Agricultural and Forest Entomology

Agricultural and Forest Entomology (2021), **23**, 203–211 DOI: 10.1111/afe.12422

Attraction of the cerambycid beetles *Tetropium gabrieli*, *T. castaneum* and *T. fuscum* to pheromones and host tree volatiles

Martin Schroeder*, Dragoş Cocoş*, Helena Johansson* and Jon Sweeney†

**Department of Ecology, Swedish University of Agricultural Sciences, P.O. Box 7044, S - 750 07, Uppsala, Sweden and* †*Natural Resources Canada, Canadian Forest Service, Atlantic Forestry Centre, 1350 Regent Street, Fredericton, NB, Canada, E3C2G6*

Abstract

1 *Tetropium gabrieli* is native to the European Alps where it breeds in European larch and may be an important pest during drought periods by killing trees. It has spread to larch plantations in several European countries including Sweden.

2 In trapping studies conducted in Sweden, we tested whether *T. gabrieli* was attracted to *E*-fuscumol, *E,Z*-fuscumol, *E,Z*-fuscumol acetate and the host volatile combination of α-pinene plus ethanol. We also compared its response with those of the native congeners, *T. fuscum* and *T. castaneum*.

3 All three *Tetropium* species were caught in significantly higher numbers in traps baited with *E*-fuscumol plus host volatiles than in traps baited with host volatiles alone or in unbaited traps.

4 There was no difference in catch of any *Tetropium* species between traps baited with *E*-fuscumol plus host volatiles versus traps baited with *E,Z*-fuscumol plus host volatiles, but the latter treatment caught more *T. fuscum* and *T. castaneum* than did *E,Z*-fuscumol acetate plus host volatiles.

5 The addition of *E*-fuscumol to host volatile-baited traps significantly reduced mean catch of *T. gabrieli,* significantly increased mean catch of *T. castaneum,* and had no significant effect on catch of *T. fuscum.* Mean catch of all three species was significantly greater in traps baited with *E*-fuscumol alone than in traps baited with host volatiles alone.

6 All three species were caught from May to August. The median date of captures was about 2 weeks earlier for *T. fuscum* compared with the other two species.

Keywords ethanol, flight periods, fuscumol, fuscumol acetate, *Larix*, *Tetropium* emergence, *Tetropium* parasitoids, trapping, α-Pinene.

Introduction

The cerambycid beetle *Tetropium gabrieli* Weise (subfamily Spondylidinae) is native to the Alps in central Europe where it breeds in European larch, *Larix decidua* Mill. The species also reproduces in other larch species non-indigenous to Europe and is considered to be a secondary pest, breeding mainly in newly felled trees or weakened standing trees. However, in some regions in Europe *T. gabrieli* is classified as an important pest species during hot and dry summers (Gorius, 1955; Evans *et al.*, 2004). Thus, the economic importance of this species may increase in the future as a result of climate change increasing the frequency of prolonged droughts during summers.

The planting of larch outside the natural distribution of European larch has enabled *T. gabrieli* to expand its distribution and establish in many countries in Europe (Sama & Löbl, 2010). In Sweden, it has been reported several times from imported larch wood (Lundberg, 1986, 1988; Lundberg & Pettersson, 1997) and in 2007 *T. gabrieli* was detected infesting larch trees in a forest adjacent to a port in the province of Blekinge in southeastern Sweden (Ericsson, 2010). Surveys conducted from 2009 to 2011 using spring-felled larch trees demonstrated the beetle was present in several locations in southeastern Sweden but absent in more northern or western locations (Lindelöw *et al.*, 2015). Although this survey method worked, it is practical

Correspondence: Martin Schroeder. Tel.: +46767924510; e-mail: martin.schroeder@slu.se

only in larch stands, requires permission to cut trees, is quite laborious, and requires either splitting of logs to remove larvae or incubation of logs to collect emerging adults for reliable species identification. A more cost-efficient method would be to capture adult *T. gabrieli* in attractant-baited traps. In recent years, a trap lure was developed for the congener *T. fuscum* (F.), a species native to Europe but which has established in Eastern Canada where it has caused considerable tree mortality among native spruce species (Silk *et al.*, 2007; Sweeney *et al.*, 2004, 2006, 2010). Traps are baited with three lures: racemic (*E*)-6,10-dimethyl-5,9-undecadien-2-ol (fuscumol), ethanol, and a blend of monoterpenes that approximates those sampled from bark of stressed spruce, i.e., racemic α-pinene, (−)-β-pinene, (+) 3-carene, (+) limonene and α-terpinolene. Male *T. fuscum* emit *S*-(*E*)-fuscumol but the synthetic racemic mixture of *R*- and *S*-(*E*)-fuscumol is as attractive as the pure *S*, and the combination of spruce host volatiles and racemic fuscumol synergizes attraction of both sexes of *T. fuscum* (Sweeney *et al.*, 2010). In addition to *T. fuscum*, *T. cinnamopterum* Kirby (native to North America) males also emit *S*-(*E*)-fuscumol and males and females of *T. cinnamopterum* and *T. castaneum* (L.) (native to Europe) are attracted to the combination of fuscumol and host volatiles (Silk *et al.*, 2007; Lemay *et al.*, 2010; Sweeney *et al.*, 2010). Thus, there is a high probability that additional *Tetropium* species may also be attracted to *E*-fuscumol and thus we wanted to test this for *T. gabrieli*.

