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Host Acceptance and Larval Competition in the Banded and European Elm Bark Beetles, *Scolytus schevyrewi* and *S. multistriatus* (Coleoptera: Scolytidae): Potential Mechanisms for Competitive Displacement between Invasive Species

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Abstract A recent survey revealed that the newly invasive banded elm bark beetle, *Scolytus schevyrewi*, was much more abundant than the long-established European elm bark beetle, *S. multistriatus,* in areas of Colorado and Wyoming, USA. This study was initiated to determine whether competitive displacement of *S. multistriatus* by *S. schevyrewi* might be mediated by a sequence of behavioral interactions between the species on and below the bark surface. At the first step in the sequence, host acceptance behavior (i.e., time to tunnel into the host) was monitored among female *S. schevyrewi* and *S. multistriatus*. There was no substantial difference in host acceptance behavior when females were offered small cut logs (bolts) of Siberian elm, *Ulmus pumila*, infested with con- or heterospecific females. At the second step, mating and oviposition usually follow after a female has excavated a gallery. Mean oviposition per parental female in 1 wk was not significantly different among treatments: *S. schevyrewi* at medium density of 2.86 parental females per dm^2, at high density of 5.71 per dm^2; *S. multistriatus* at medium density, at high density; and mixed species (i.e., *S. schevyrewi* and *S. multistriatus* combined, with each at medium density). At the third step, progeny production and progeny size were monitored among the same density treatments, but the number of parental beetles and size of bolts were doubled. Differences in progeny production would reflect

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larval competition, since the number of eggs initially laid was not different. Both *S. schevyrewi* and *S. multistriatus* were sensitive to intraspecific competition because size of progeny was smaller in high than medium density treatments, but total progeny production was similar at both densities. *Scolytus schevyrewi* was a stronger interspecific competitor than *S. multistriatus*. Smaller *S. multistriatus* progeny, and four-fold more *S. schevyrewi* progeny were produced when both species developed on the same host. The contributions of these proximal behavioral events toward the mechanism for competitive displacement are described in the context of the host colonization behavior of *Scolytus* spp. The competitive advantage of *S. schevyrewi* larvae established through this study, and the more rapid response of *S. schevyrewi* to elm hosts established through other investigations, may be the key mechanistic components that facilitate the displacement of *S. multistriatus* by *S. schevyrewi*.

Keywords Host acceptance · oviposition · resource acquisition · *Scolytus multistriatus* · *Scolytus schevyrewi* · *Ulmus pumila*

Introduction

The European elm bark beetle, *Scolytus multistriatus* (Marsham) [Coleoptera: Scolytidae, *sensu* Wood (2007)], now occurs throughout most of the continental USA (Claflin and Dooling 1973) after its first detection in Massachusetts a century ago (Chapman 1910). The banded elm bark beetle, *Scolytus schevyrewi* Semenov, which originates from Asia, was first detected in 2003 in Colorado and Utah. Now it occurs in 28 states (Lee et al. 2009a) and southern Alberta in Canada (Langor et al. 2009). These two species have allopatric distributions in Eurasia, but now share a relatively broad zone of sympatry in the USA (Lee et al. 2009a). *Scolytus multistriatus* has been a principal vector of Dutch elm disease, which has decimated elms in the northern and eastern USA (Readio 1935). Likewise, *S. schevyrewi* may vector one of the fungi that causes Dutch elm disease (Jacobi et al. 2007), and heavy infestations alone have killed drought-stressed elms in Colorado (Negrón et al. 2005; Lee et al. 2006). A seven-state survey revealed that the newly invasive *S. schevyrewi* was relatively more abundant than the established invasive *S. multistriatus* in some locations (Lee et al. 2009a). In 2006 and 2007, the relative abundance of *S. schevyrewi* (percent of *S. schevyrewi* out of both *Scolytus* species collected) from plexiglass traps, baited funnel traps, and trap logs of Siberian elm, *U. pumila* L., was 90% and 89%, respectively, around Denver, Colorado, and 90% and 83% in Newcastle, Wyoming. There was a sharp decline in relative abundance in samples collected to the east [Manhattan, Kansas and Columbia, Missouri (3.3% and 2.7% in 2007)]; a more gradual decline in relative abundance in samples collected to the west [around Ogden, Utah (60% and 65% in 2006 and 2007, respectively), Reno, Nevada (43%, 68%), and Sacramento, California (11%, 13%)]. Although a longer-term survey would validate that displacement is occurring, cut elm logs (bolts) from Colorado had high population densities of *S. multistriatus* during the 1970s (Hostetler and Brewer 1976), and our two-year data suggest that a shift in the relative abundance of *S. multistriatus* may be taking place. This may occur through competitive displacement, 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). Because the two *Scolytus* species have existed allopatrically in Eurasia, but now have been introduced into North America and formed a zone of sympatry, they appear to share the same niche as phloem feeders co-occurring on the same *Ulmus* spp. hosts (Negrón et al. 2005; Lee et al. 2009a).

