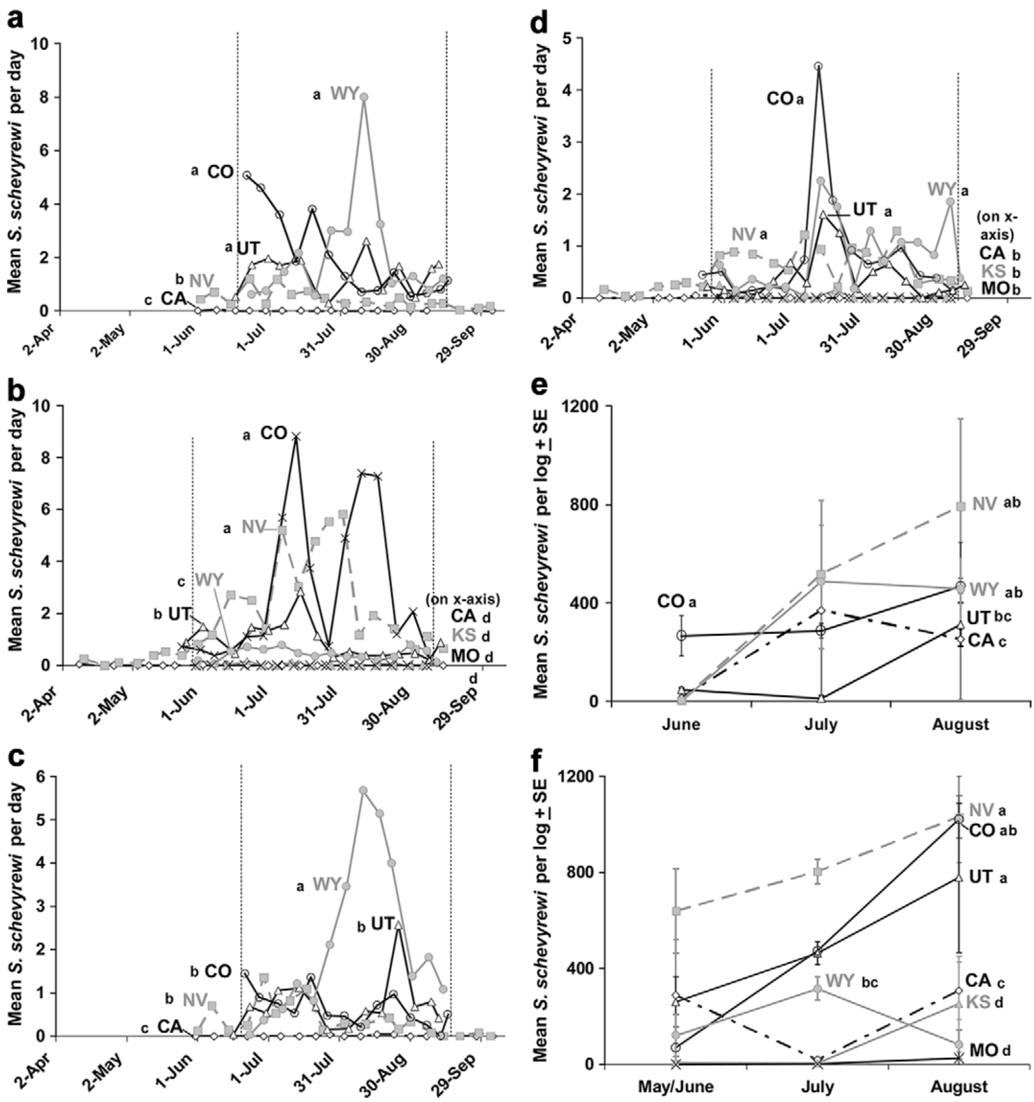

Fig. 4. Mean number of *S. schevyrewi* in funnel traps in 2006 (a) and 2007 (b), in panel traps in 2006 (c) and 2007 (d), and recovered from trap logs in 2006 (e) and 2007 (f). Vertical dotted lines in a–d indicate the beginning and ending of the sampling periods when all sites were analyzed statistically. Letters denote significant differences ($P < 0.05$) by Ryan's Q on $\log_{10}(x + 1)$-transformed data; untransformed data are shown.