We also wanted to test response of *T. gabrieli* to the structurally related (*E*)-6,10-dimethyl-5,9-undecadien-2-yl acetate (termed fuscumol acetate). Fuscumol, fuscumol acetate, and geranyl acetone [(*E*)-6,10-dimethyl-5,9-undecadien-2-one] are attractive to several species of longhorn beetles in the subfamily Spondylidinae (Silk *et al.*, 2007; Halloran *et al.*, 2018; Žunič-Kosi *et al.*, 2019) and Lamiinae (Mitchell *et al.*, 2011; Hughes *et al.*, 2013, 2016; Hanks & Millar 2016; Meier *et al.*, 2016, 2020; Halloran *et al.*, 2018). Because the fuscumol/fuscumol acetate motif appears to be common in Spondylidinae, we hypothesized that fuscumol acetate might be attractive to *T. gabrieli*. Finally, we wanted to compare the efficacy of racemic *E*-fuscumol to racemic *E,Z*-fuscumol and *E,Z*-fuscumol acetate, because the latter compounds are simpler and cheaper to synthesize than *E*-fuscumol, using *E,Z*-geranylacetone as the starting material (Mitchell *et al.*, 2011).

Although the main focus of the study was *T. gabrieli*, we also expected catches of *T. fuscum* and *T. castaneum* which both are common all over Sweden (Ehnström & Holmer, 2007). The following questions were addressed by the study: (i) Is *T. gabrieli* attracted to fuscumol or fuscumol acetate? (ii) Does addition of the host tree volatiles α-pinene and ethanol increase attraction of *T. gabrieli* compared with pheromone alone? (iii) Does the phenology of adult flight differ among the three species? (iv) How long is the emergence period of *T. gabrieli*? (v) What parasitoids species are associated with *T. gabrieli*? The host volatile α-pinene was chosen because it is one of the major monoterpenes in larch (Holm & Hiltunen, 1997; Ruuskanen *et al.*, 2007; Kajos *et al.*, 2013) while ethanol is released from stressed or decayed trees. Phenology of flight, emergence period and parasitoids are of interest for understanding the invasion biology of the species.

Materials and methods

Study area

The study was conducted in a 4.3 × 3.3 km (1440 ha) rectangular area in south-eastern Sweden (56°19′13.8"N 14°49′32.2″E, province of Blekinge) in 2017 in which *T. gabrieli* had been detected in earlier surveys using cut larch trees (Lindelöw *et al.*, 2015). Managed forest stands comprised 986 ha (72.6%) of the study area, including 60.5 ha (4.2% of study area) of hybrid larch stands, *Larix x eurolepis* A. Henry, (13 stands including one fresh clear-cut) and 925.5 ha (68.4% of study area) of Norway spruce, *Picea abies* (L.) H. Karst., and Scots pine, *Pinus sylvestris* L., dominated stands. The remainder of the study area included pastures and swamps (20.8%) and lakes (6.6%). In a 1.2 km buffer zone (2420 ha) around the study area, there was only one larch stand (4.6 ha, 0.2% of buffer area). The proportion of larch in the study area is much higher than the average for southern Sweden which is 0.1% of the total growing stock including all tree species (Anonymous, 2016).

Lures

Racemic *E*-fuscumol, racemic *E,Z*-fuscumol, and racemic *E,Z*-fuscumol acetate (99% purity) lures were purchased from Sylvar Technologies Inc. (Fredericton, New Brunswick, Canada). The lures were natural red rubber septa (sleeve stoppers), 5 × 11 mm (OD) (Wheaton, Millville, NJ) loaded with 50 mg of fuscumol or fuscumol acetate; release rates were 0.5–2.0 mg/day at 20 °C (measured indoors by weight loss). The host volatiles ethanol (95%) and (−)-α-pinene (98%, optical purity ee: ≥81%, GLC, Aldrich) were released from separate, sealed 50 ml PVC-containers filled with 30 ml of compound, with holes bored through the sides of the container just below the lid. Ethanol dispensers had four 0.5 mm-holes and (−)-α-pinene dispensers had eight 2 mm-holes. Release rates (determined by weight loss in the laboratory at 20 °C) were 140 mg/day for ethanol and 940 mg/day for (−)-α-pinene. We also measured host volatile release rates in the field as follows. At each trap check, the dispensers were refilled if more than half of the compound had been released and the amount that was added to each dispenser was recorded. By this method, we estimated average release rates in the field of 272 and 1605 mg/day for ethanol and (−)-α-pinene, respectively. However, this is an underestimate of the mean outdoor release rate of (−)-α-pinene because about half of the (−)-α-pinene dispensers were found empty during trap checks, i.e., all 30 ml dispensers had volatilized since the previous trap check 1–3 weeks earlier. This means that some traps were releasing no (−)-α-pinene for at least a portion of the experimental trapping period.

Field experiments

Three trapping experiments were conducted sequentially with the same traps, each with three treatments. In all three experiments, we used α-pinene and ethanol as host volatiles, released from the dispensers described above. The first experiment, conducted 8 May–13 June, compared catch of *T. gabrieli* in traps baited with *E*-fuscumol plus host volatiles, host volatiles alone, or left unbaited. The aim of this experiment was to test whether *T. gabrieli* was attracted by the combination of *E*-fuscumol and host tree volatiles as demonstrated for other *Tetropium* species. The second experiment, conducted 13 June–29 June, compared *E*-fuscumol, *E,Z*-fuscumol, and *E,Z*-fuscumol acetate, each paired with host volatiles. The objective here was to compare the response of *T. gabrieli*, as well as the native *Tetropium* species, to *E,Z*-fuscumol and *E,Z*-fuscumol acetate. The third experiment, conducted 29 June–12 September, compared catches in traps baited with *E*-fuscumol alone, *E*-fuscumol plus host volatiles, and host volatiles alone. Here, our objective was to determine whether the combination of fuscumol and host volatiles synergized attraction of *T. gabrieli* as has been observed with *T. fuscum* and *T. castaneum* (Sweeney *et al.*, 2010). In addition, because traps baited with *E*-fuscumol plus host volatiles were included in all three experiments, this allowed us to compare the seasonal phenology of adults of the three *Tetropium* species.