Mechanisms of competitive displacement include differential resource acquisition, female fecundity, searching ability, resource preemption, resource degradation, direct physical agonistic interactions, reproductive interference, and intraguild predation (Reitz and Trumble 2002). In a well-studied system of two invasive cerambycid beetles, changes in the abundance of *Phoracantha semipunctata* F. and *P. recurva* Newman were observed in southern California from 1995 to 1998 (Hanks et al. 1997; Bybee et al. 2004). *Phoracantha recurva* comprised 0.01% of *Phoracantha* beetles emerging from eucalyptus in 1995 and more than 95% in 1998. Luhring et al. (2004) suggested three possible causes for this replacement: 1) *P. recurva* having a greater rate of increase; 2) *P. recurva* being a better direct or indirect competitor for the same host resources; and 3) an egg parasitoid having differential rates of parasitism on the species. From experiments, *P. recurva* did not have substantially different fecundity and activity periods than *P. semipunctata* (Bybee et al. 2004). Replacement was likely mediated by the preference of the egg parasitoid to oviposit on *P. semipunctata* eggs, and its lower survival rate on *P. recurva* eggs (Luhring et al. 2004).

The current invasion of North America by *S. schevyrewi* provides a timely opportunity to examine newly formed interspecific interactions especially since these two congeneric invasive species have not previously overlapped in their indigenous geographic ranges (Lee et al. 2009a), but are now observed occupying the same niches in their elm hosts (Negrón et al. 2005). From the literature, *S. schevyrewi* appears to have slightly greater fecundity and a shorter generation time (Wang 1992; Negrón et al. 2005) than *S. multistriatus* (Cannon 1985; Drooz 1985). Yet, comparisons where both species are monitored under controlled conditions are needed. A comparison of flight behavior between the two species in the field in North America suggested that both sexes of *S. schevyrewi* may locate available hosts quickly *via* host volatiles, but this species did not appear to produce an aggregation pheromone at the early stages of infestation (Lee et al. 2009b). The same study suggested that *S. multistriatus* would also locate hosts *via* host volatiles, but a greater flight response occurred a few days later when the first colonizing females produced an aggregation pheromone.

Although *S. schevyrewi* may have an advantage due to a strong response to host volatiles during the dispersal phase of host colonization, we wished to investigate potential mechanisms for displacement once these beetles came in close proximity on the bark during the selection phase (Wood 1982) and when larvae are developing in the phloem. Since more beetles will land on the bark than will bore galleries, whether a potential host is accepted is influenced by proximal gustatory or olfactory responses to host chemicals (Doskotch et al. 1970), internal physiological state of the beetle (Wallin and Raffa 2000), and behaviors of the beetle on the bark surface (Elkinton and Wood 1980; Bishir et al. 2004). The first objective of this study was to examine host acceptance of uninfested elms and elms infested by con- and heterospecific females among presumably unmated female *S. schevyrewi* and *S. multistriatus*. Upon host acceptance, female *S. multistriatus* have been observed to mate at the entrance of their gallery and lay eggs (Chapman 1910). Given this sequence of behavior, the second objective was to examine oviposition rates among mated females in the presence of intra- and interspecific competition. The third objective was to examine progeny production, which can reflect larval competition, in the context of intra- and inter specific competition.

Materials and Methods

Host Material and Insects

All studies used logs of Siberian elm, *U. pumila* L., collected on June 19, 2006 from Washoe Co., NV. Logs were sealed on each end with wax to prevent water loss and stored at 10°C until use. All beetles were reared from infested *Ulmus* spp. logs (collection details below), which were placed in large rearing boxes with a refrigerated collection unit (Browne 1972). Emerging females were presumably unmated since they were stored at 4°C after emerging from the brood logs. *Scolytus schevyrewi* and *S. multistriatus* were easily separated based on external morphological characteristics (Negrón et al. 2005), and males were distinguished from females by a concave frons with abundant setae; females have a convex frons with fewer setae.

Host Acceptance Behavior

For this study, *U. pumila* logs of ~7–9 cm diameter were cut to 10–13 cm lengths to yield smaller sections (bolts) of 2.8 dm^2 of bark surface. Adult *S. multistriatus* were reared from infested *Ulmus* spp. logs collected in Sept. 2006 from Yolo Co., CA. *Scolytus schevyrewi* were reared from infested *U. pumila* collected on Sept. 20, 2006 from Washoe Co., NV. Newly emerged adult beetles (<1 wk old) were used in all experiments.

To compare host acceptance between *Scolytus* species on uninfested hosts, a cohort of ten female *S. schevyrewi* or *S. multistriatus* were released onto a paper towel beneath an elm bolt kept in a 2.4 l plastic container with a mesh opening (3.51 females per dm^2 on or below the bark surface). Observations of beetles were made at 2, 4, 6, 8, 12, 24, 36, 48, 60, and 72 hr. Each entrance hole was counted and labeled. Construction of entrance holes by females may reflect host acceptance since unmated *S. multistriatus* females are known to tunnel through the bark, release a pheromone, and then mate (Peacock et al. 1973; Švihra and Clark, 1980). To compare host acceptance between species on currently infested hosts, a second cohort of six females was added at 72 hr to create four species-combination treatments: 1) *S. schevyrewi* 1st cohort, *S. schevyrewi* 2nd cohort; 2) *S. schevyrewi* 1st cohort, *S. multistriatus* 2nd cohort; 3) *S. multistriatus* 1st cohort, *S. multistriatus* 2nd cohort; and 4) *S. multistriatus* 1st cohort, *S. schevyrewi* 2nd cohort. Bolts initially contained ten total females on or below the surface, or 3.51 females per dm^2, and eventually contained 16 females after addition of the second cohort, or 5.71 females per dm^2. Each female of the second cohort was painted on the elytra with a different color (Testors Inc., Rockford, IL) red, orange, blue, yellow, white, or green, to distinguish them from the 1st cohort and record individual movement. Preliminary observations showed that painting the elytra was not detrimental to beetles for the short term, and painted beetles readily tunneled into the bark usually wearing off the paint within a day. Females were released as a group on a paper towel beneath the bolt, and each differently colored female was observed individually. During the first 30 min, movements of the second cohort of beetles were observed continuously. Later, the position of each second cohort female was recorded at 30, 60, 120, 150, 180, 210, and 240 min. Bolts were then debarked to confirm the positions of females beneath the bark. Treatments were replicated ten times between Oct. 13 and Nov. 16, 2006.