ulations in hardwood forests and urban landscapes. *U. americana* has been a favored shade tree throughout the United States for its fast growth, esthetically pleasing crown, and tolerance to stress. It was distributed in native forests throughout eastern North America, but during the 20th Century it also became a valuable part of the urban landscape across the United States. The devastating DED–bark beetle complex killed between 50 and 75% of the pre-1930s elm population in northeastern North America (Bloomfield 1979; Tainter and Baker 1996; R. J. Hauer, unpublished data), including primarily *U. americana* as well as six other species of elms (Strobel and Lanier 1981). However, through natural regeneration, planting of resistant varieties, and good sanitation practices, *U. americana,* and, to a lesser extent, *U. pumila,* continue to be important urban trees, particularly in the Upper Midwest, the Great Plains, the Intermountain West, and California (R. J. Hauer, unpublished data; McPherson 1998; McPherson et al. 2004; Peper et al. 2004).

Our trap logs revealed how quickly *S. schevyrewi* populations could build up among weakened elm trees or debris. In Colorado, trap logs with ≈14.1-dm^2 surface area recruited up to 1,000 *S. schevyrewi* adults within 2 mo (Fig. 4e and f). The Intermountain West and Midwest may be vulnerable because *U. pumila* is one of the few shade trees present in communities such as Lovelock, Winnemucca, and Battle Mountain, NV; Edgemont, SD; and Lusk (personal observations), and Newcastle, WY, where 333 infested elm trees were