Treatments were replicated 12 times in a randomized complete block design, with re-randomization between experiments. The 12 blocks were distributed among 10 sites, 9 of which consisted of larch stands (each with one block) and one which was a fresh larch clear-cut (with three blocks). The average size of the larch stands was 4.6 ha (SE = 0.7 ha) while the clear-cut was 11.8 ha. Minimum distance between sites was 300 m and maximum distance 3700 m. Traps were spaced 50 m apart within blocks and at least 10 m from the edge of the stands.

Beetles were caught in 12-unit multiple funnel traps (ECONEX MULTIFUNNEL-12®, Econex SL) hung from 1.8 m wooden poles with 50% solution of ethylene glycol in the collecting cups. The traps were emptied seven times (exp. 1: twice; exp. 2: twice; exp. 3: three times) with intervals from 1 to 3 weeks (except for the last one with almost 5 weeks).

Tetropium adults were determined to species based on Pfeffer (1995) and Ehnström and Holmer (2007). The beetles were sexed by inspection of the tip of the abdomen. As is common in many Cerambycidae, a portion of the sixth abdominal tergite is visible beyond the pygidium of males (Yanega, 1996), whereas the female's pygidium is flatter and broader and the tip of the ovipositor is often visible.

On May 8–9 2017, we felled a larch tree in each of five larch stands in which we had traps and on September 11–14, we inspected them for colonization by *Tetropium* by debarking parts of the trunk every 3 m. In addition, 2 m logs were cut from the three trees that were colonized by *Tetropium* and also from a colonized wind-felled tree. The logs were stored outside the laboratory in Uppsala. On March 13, two 60 cm stem sections were cut from each of the logs and ends were waxed. Each stem section was placed in a separate cage in a climate chamber (20.4 °C, 18 h day-length) and checked each day (except weekends) for emerging insects for 78 days. On April 9, additional two 60 cm stem sections were cut from logs of the same four trees and handled in the same way as the first batch of stem sections. Mean diameter of the 16 stem sections was 21.3 cm (SE = 0.4). Emerging parasitoids were identified by Niklas Johansson at the Swedish Species Information Centre, Swedish University of Agricultural Sciences. Rate of parasitism was estimated for each tree by dividing the number of emerging parasitoids by the sum of emerging *Tetropium* beetles and parasitoids (assuming that each parasitoid killed one *Tetropium* larvae).

In addition, part of the colonized logs from three of the trees (40, 73 and 33 cm length stem sections respectively) were split on 15 March to count and collect *Tetropium* larvae. For each larva, the width of head-capsule was measured and it was noted if it occurred under the bark or in a gallery in the wood. The lengths of all galleries in wood, and of the plug blocking their entrances, were measured.

All nine larch stands used for trapping were inspected for occurrence of wind-felled larch trees which were checked for colonization by *Tetropium* by debarking. In addition to the cut and wind-felled trees, we also checked 30 stumps (30–40 cm in height) in the fresh clear-cut (cut winter 2016/2017) in early April 2018 for colonization by *Tetropium*.

Statistical analyses

For each species, catches were totalled for each treatment and block over the entire trapping period for each experiment and analysed using generalized linear models (SAS PROC GLIMMIX) with treatments fixed and blocks random. Blocks in which all three lure treatments had zero catch were deleted from analysis. The models were run with Gaussian, Poisson, and negative binomial distributions; results are reported for the distribution that best fit the data, according to the lowest value of the corrected Aikaike's Information Criterion (AIC_c). Post-hoc comparisons of least square means were done with Tukey–Kramer multiple comparisons which control the experiment-wise error rate ($P \leq 0.05$). We also analysed the raw data and data transformed by log $(y+1)$ using standard ANOVA (SAS PROC GLM), testing residuals for normality using Shapiro-Wilks test, and compared results with those from the generalized linear mixed models. When results from the GLM and GLIMMIX analyses differed greatly, e.g., zero values for F in the generalized mixed model and significant F values in the GLM for the same data, we assumed the data were not suitable for analysis by the mixed models. This occurred in two cases (Experiment 3), possibly because the host volatile treatment caught zero *T. gabrieli* and *T. fuscum*. In these cases, count data were converted to ranks and analysed by Friedman's nonparametric ANOVA for randomized blocks, followed by the Ryan-Einot-Gabriel-Welsh multiple range test. For each *Tetropium* species, chi-square contingency tables (or Fischer's exact test in cases when expected values were below 5) were used to test whether sex ratio of trapped beetles was affected by lure treatment. Only treatments with at least four caught individuals were included in the sex ratio tests.

Results

Three *Tetropium* species were caught in the trapping experiments: the native *T. fuscum* (154 specimens) and *T. castaneum* (2230), and the exotic *T. gabrieli* (57). All three species were caught in all 12 blocks. Total catch per block (all experiments and treatments pooled per species) for *T. fuscum* was positively correlated with that of *T. castaneum* ($r = 0.81, N = 12, P = 0.001$) while there was no correlation between catches of *T. gabrieli* and

Table 1 Mean of total catch, SE and sex ratio (% males) of *T. gabrieli*, *T. fuscum* and *T. castaneum* in traps baited with *E*-fuscumol plus host volatiles (α-pinene and ethanol), host volatiles alone or in unbaited traps from 8 May to 13 June 2017

	T. gabrieli ($n = 10$)			*T. fuscum* ($n = 11$)			*T. castaneum* ($n = 12$)		
Treatment	Mean	SE	Males (%)	Mean	SE	Males (%)	Mean	SE	Males (%)
Host volatiles	0.50b	0.34	60	0.36b	0.20	75	6.67b	1.60	50
E-fuscumol + host volatiles	2.80a	0.80	39	10.20a	2.60	53	104.00a	21.20	58
Unbaited	0.10b	0.10		0.18b	0.12		1.67c	1.42	60
F	10.9			36.5			35.5		
df	2,27			2,30			2,33		
P	0.0003			<0.0001			<0.0001		
Distribution with best fit	Poisson			Poisson			Negative binomial		

For each species, blocks in which all three lure treatments had zero catches were deleted from analysis and n gives the number of remaining blocks. Data analysed by generalized linear models using distribution with best fit as measured by corrected Aikaike's information criterion. Means followed by different letters differed significantly, Tukey–Kramer multiple comparison test, $P \leq 0.05$. Sex ratio only given for treatments with ≥ 4 caught individuals.