To compare general host acceptance, the proportion of the first or second cohort tunneling into the elm over time was tested with a repeated measures ANOVA following transformation of the proportions by arcsin(√x). The cumulative number of holes excavated was likewise analyzed over time. Next, an ANOVA tested for treatment differences among the second cohort for: 1) The time (min) a beetle took to first tunnel in the elm bolt; 2) the number of visits to the bolt; 3) time (min) spent tunneling and on the bolt surface; 4) total number of holes visited; and 5) proportion of beetles that tunneled into new holes at 240 min [following transformation by arcsin(√x)]. All statistical analyses were conducted with the bolt as the experimental unit and the six beetles per bolt as observational units by using the software package JMP® 7 (SAS Institute 2007).

Ovipositional Activity

Scolytus schevyrewi and *S. multistriatus* were reared from an overwintering laboratory colony started from infested *U. pumila* collected on Sept. 20, 2006 from Washoe Co., NV. Elm bolts ~7–8 cm diameter were cut to yield 2.8 dm^2 of bark surface and placed in a 2.4 l plastic container with a mesh opening. Five treatments were tested: 1) medium density of *S. schevyrewi*; 2) high density of *S. schevyrewi*; 3) medium density of *S. multistriatus*; 4) high density of *S. multistriatus*; and 5) mixed with medium densities each of *S. schevyrewi* and *S. multistriatus*. Eight females and five males were released onto each elm bolt in medium density treatments (2.86 parental females per dm^2), and 16 females and 10 males in high density treatments (5.71 females per dm^2). The mixed treatment contained eight females and five males for each species. Densities were based on reported attack densities of *S. multistriatus* in the field on elm branches less than 10 cm in diameter: 1–7 attacks per dm^2 (Švihra and Koehler 1982), and 5–9.9 attacks per dm^2 resulted in 72–78% mortality of *S. multistriatus* (Hajek and Dahlsten 1985b). Fewer males were added to bolts since males of both species have a propensity for multiple matings (Bartels and Lanier 1974; Wang 1992). Beetles were left undisturbed on elm bolts to tunnel, mate, and oviposit. After one week, we debarked bolts, counted galleries and eggs, and measured the length of galleries. Although beetles may continue to oviposit after a week, observations were made at one week since some eggs started hatching and larval development could confound the experiment. Treatments were initiated and replicated seven times between Mar. 29, and April 6, 2007.

The number of eggs and galleries per parental female, eggs per gallery, and gallery length were compared in a two-factor ANOVA that tested the effect of density/composition (medium, high, mixed), parental species (*S. schevyrewi* and *S.*

multistriatus), and density/composition*parental species interaction. Although the number of eggs per gallery was counted, females sometimes moved into other galleries upon debarking. Hence, it was not possible to determine the exact number of egg galleries initiated and eggs laid by each parental female. To adjust for the different numbers of parental females among treatments, the total number of eggs laid or galleries on a bolt was standardized by the number of parental females introduced (# total eggs in bolt/# parental females introduced). Among mixed treatment bolts, an egg gallery was designated as *S. schevyrewi* or *S. multistriatus* if a beetle of that species was found inside the gallery upon debarking.

Larval Competition

Both species of beetles were reared from the same overwintering lab colony as in the previous experiment. The same five treatments from the oviposition study were used except that elm bolts ~11 cm diameter were cut to yield 5.6 dm^2 of bark surface. Twice the number of beetles were released onto bolts with twice the surface area of the previous experiment: 16 females and 10 males for medium density and mixed treatment bolts, and 32 females and 20 males for high density. Bolts were reared in individual rearing buckets with aeration to prevent fungal growth (Lee et al. 2008) for 2 mo since *S. schevyrewi* can develop within 30–45 d (Wang 1992; Negrón et al. 2005), and *S. multistriatus* within 35–60 d (Drooz 1985; Cranshaw et al. 1993). After 2 mo, bolts were stored in the refrigerator to halt development, and debarked so that we could count the number of exit holes, galleries, and progeny. Up to 50 beetles for each species-sex combination emerging from a log were measured for elytral length as a measure of fitness. Body size influences fitness, and it has been assessed for bark beetles in the past by weight, length from the anterior margin of the pronotum to the posterior margin of the elytra (Pureswaran and Borden 2003), and pronotal width (Safranyik 1976). We measured elytral length since the pronota on some beetles were loosened during the debarking process, which could affect the measurement. Treatments were replicated seven times and initiated during April 4–27, 2007.