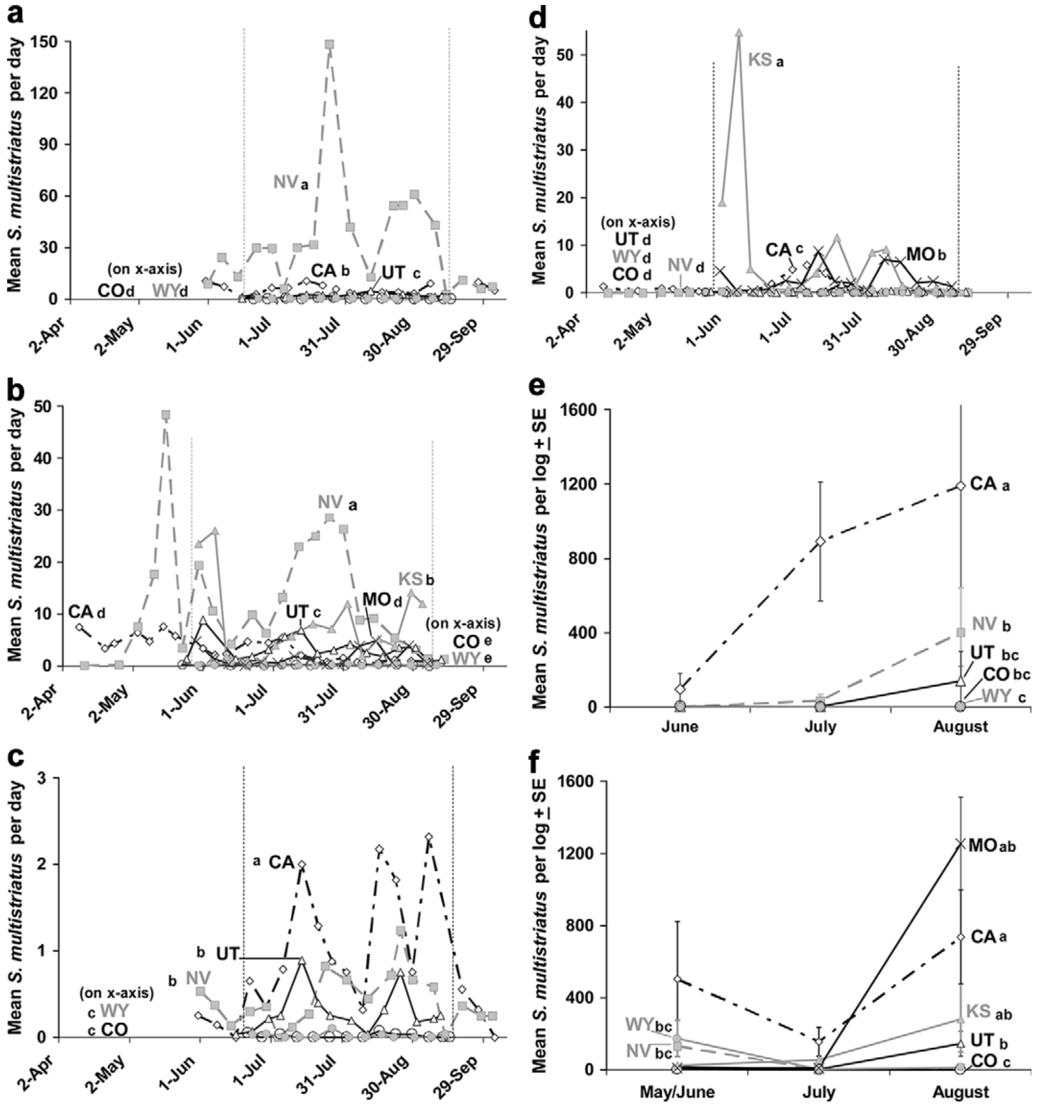

Fig. 5. Mean number of *S. multistriatus* in funnel traps in 2006 (a) and 2007 (b), in panel traps in 2006 (c) and 2007 (d), and recovered from trap logs in 2006 (e) and 2007 (f). Vertical dotted lines in a–d indicate the beginning and ending of the sampling periods when all sites were analyzed statistically. Letters denote significant differences ($P < 0.05$) by Ryan's Q on $\log_{10}(x + 1)$-transformed data; untransformed data are shown.

removed in 2004 (Lee et al. 2006). In Fort Collins, CO, *U. americana* and *U. pumila* make up 18.5 and 9.5% of canopy cover, respectively (McPherson et al. 2004). Loss of these trees could lead to a substantial increase in energy use and reduction of air quality. Minnesota has reported 9,706, 10,869, 16,617, and 36,537 elm trees removed because of DED from 2001 to 2004, respectively, corresponding to a 12% increase from 2001 to 2002, 53% increase from 2001 to 2003, and 220% increase from 2001 to 2004 (Burks 2005). Although the cause for this increase is not known, the role of *S. schevyrewi* may be of interest. In laboratory and field cage trials, *S. schevyrewi* reared from diseased elms were allowed to feed on elms and found to transmit the pathogen to the new wound (Koski and Jacobi 2007). This suggests that *S. schevyrewi* may transfer DED, although the vectoring efficiency is still being investigated. However, if *S. schevyrewi* is a less efficient vector of DED than *S. multistriatus,* which has yet to be determined, a displacement event may eventually be beneficial for elm populations in the United States.

Our 2-yr monitoring survey indicates how predominant *S. schevyrewi* is in parts of Colorado and Wyoming, with substantial populations in Utah and Nevada, and low populations thus far in California, Kansas, and Missouri. Although the point or points where *S. schevyrewi* was introduced to the United States are unknown, the data collected here and previous collection data are consistent with *S. schevyrewi* establishing founder populations in Colorado and Wyoming. The earliest pinned specimens were from Colorado and New Mexico, which supports the hypothesis of founder populations in Colorado and surrounding areas. We might better understand the invasion pattern of *S. schevyrewi* by conducting population genetic studies to elucidate how closely related the populations are over the adventive geographic range, and whether one or more points of introduction occurred.

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