T. fuscum ($r = -0.32$, $N = 12$, $P = 0.305$) or *T. gabrieli* and *T. castaneum* ($r = -0.22$, $N = 12$, $P = 0.492$).

Experiment 1. Catches of *T. gabrieli*, *T. fuscum* and *T. castaneum* were 28, 55 and 62 times higher in traps baited with *E*-fuscumol plus host volatiles than in unbaited traps and these differences were significant (Table 1). All three were also caught in significantly higher numbers in traps baited with *E*-fuscumol plus host volatiles than in traps baited with only host volatiles (Table 1). Traps baited with host volatiles alone caught 2–5 times more beetles than unbaited traps but the difference was significant only for *T. castaneum* (Table 1). Presence of *E*-fuscumol (i.e., *E*-fuscumol plus host volatiles vs. host volatiles alone) did not significantly affect sex ratio of *T. gabrieli* ($P = 0.63$) or *T. fuscum* ($P = 0.70$) (Fischer's exact test). (Table 1). Neither was there any significant difference in sex ratio between all three treatments for *T. castaneum* ($P = 0.38$, chi-square test).

Experiment 2. Mean catch of *T. gabrieli* did not differ significantly among traps baited with *E*-fuscumol plus host volatiles, *E,Z*-fuscumol plus host volatiles, or *E,Z*-fuscumol acetate plus host volatiles (Table 2). Catches of *T. fuscum* and *T. castaneum* were significantly higher (9 times and 6 times, respectively) in traps baited with *E,Z*-fuscumol plus host volatiles than in traps baited with *E,Z*-fuscumol acetate plus host volatiles (Table 2). In contrast, there was no significant difference in catch between *E*-fuscumol plus host volatiles and *E,Z*-fuscumol plus host volatiles for either *T. fuscum* or *T. castaneum* (Table 2). There was no significant difference in sex ratio between treatments for any of the species (*T. gabrieli*, $P = 0.91$, *T. fuscum*, $P = 0.84$, Fischer's exact test, *T. castaneum*, $P = 0.12$, chi-square test) (Table 2).

Experiment 3. Contrary to our expectations, adding α-pinene plus ethanol to traps baited with *E*-fuscumol significantly reduced mean catch of *T. gabrieli*; in fact mean catch in traps baited with *E*-fuscumol plus host volatiles was less than half of that in traps baited with *E*-fuscumol alone (Table 3). In contrast, traps baited with *E*-fuscumol plus host volatiles caught significantly more *T. castaneum* (5 times as many) than traps baited with *E*-fuscumol alone, which, in turn, caught significantly more *T. castaneum* (12 times as many) than traps baited with host volatiles alone (Table 3). Catches of *T. fuscum* were low. Mean catches in traps baited with *E*-fuscumol and *E*-fuscumol plus host volatiles did not differ, but both were significantly greater than

Table 2 Mean of total catch, range and sex ratio (% males) of *T. gabrieli*, *T. fuscum* and *T. castaneum* in traps baited with *E*-fuscumol plus host volatiles (α-pinene and ethanol), *E,Z*-fuscumol plus host volatiles or *E,Z*-fuscumol acetate plus host volatiles from 13 June to 29 June 2017

	T. gabrieli ($n = 9$)			*T. fuscum* ($n = 12$)			*T. castaneum* ($n = 12$)		
Treatment	Mean	SE	Males (%)	Mean	SE	Males (%)	Mean	SE	Males (%)
E-fuscumol + host volatiles	1.78a	0.72	56	2.50ab	0.93	43	65.08a	22.7	53
E,Z-fuscumol + host volatiles	2.11a	0.70	63	6.83a	2.25	41	71.83a	19.7	51
E,Z-fuscumol acetate + host volatiles	0.78a	0.36	71	0.75b	0.25	33	11.92b	2.96	60
F	2.6			7.89			22.5		
df	2,24			2,33			2,33		
P	0.0953			0.0016			<0.0001		
Distribution with best fit	Poisson			Negative binomial			Negative binomial		

For each species, blocks in which all three lure treatments had zero catches were deleted from analysis and n gives the number of remaining blocks. Data analysed by generalized linear models using distribution with best fit as measured by corrected Aikaike's information criterion. Means followed by different letters differed significantly, Tukey–Kramer multiple comparison test, $P \leq 0.05$. Sex ratio only given for treatments with ≥ 4 caught individuals.