The number of progeny that emerged per log was normalized on a per parental beetle basis, and tested in a two-factor ANOVA for the effect of density/composition (medium, high, mix), parental species, and density/composition*parental species interaction. The elytral length for each species and sex was tested in separate one-way ANOVAs for the effect of density/composition. Sizes of adults were expected *a priori* to be larger among *S. schevyrewi* than *S. multistriatus* (Negrón et al. 2005), and larger among females than males, and hence comparisons between species and sex were not made. Multiple comparisons were tested by Tukey HSD ($\alpha=0.05$).

Results and Discussion

Host Acceptance Behavior

In general, host acceptance behavior between *S. schevyrewi* and *S. multistriatus* was not substantially different (Table 1, 2). The first cohort of beetles that colonized an uninfested *U. pumila* bolt, tunneled into the bolt and excavated holes at similar rates,

Table 1 Host Acceptance Behaviors of the First and Second Cohorts of *Scolytus schevyrewi (schevy)* and *S. multistriatus (multi)* Females on *Ulmus pumila* Bolts in the Laboratory

Behavioral parameter	Mean over all times ± SE (*N*=10 bolts)			
	schevy 1st *schevy* 2nd	*schevy* 1st *multi* 2nd	*multi* 1st *multi* 2nd	*multi* 1st *schevy* 2nd
Prop. of 1st cohort beetles inside uninfested elm [arcsin(√x)]	0.81±0.021	0.83±0.021	0.75±0.021	0.78±0.23
Cumulative number of holes excavated by 1st cohort	7.8±0.41	7.6±0.38	7.5±0.40	6.8±0.41
Prop. of 2nd cohort beetles inside infested elm [arcsin(√x)]	0.82±0.025	0.68±0.033	0.8±0.26	0.84±0.24

regardless of species as indicated by non-significant effects of the species-combination factor in the model (Table 3). After introduction of the second cohort, rates of *S. multistriatus* tunneling into a *S. schevyrewi*-infested elm appeared to be the slowest (Fig. 1), but differences were not significant (Table 3). Only one observation during the first 30 min was different among groups. The mean time (min) until *S. schevyrewi* would tunnel into a *S. multistriatus*-infested elm was shorter than *S. multistriatus* tunneling into a *S. schevyrewi*-infested elm (Table 2, 3).

Table 2 Means of the Host Acceptance Behaviors of the Second Cohort of *Scolytus schevyrewi* (*schevy*) and *S. multistriatus* (*multi*) Females on *Ulmus pumila* Bolts in the Laboratory

Behavioral parameter	Mean ± SE (*N*=8 or 10 bolts, 6 females per bolt)			
Continuous observations during first 30 min[a]	*schevy* on *schevy*-infested elm	*schevy* on *multi*-infested elm	*multi* on *multi*-infested elm	*multi* on *schevy*-infested elm
Time to first tunnel in elm (min)	3.5±0.81 ab[b]	2.6±1.5 a	5.5±1.3 ab	7.4±1.7 b
No. visits on elm (walk on and off)	1.4+0.10	1.1±0.04	1.2±0.05	1.3±0.08
Time tunneled in elm (min)	13.2±1.5	14.0±1.9	12.8±2.2	8.1±1.4
Time on surface of elm (min)	9.6±1.1	10.3±1.6	7.2±1.7	7.8±1.6
Observations at other times				
No. holes visited per beetle, observations during 30–240 min	1.4±0.10	1.3±0.10	1.2±0.06	1.1±0.07
Prop. of beetles in new holes at 240 min [arcsin(√x)]	0.7±0.07	0.78±0.06	0.79±0.04	0.72±0.09

[a] Replicates 1 and 2 out of 10 were not included because of visual difficulties during continuous observation.

[b] Different letters next to means within a row indicate significant difference based on Tukey HSD ($\alpha=0.05$). Time to first tunnel into elm was significantly different among groups in an ANOVA (Table 3); there was no significant treatment effect for the remaining parameters listed in this table.

Table 3 Repeated Measures and ANOVA of Host Acceptance Behaviors of *Scolytus schevyrewi* and *S. multistriatus* on *Ulmus pumila* Bolts in the Laboratory

Behavioral parameter 1st cohort	 Repeated Measures	*F*	df	*P*
Prop. of 1st cohort beetles inside uninfested elm [arcsin(√x)]	Species combination	1.15	3, 36	0.34
	Time (2–72 hr)	37.7	9, 324	<0.001
	Species comb.*time	1.16	27, 324	0.27
Cumulative number of holes excavated by 1st cohort	Species combination	0.43	3, 36	0.74
	Time (2–72 hr)	179	9, 324	<0.001
	Species comb.*time	0.55	27, 324	0.97
2nd cohort				
Prop. of 2nd cohort beetles inside infested elm [arcsin(√x)]	Species combination	2.02	3, 36	0.13
	Time (0.5–4 hr)	6.6	4, 144	<0.001
	Species comb.*time	0.91	12, 144	0.54
	ANOVA			
Time to first tunnel in elm (min)	Species combination	3.3	3, 28	0.036
No. visits on elm (walk on and off)	Species combination	2.0	3, 28	0.13
Time tunneled in elm (min)	Species combination	2.2	3, 28	0.12
Time on surface of elm (min)	Species combination	0.94	3, 28	0.44
No. holes visited per beetle, observations during 30–240 min	Species combination	2.6	3, 36	0.064
Prop. of beetles in new holes at 240 min [arcsin(√x)]	Species combination	0.50	3, 36	0.69