Table 3 Mean of total catch, range and sex ratio (% males) of *T. gabrieli*, *T. fuscum* and *T. castaneum* in traps baited with *E*-fuscumol plus host volatiles (α-pinene and ethanol), E-fuscumol alone or host volatiles alone from 29 June to 13 September 2017

	T. gabrieli (*n* = 12)			*T. fuscum* (*n* = 8)			*T. castaneum* (n = 12)		
Treatment	Mean	SE	Males (%)	Mean	SE	Males (%)	Mean	SE	Males (%)
E-fuscumol + host volatiles	1.08b	0.60	62	1.50a	0.50	25	16.75a	3.53	37
E-fuscumol	2.75a	1.21	45	0.75a	0.25	17	3.08b	1.15	27
Host volatiles	0c	0		0b	0		0.25c	0.13	
F	11.59			5.93			23.7		
df	2,22			2,14			2,33		
P	0.0004			0.0136			<0.0001		
Distribution with best fit	NA			NA			Negative binomial		

For each species, blocks in which all three lure treatments had zero catches were deleted from analysis and n gives the number of remaining blocks. Data for *T. castaneum* analysed by generalized linear models using distribution with best fit as measured by corrected Aikaike's information criterion; means followed by different letters differed significantly, Tukey–Kramer multiple comparison test, $P \leq 0.05$. Data for *T. gabrieli* and *T. fuscum* analysed by Friedman's test (ANOVA on ranks) followed by Ryan-Einot-Gabriel-welsh multiple range test ($P \leq 0.05$). Sex ratio only given for treatments with ≥4 caught individuals.

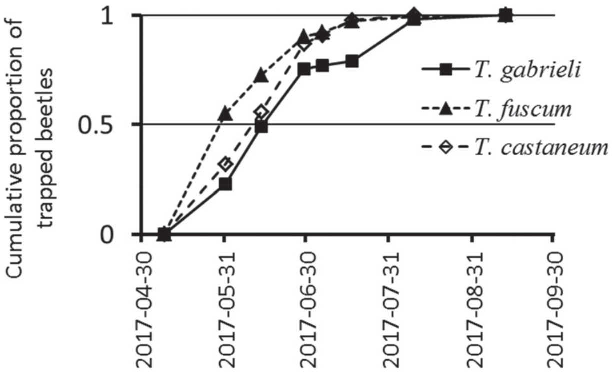

Figure 1 Seasonal patterns of catches of the exotic *T. gabrieli* and the native *T. fuscum* and *T. castaneum* in 12 multi-funnel traps baited with *E*-fuscumol, α-pinene and ethanol in larch stands. The total number of individuals caught was 57 *T. gabrieli*, 154 *T. fuscum* and 2230 *T. castaneum*.

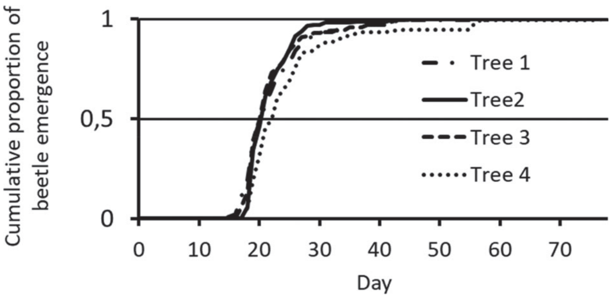

Figure 2 Emergence pattern of *T. gabrieli* from stem sections cut from four naturally infested cut and wind-felled larch trees in southern Sweden. From each tree, four 60-cm stem sections were cut in early spring and placed separately in cages in a climate room. The number of emerging adults were 276, 212, 142 and 152, respectively, from tree 1, 2, 3 and 4.

the zero catch in traps baited with host volatiles alone (Table 3). The addition of host volatiles to *E*-fuscumol did not affect the sex ratio for any of the three species (*T. gabrieli*, $P = 0.33$, chi-square test, *T. fuscum*, $P = 1$, Fischer's exact test, *T. castaneum*, $P = 0.25$, chi-square test) (Table 3).

Seasonal phenology of Tetropium spp. All three species were caught from May to August (Fig. 1). Most of the flight activity occurred in May and June. The median date of captures was about 2 weeks earlier for *T. fuscum* compared with the other two species. For both *T. fuscum* and *T. castaneum* (catches of *T. gabrieli* were too low for evaluation) a somewhat larger part of the flight activity of females than that of males occurred late in the season: 90% of the cumulative catches occurred about 10 days later for females than for males (data not shown).

Three of the five larch trees cut in the spring 2017 were colonized by *Tetropium*. About 75% of the tree stems were colonized. No other bark- and wood-boring beetle species were found on the stems. Wind-felled larch trees were found in two of the nine stands: six trees colonized in 2016 in one stand and one tree colonized in 2017 in another stand (same stand in which a cut tree was not colonized). There were no *Tetropium* emergence holes in the autumn in the colonized trees cut in the spring the same year. None of the 30 larch stumps inspected on the clear-cut were colonized by *Tetropium* spp.

Tetropium gabrieli was the only bark- and wood-boring insect species emerging from the 16 stem sections cut from four naturally infested cut and wind-felled larch trees except for four individuals of *Urocerus gigas* (L.) (Hymenoptera, Siricidae). A total of 782 individuals of *T. gabrieli* emerged: 276 (50% males), 212 (52% males), 142 (44% males) and 152 (50% males) individuals respectively from tree 1, 2, 3 and 4. The average production of *T. gabrieli* adults was 122 per m^2 bark (SE = 19, $N = 4$) and 2309 per m^3 wood (SE = 347) individuals. The emergence pattern was similar among trees: starting 14–17 days after stem sections were put in the climate chamber, 50% emergence after 19–21 days and 90% emergence after 25–32 days (Fig. 2). There was almost no difference in emergence pattern between sexes, 50% emergence of males occurred less than 1 day earlier than that for females (data not shown).

A total of 97 *Tetropium* larvae were found during the splitting of stem sections from three colonized trees. The *Tetropium* larvae were not determined to species but because only *T. gabrieli*

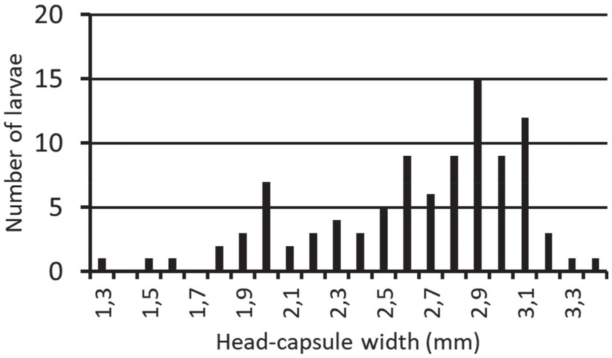

Figure 3 Size distribution of head-capsule widths among the 93 hibernating *Tetropium* larvae collected from the splitting of wood in early spring from three of the naturally infested larch trees.

adults emerged from the stem sections it is highly unlikely that the larvae were another species. All larvae were alive. About 34% of the larvae were found in galleries in the wood while the remaining 66% were found under the bark. Head-capsule width ranged from 1.3 to 3.4 mm with the majority (92%) >1.9 mm (Fig. 3). Head-capsule width was significantly larger for larvae in galleries in the wood than for larvae under bark: mean = 2.84 mm (SE = 0.06) and 2.53 mm (SE = 0.06) respectively ($P < 0.001$, *t*-test). Average length of galleries in the wood was 45 mm (SE = 2) and the entrance of all galleries were blocked with a plug (mean length = 7.4 mm, SE = 0.7 mm).

In addition to emergence of *T. gabrieli* adults, 110 parasitoid adults emerged from the stem sections: 28, 15, 38 and 29, respectively, from tree 1, 2, 3 and 4. They belonged to three species: *Rhimphoctona xoridiformis* Holmgren (Ichneumonoidea) (77 specimens, 60% males), *Helconidea dentator* (F.) (Braconidae) (31, 45% males) and *Neoxorides collaris* Gravenhorst (Ichneumonoidea) (2, 50% males). The average rate of parasitism was 13.2% (SE = 3.3%). Median emergence of *R. xoridiformis* occurred after 20 days while for *H. dentator* it occurred after 30 days.

Discussion

We present evidence from field-trapping experiments that *T. gabrieli* is attracted to racemic *E*-fuscumol. This is the fourth *Tetropium* species demonstrated to be attracted by *E*-fuscumol. *Tetropium castaneum*, *T. fuscum* and *T. cinnamopterum*, all with spruces as the main host tree species, are significantly attracted to the combination of *E*-fuscumol and host tree volatiles, and males of the latter two species emit *S*-fuscumol (Silk *et al.*, 2007; Sweeney *et al.*, 2010). These results suggest that *T. gabrieli* males may also emit fuscumol, but this must be confirmed by volatile collection and chemical analysis.

The effects of the host volatiles, α-pinene and ethanol, on trap catches varied among species. The addition of (−)-α-pinene plus ethanol to either unbaited traps or traps baited with *E*-fuscumol significantly increased catches of *T. castaneum*. The combination of *E*-fuscumol and host volatiles appeared to synergize attraction of *T. castaneum*, similar to what Sweeney *et al.* (2010) observed using a different blend of host volatiles that included α-pinene, ethanol, and four other monoterpenes. In contrast, neither *T. gabrieli* nor *T. fuscum* were attracted to (−)-α-pinene plus ethanol by themselves, and adding them to traps baited with *E*-fuscumol reduced catch of *T. gabrieli* and had no effect on catch of *T. fuscum*. These results suggest that *T. gabrieli* and *T. fuscum* respond to additional host-specific volatiles or volatile blends when searching for hosts. This was previously demonstrated for *T. fuscum* by Sweeney *et al.* (2004) who showed that trap catch of *T. fuscum* was significantly lower in traps baited with ethanol plus racemic α-pinene than in traps baited with ethanol plus a blend of five monoterpenes that approximated volatiles emitted from the boles of stressed spruce trees. Although there is variation among and within *Larix* species in the relative amounts of terpenes in leaves and twigs, common major components include (−)- and (+)-α-pinene, (−)-β-pinene, (+)-3-carene, and myrcene (Von Rudloff, 1987; Holm & Hiltunen, 1997; Ruuskanen *et al.*, 2007; Kajos *et al.*, 2013). Future research should compare the attraction of *T. gabrieli* to a synthetic blend of major monoterpenes emitted from larch trees (i.e., a larch blend) plus ethanol *versus* the (−)-α-pinene plus ethanol used in this study. These host volatile treatments should be also be tested with and without *E*-fuscumol and compared to *E*-fuscumol alone to determine whether the host volatiles synergize attraction of *T. gabrieli* to fuscumol.

Traps baited with host volatiles plus *E,Z*-fuscumol acetate caught significantly fewer individuals of *T. fuscum* and *T. castaneum* than did traps baited with host volatiles and *E,Z*-fuscumol, suggesting *E,Z*-fuscumol acetate is not attractive to these species. Lack of attraction of *T. fuscum* to fuscumol acetate is consistent with males not producing this compound (Silk *et al.*, 2007; Sweeney *et al.*, 2010); however, volatiles emitted by males of *T. castaneum* and *T. gabrieli* have not yet been determined. Catches of *T. gabrieli* in traps baited with host volatiles plus *E,Z*-fuscumol acetate were very low but did not differ significantly from catches in traps baited with host volatiles plus *E,Z*-fuscumol or *E*-fuscumol. However, to confirm whether or not *E,Z*-fuscumol is attractive to these species, one would have to compare catches in traps baited with *E,Z*-fuscumol acetate versus host volatiles versus *E,Z*-fuscumol acetate plus host volatiles versus unbaited traps.