This difference suggests *S. schevyrewi* may be slightly quicker to colonize *S. multistriatus*-infested elms, but the differences are probably not substantial enough to affect colonization rates in the field. The chemical ecology and host acceptance behavior of *S. schevyrewi* are unknown, but *S. multistriatus* is able to excavate galleries on an appropriate host elm after encountering feeding stimulants (Doskotch et al. 1970) and avoid gallery construction on nonhosts after encountering feeding deterrents (Baker and Norris 1968). Also, unmated female *S. multistriatus* appeared non-responsive to frass produced by conspecific unmated females in the laboratory (Peacock et al. 1973). Some bark beetles may rely on cuticular hydrocarbons for recognition of con- and heterospecifics (Page et al. 1997), but from our observations of these two *Scolytus* spp., when beetles are in close proximity, the presence of heterospecific females did not appear to inhibit females of either species from tunneling into the occupied host.

Ovipositional Activity

Though not significantly different, the mean number of eggs laid in a week per parental female appeared ~25% greater among treatments involving *S. schevyrewi* than *S. multistriatus* (Fig. 2). Similar numbers of galleries were excavated per parental female for both species and for all density/composition treatments (0.74±

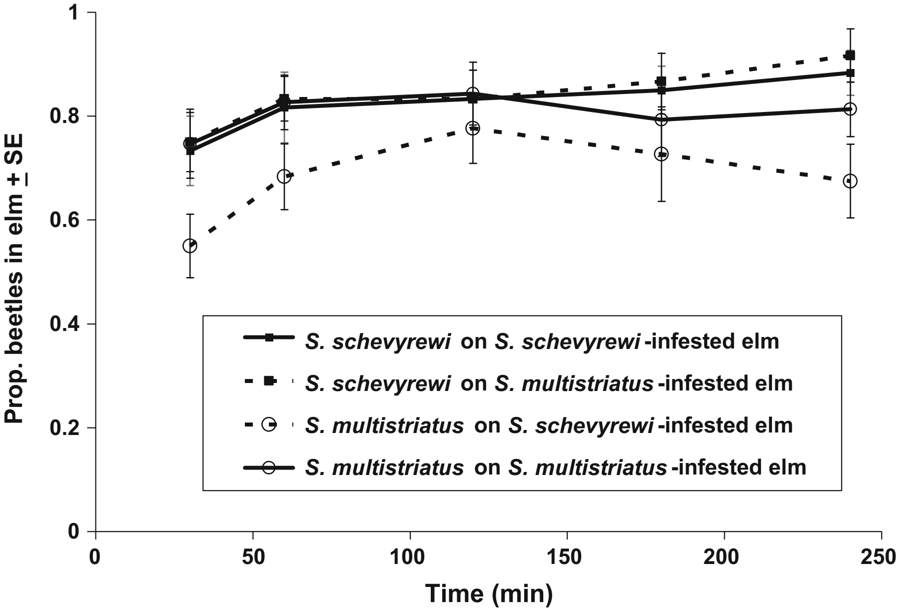

Fig. 1 Mean proportion of second cohort of female *Scolytus schevyrewi* and *S. multistriatus* tunneling over time into a bolt of Siberian elm, *Ulmus pumila*, infested previously with females of either species. Back-transformed data have been plotted.

0.04 SE) (Density/composition F=0.28, df=2, 36, P=0.76; Parental species F=0.36, df=1, 36, P=0.55; Density/composition*species F=0.25, df=2, 36, P=0.78). Although overall egg output per parental female was not different, the mean (± SE) number of eggs per *S. schevyrewi* gallery was 19.49±1.5 and higher than *S. multistriatus* (14.4±1.6 eggs per gallery) (Density/composition F=0.081, df=2, 35, P=0.92; Parental species F=5.6, df=1, 35, P=0.024; Density/composition*species F=1.2, df=2, 35, P=0.31). Not surprisingly, *S. schevyrewi* (the larger beetle) had significantly longer egg galleries than *S. multistriatus* (11.1±0.68 vs. 8.38 mm± 0.53; Density/composition F=0.054, df=2, 35, P=0.94; Parental species F=10.7, df=1, 25, P=0.0024; Density/composition*species F=1.6, df=2, 35, P=0.22). Mean gallery lengths of *S. schevyrewi* were similar at medium and high densities and in the presence of the heterospecific. Likewise mean gallery lengths of *S. multistriatus* were similar among those three treatments. Although we found no evidence of an impact of intraspecific competition on oviposition with densities of 2.86 and 5.71 parental females per dm^2, Cannon (1985) found differences when releasing densities of 4 and 20 female *S. multistriatus* per dm^2. At that higher density, *S. multistriatus* produced significantly shorter maternal galleries, 20 vs. 23 mm, and significantly fewer eggs, 37 vs. 43 eggs.

From the literature, *S. schevyrewi* can lay 20–120 eggs (Wang 1992), and *S. multistriatus* can lay 9–86 eggs (Cannon 1985). In our study, a lower than expected number of eggs was laid per gallery or per parental female for both species probably because: 1) some of our parental females may not have laid eggs; 2) moderate room temperatures or seasonality was not optimal for full reproductive capacity; and 3)

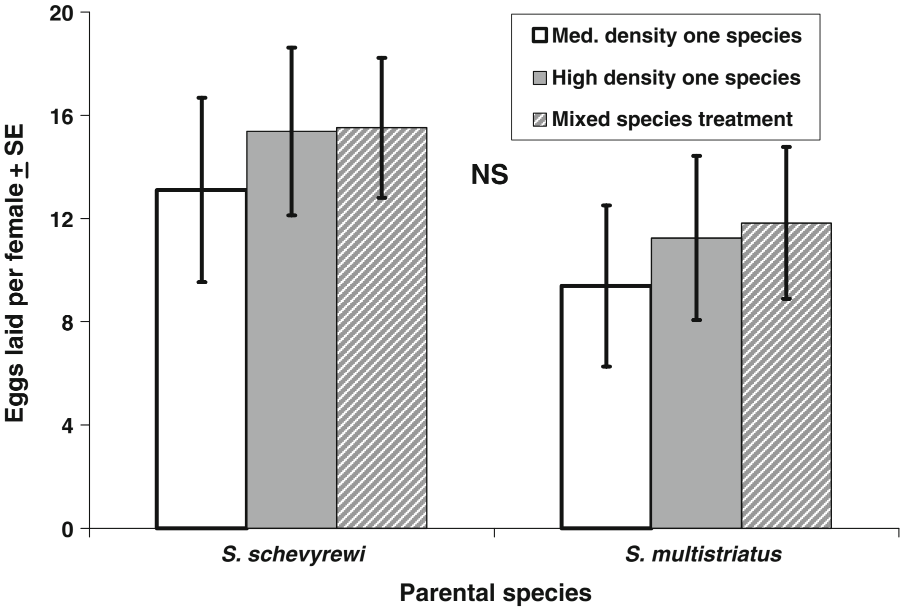

Fig. 2 Mean number of eggs laid (adjusted per parental female) after 1 wk on a host Siberian elm, *Ulmus pumila*, bolt with parental *Scolytus schevyrewi* and *S. multistriatus* at three density/compositions: medium and high densities of a single species, and mixed species. Two-way ANOVA: Density/composition $F=0.35$, df=2, 36, $P=0.71$. Parental species $F=2.3$, df=1, 36, $P=0.14$. Density/composition*species $F=0.003$, df=2, 36, $P=0.99$.

oviposition was not fully completed at one week when bolts were debarked. For the first point, some bolts contained fewer egg galleries than the number of parental females introduced indicating that some females did not lay eggs. Other bolts contained more egg galleries than the number of parental females indicating that females of both species can initiate more than one egg gallery. For the second point, our study was conducted with early spring emerging beetles that may require more time to mature and to lay more eggs. The moderate room temperatures of 25° in our trials should not have delayed oviposition, temperatures of 25° and 30°C have had no differential effect on oviposition patterns of *S. multistriatus* in the laboratory (seasonality not specified) (Cannon 1985). For the third point, our larval competition study (below) suggested that additional oviposition may occur after 1 wk for *S. multistriatus*. When infested logs were reared for 2 mo, *S. multistriatus* produced 16.7±1.8 (mean ± SE) progeny per parental female at the medium and high density treatments (Fig. 3), which was more than the 10.3±2.2 eggs laid per female in a week from similar treatments (Fig. 2, *t*-test of progeny and egg output across experiments, $t=2.7$, df=26, $P=0.032$). A higher oviposition rate may have also occurred in the larval competition study since bolts used for progeny production were larger in diameter with a thicker phloem layer than bolts used for the oviposition study. Natural attacks by *S. multistriatus* on elm branches have been observed to increase as branch diameter increased (Hajek and Dahlsten 1985b).