There was no difference in catches of any of the *Tetropium* species between traps baited with *E,Z*-fuscumol plus host volatiles versus traps baited with *E*-fuscumol plus host volatiles, suggesting that the presence of *Z*-fuscumol did not inhibit response to *E*-fuscumol. This is further reinforced by the fact that the release rate of the attractive *E* isomer from the *E,Z* fuscumol lures was only about half of that from the *E*-fuscumol lures, because both lures were loaded with the same volume of *E,Z*-fuscumol or *E*-fuscumol. Flaherty *et al.* (2019) observed that traps baited with *E,Z*-fuscumol, *E,Z*-fuscumol acetate and ethanol captured significantly more *T. fuscum* and *T. cinnamopterum* than traps baited with monochamol, ipsenol, α-pinene and ethanol, whereas the converse was true for *T. castaneum*, suggesting the optimal combination of host volatiles and pheromone differs among these species.

The total catch (all experiments combined) of *T. gabrieli* was considerably lower than that of the other two *Tetropium* species. This is not surprising because *T. gabrieli* is monophagous on larch (Gorius, 1955) and larch stands constitute only 0.1%

(0.9 million m^3) of the total growing stock (i.e. all tree species) in southern Sweden compared with 48.5% (431 million m^3) for Norway spruce (Anonymous, 2016).

The positive correlation between *T. castaneum* and *T. fuscum* may be explained by the two species sharing the same host tree species Norway spruce. This result is in agreement with an earlier study conducted on these two species in Poland and on *T. fuscum* and *T. cinnamopterum* (also sharing the same host tree species) in Canada (Sweeney *et al.*, 2010). Because the experimental stands only included larch, all trapped *T. castaneum* and *T. fuscum* must have dispersed from colonized spruces in the surrounding landscape which means that the correlation in catches was not caused by the presence of previously colonized breeding substrates in the immediate vicinity of the traps. In contrast, there was no correlation between catches of *T. gabrieli* and those of *T. castaneum* and *T. fuscum*, and this was expected because of differences in host tree species.

An earlier study conducted in eastern Canada demonstrated that the exotic *T. fuscum* had a somewhat earlier flight period than the native *T. cinnamopterum* (Rhainds *et al.*, 2010). The median date of captures was >2 weeks earlier for *T. fuscum*. The present study demonstrates that also in its native range *T. fuscum* is an early occurring *Tetropium* species. In Sweden, the median date of captures was about 2 weeks earlier for *T. fuscum* compared with the native *T. castaneum* and the exotic *T. gabrieli*. Thus, *T. fuscum* should have an advantage compared with *T. castaneum* regarding colonization of the generally limited amounts of wind-felled or weakened standing spruce trees in the managed forests of Sweden.

The only *Tetropium* species emerging from the larch stem sections was *T. gabrieli*. This is in accordance with an earlier Swedish study, including stem sections from 17 trees in 6 stands, in which also only *T. gabrieli* emerged (Lindelöw *et al.*, 2015). Most *T. gabrieli* emerged during a relatively short time period after the breeding material was brought in to the climate room. Emergence started after about 2 weeks and after 4 weeks 90% of the beetles had already emerged. This is similar to what have been demonstrated for *T. fuscum* in Canada (Rhainds *et al.*, 2010). The synchronized emergence is in accordance with the fact that most of the flight activity occurred during May and June. *Tetropium gabrieli* most commonly overwinters as a mature pre-pupal larva, though a proportion of the population may overwinter as immature larvae (Crawshay, 1907; Schimitschek, 1929). This is in accordance with the variation in larval head-capsule width found in the present study for hibernating larvae of which the smaller ones may represent individuals emerging and flying later in the season.

The three species of parasitoids that emerged from the stem sections have all earlier been demonstrated to use *T. gabrieli* as a host (Kenis & Hilszczanski, 2004). They are also commonly associated with the native *T. castaneum* and *T. fuscum*. All three species have earlier been recorded from Sweden and are classified as native (www.dyntaxa.se). The rate of parasitism in the present study is low compared with earlier studies on *Tetropium* (see Kenis & Hilszczanski, 2004 for an overview). It is highly unlikely that this was a result of the methodology used because the *Tetropium* larvae in the cut larch trees were exposed to parasitoids during the whole summer before the stem sections were cut in September. The two most common parasitoids we collected, *R. xoridiformis* and *H. dentator*, are endoparasitic koinobionts, i.e., females oviposit in the early instar host larva which continues to develop to a mature larva or prepupa before the parasitoid consumes the host, emerges to spin a cocoon and pupates. Both *R. xoridiformis* and *H. dentator* overwinter as pupae and emerge as adults the following spring, shortly after emergence of *Tetropium* adults (Schimitschek, 1929). The median emergence of *R. xoridiformis* and *H. dentator* in our study was only 5 and 15 days, respectively, after median emergence of *T. gabrieli*, providing evidence that these species likely parasitize early instar larvae. The ectoparasite, *Neoxorides collaris*, develops externally on parasitized larvae and overwinters as a pupa between the bark and the wood (Kenis & Hilszczanski, 2004). Thus, exposure of fresh larch logs in May and removal of logs from the field in September would have provided ample opportunity for parasitism by these species.

Tetropium gabrieli seems to be able to establish, and continuously maintain populations, in forest landscapes with only a low proportion of larch stands (4.2% in the present study area) and with few wind-felled larch trees. In an earlier study, conducted during 2 years (2009 and 2010) in the same area as the present study, *T. gabrieli* colonized most cut larch trees (Lindelöw *et al.*, 2015). In the present study, it colonized wind-felled trees in 2016 (assuming the *Tetropium* larval galleries belonged to *T. gabrieli*, one adult found under bark in one of the trees) and cut and wind-felled trees in 2017. Factors explaining the ability to maintain populations in landscapes with low proportions of host trees may be a high production of adults per tree, a synchronized emergence and flight activity, and a strong attraction to their pheromones ensuring a high probability of mate finding. Low levels of interspecific competition and rate of parasitism should have contributed to the high production. No other bark- and wood-boring insects, except a few *U. gigas*, utilized the stems of the larch trees in this study and only a few in the earlier study (Lindelöw *et al.*, 2015).