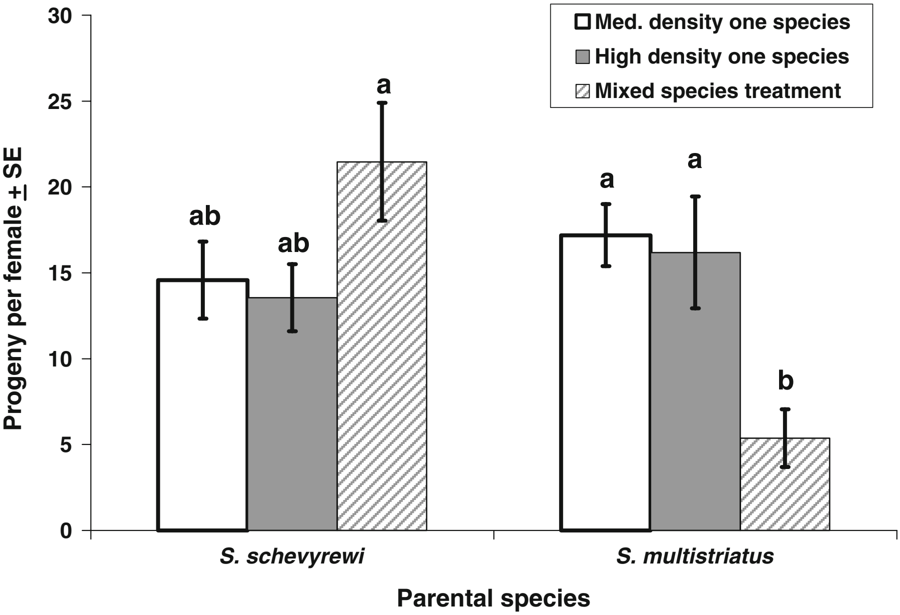

Fig. 3 Mean number of progeny produced (adjusted per parental female) on a host Siberian elm, *Ulmus pumila*, bolt with parental *Scolytus schevyrewi* and *S. multistriatus* at three density/compositions: medium and high densities of a single species, and mixed species. Two-way ANOVA: Density/composition $F=0.49$, df=2, 36, $P=0.62$. Parental species $F=3.15$, df=1, 36, $P=0.08$. Density/composition*species $F=9.4$, df=2, 36, $P<0.001$. Letters above histogram bars denote significant differences, Tukey HSD ($\alpha=0.05$).

Larval Competition

Given that oviposition was similar between density/composition treatments and parental species in the previous experiment, a substantial difference in the number of progeny produced would likely reflect larval competition. For within-species comparisons of *S. schevyrewi* and *S. multistriatus* (Fig. 3), medium and high densities resulted in similar numbers of progeny per parental female suggesting that intraspecific competition at 2.86 and 5.71 females per dm^2 was not a limiting factor. Hajek and Dahlsten (1985b) surveyed a wider range of attacks, 1–16 per dm^2, and found that *S. multistriatus* mortality increased from 30% to 88% as attack density increased and branch diameter decreased. We did not assess the effect of colonization density on mortality, but we did find that the elytral lengths of *S. schevyrewi* and *S. multistriatus* progeny were shorter in the high versus medium densities (Fig. 4), suggesting that larval intraspecific competition at these densities had qualitative physiological effects on reducing adult size rather than total progeny production. Similarly, Beaver (1974) found that intraspecific competition among *S. multistriatus* did not affect the number of emerging adults, but did affect the weight of new adult progeny. In that study, logs were naturally attacked, and the attack (parental) densities were not known, but the number of emerging progeny ranged from 12.5 to 126 per dm^2, which overlapped with the range of our

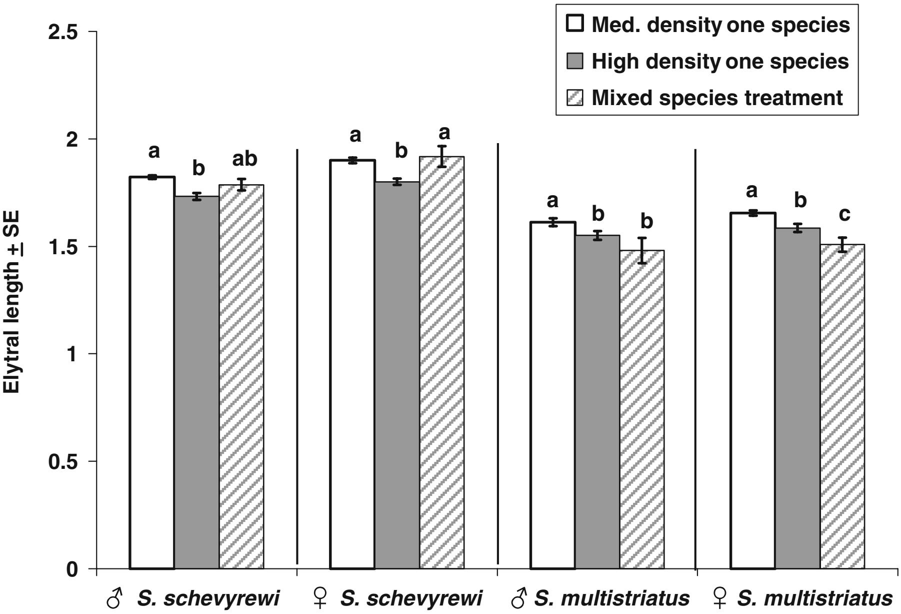

Fig. 4 Mean elytral length of progeny of both sexes of *Scolytus schevyrewi* and *S. multistriatus*. Separate ANOVA for each sex-species combination: Male *S. schevyrewi* $F=6.4$, df=2, 18, $P=0.008$; female *S. schevyrewi* $F=7.3$, df=2, 18, $P=0.005$; male *S. multistriatus* $F=7.8$, df=2, 18, $P=0.004$; female *S. multistriatus* $F=13.1$, df=2, 18, $P<0.001$. Letters above histogram bars denote significant differences within each sex-species group, Tukey HSD ($\alpha=0.05$).

experiments (17–182 progeny per dm^2). When evaluating within-species comparisons from Beaver (1974), Hajek and Dahlsten (1985b), and our study, intraspecific competition among *S. schevyrewi* and *S. multistriatus* reduces length/weight of adult progeny, and very high competitive pressure may reduce the quantity of progeny. Although the fitness consequences of smaller sized *S. schevyrewi* and *S. multistriatus* are not known, size has been shown to affect other bark beetles. Larger sized adults have had higher survival in cold temperatures (Safranyik 1976), produced more progeny (Reid and Roitberg 1995), produced more pheromone (Anderbrant et al. 1985), and produced more antiaggregation pheromone to avoid resource competition (Pureswaran and Borden 2003). Also, high densities of *Ips typographus* larval bark beetles developing in the same host led to the production of adult beetles that had lower reproductive capacity and survival (Anderbrant and Schlyter 1989).

Regarding interspecific interactions, *S. schevyrewi* larvae have a competitive advantage over *S. multistriatus* larvae. When the same numbers of parental beetles of the two species were released simultaneously onto a log, the number of *S. schevyrewi* progeny produced was four-fold greater than *S. multistriatus* on the same bolt (Fig. 3). *Scolytus schevyrewi* was not negatively affected by interspecific competition. Progeny production per parental female was numerically greater, but was statistically similar for *S. schevyrewi* from mixed bolts versus medium and high density bolts (Fig. 3), and size of progeny of *S. schevyrewi* from mixed bolts was similar to those developing under medium density conditions (Fig. 4). On the other hand, *S. multistriatus* was negatively affected by interspecific competition. *Scolytus multistriatus* progeny production per parental female from mixed bolts was only one-third that of medium or high density bolts (Fig. 3). Also, the elytral length of *S. multistriatus* progeny from mixed species bolts was either as short as or shorter than progeny from the medium or high density treatments (Fig. 4).

The presence of *S. schevyrewi* larvae developing in the same host had detrimental effects on the survival and fitness of *S. multistriatus* larvae. This may be due to resource degradation. When one species qualitatively degrades or alters the food/ breeding site, then development by the other species is inhibited (Hougen-Eitzman and Karban 1995). *Scolytus schevyrewi* larvae tunnel more unpredictably, crossing over one another, and take up more space than *S. multistriatus* whose larval tunnels radiate uniformly from the egg gallery (Negrón et al. 2005; Lee et al. 2007). The larval tunneling pattern of *S. schevyrewi* may interfere with the development and survival of larval *S. multistriatus*.

Competitive Displacement Mechanisms

This study describes a possible mechanism leading to the displacement of the established invasive *S. multistriatus* by the newer invasive *S. schevyrewi,* in which displacement is suspected to be occurring in sites in Colorado and Wyoming (Lee et al. 2009a). In 2006 and 2007, *S. schevyrewi* comprised 83–90% of the *Scolytus* population in our survey, and *S. multistriatus* comprised the remaining percentage in those sites. The high relative abundance of *S. schevyrewi* in the Intermountain West where *U. pumila* is also planted abundantly and grows at relatively high densities as an escapee (Lee et al. 2009a), suggests that *S. schevyrewi* has an advantage in colonizing *U. pumila*. This is not unexpected because both the tree and the beetle share the same native range (Wang 1992; Moore 2003). Although *S. multistriatus* is not found infesting *U. pumila* in the tree's native range, *S. multistriatus* has been observed to infest *U. pumila* in its adventive range in the USA (Hostetler and Brewer 1976; Hajek and Dahlsten 1985a; Negrón et al. 2005), and over 90 progeny per dm^2 were observed to emerge from *U. pumila* bolts in this study.

In an attempt to explain the rather pronounced relative abundance of *S. schevyrewi* in the center of its adventive North American range, we investigated the behavioral advantages that *S. schevyrewi* may have over *S. multistriatus* during host colonization and at later stages in their life cycles. First, when beetles are at a distance and in flight, *S. schevyrewi* aggregated very strongly towards elm volatiles, whereas *S. multistriatus* aggregated moderately to the same stimuli (Lee et al. 2009b). We found that more *S. multistriatus* aggregated towards pheromones produced by pioneer females that had infested a host for 48–96 hr compared to 0–48 hr. With these differences, *S. schevyrewi* may have a 2–3 d advantage in colonizing an elm host relative to *S. multistriatus*. Also from the same study, *S. schevyrewi* did not appear to fly differentially towards elms infested by con-, hetero-specifics, or both species. In the present study, we examined the behavior of beetles on or below the bark surface for host acceptance, oviposition, and competition between developing larvae. Both species appeared to accept hosts similarly by tunneling into hosts infested by con- and hetero-specifics at similar rates, although female *S. schevyrewi* tunneled more quickly into bolts previously infested with female *S. multistriatus* (Table 2) and a numerically lower proportion of female *S. multistriatus* tunneled into bolts previously infested with female *S. schevyrewi* (Fig. 1). Oviposition rates of the two species were not substantially different, although in all cases female *S. schevyrewi* laid numerically more eggs (Fig. 2). Most strikingly, however, *S. schevyrewi* appeared to be a stronger competitor at the larval stage than *S. multistriatus* when developing on the same host (Fig. 3). The competitive advantage of *S. schevyrewi* larvae (this study), and the quicker response of *S. schevyrewi* to elm hosts (Lee et al. 2009b), may be important mechanistic components that are facilitating the displacement of *S. multistriatus* by *S. schevyrewi*.

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