The results demonstrate that *E*-fuscumol and *E,Z*-fuscumol can be used for early detection of *T. gabrieli* in areas where the species has not yet established. However, more research is needed to develop a synthetic blend of host volatiles that is more representative of those emitted by freshly felled larch trees than the α-pinene and ethanol used in this study, and to determine the enantiomer or enantiomers of fuscumol emitted by *T. gabrieli*. Combining *E*-fuscumol with an attractive 'larch blend' host volatile lure plus ethanol may result in even greater attraction of *T. gabrieli*, in much the same way as the combination of spruce blend, ethanol, and *E*-fuscumol synergizes attraction of *T. fuscum*. Trap catches would also likely be improved by coating trap surfaces with Fluon to reduce friction (Allison *et al.*, 2011; Graham & Poland, 2012; Allison *et al.*, 2016). Even though *T. gabrieli* is considered to be more of a secondary pest species in Europe, it may become more aggressive if encountering new host tree species, for example, different larch species in North America, as was the case with *T. fuscum* when it established in North America. Furthermore, the results of the present study demonstrate that the species is able to also establish in regions where its habitat is strongly fragmented and constitutes only a very small proportion of total forest cover which is a strong argument for including this species in early detection programs. In addition, the bait may also be useful for monitoring population levels in areas where it is already established and for documenting the spread in areas where it has recently established.

Acknowledgements

We thank Sveaskog for giving access to larch stands and for allowing of cutting larch trees and Minna Jacklin (Sveaskog) for information about locations of suitable larch stands. Niklas Johansson identified the parasitoids and Claudia Von Brömssen helped with statistics. Financial support was provided by the Swedish Research Council for Environment, Agricultural Sciences and Spatial Planning (Project no. 2016-01049 and 942-2016-11).

Data availability statement

Data available on request from the authors

References

Allison, J.D., Johnson, C.W., Meeker, J.R., Strom, B.L. & Butler, S.M. (2011) Effect of aerosol surface lubricants on the abundance and richness of selected forest insects captured in multiple-funnel and panel traps. *Journal of Economic Entomology*, **104**, 1258–1264.

Allison, J.D., Graham, E.E., Poland, T.M. & Strom, B.L. (2016) Dilution of Fluon before trap surface treatment has no effect of longhorned beetle (Coleoptera: Cerambycidae) captures. *Journal of Economic Entomology*, **109**, 1215–1219.

Anonymous (2016) Forest statistics 2016 - official statistics of Sweden, Swedish University of Agricultural Sciences, Umeå 2016, 150 pp.

Crawshay, G.A. (1907) The life history of *Tetropium gabrieli*, Ws. – *T. fuscum*, Sharp – *T. crawshayi*, Sharp, etc. *Transactions of the Entomological Society of London*, **Part II**, 183–212.

Ehnström, B. & Holmer, M. (2007) *Nationalnyckeln till Sveriges flora och fauna*. Långhorningar, Skalbaggar Coleoptera: Cerambycidae. Artdatabanken, SLU, Uppsala. 302 pp.

Ericson, B. (2010) Two species of beetles new to Sweden feeding on larch. *Entomologisk Tidskrift*, **131**, 131–136 (in Swedish with English abstract).

Evans, H.F., Moraal, L.G. & Pajares, J.A. (2004) Biology, ecology and economic importance of Buprestidae and Cerambycidae. *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans). Kluwer Academic Publishers, Dordrecht.

Flaherty, L., Gutowski, J.M.G., Hughes, C. *et al.* (2019) Pheromone-enhanced lure blends and multiple trap heights improve detection of bark and wood-boring beetles potentially moved in solid wood packaging. *Journal of Pest Science*, **92**, 309–325.

Gorius, U. (1955) Unterzuchungen über den Lärchenbock, *Tertropium gabrieli* Weise mit besonderen Berücksichtigung seines Massenwechels. *Zeitschrift für Angewandte Entomologie*, **38**, 157–205.

Graham, E.E. & Poland, T.M. (2012) Efficacy of Fluon conditioning for capturing cerambycid beetles in different trap designs and persistence on panel traps over time. *Journal of Economic Entomology*, **105**, 395–401.

Halloran, S.T., Collignon, R.M., McElfresh, J.S. & Millar, J.G. (2018) Fuscumol and geranylacetone as pheromone components of Californian longhorn beetles (Coleoptera: Cerambycidae) in the subfamily Spondylidinae. *Environmental Entomology*, **47**, 1300–1305.

Hanks, L.M. & Millar, J.G. (2016) Sex and aggregation-sex pheromones of cerambycid beetles: basic science and practical applications. *Journal of Chemical Ecology*, **42**, 631–654.

Holm, Y. & Hiltunen, R. (1997) Variation and inheritance of monoterpenes in *Larix* species. *Flavour and Fragrance Journal*, **12**, 335–339.

Hughes, G.P., Zou, Y., Millar, J.G. & Ginzel, M.D. (2013) (*S*)-fuscumol and (*S*)-fuscumol acetate produced by a male *Astyleiopus variegatus* (Coleoptera: Cerambycidae). *The Canadian Entomologist*, **145**, 327–332.

Hughes, G.P., Meier, L.R., Zou, Y., Millar, J.G., Hanks, L.M. & Ginzel, M.D. (2016) Stereochemistry of fuscumol and fuscumol acetate influences attraction of longhorned beetles (Coleoptera: Cerambycidae) of the subfamily Lamiinae. *Environmental Entomology*, **45**, 1271–1275.

Kajos, M.K., Hakola, H., Holst, T. *et al.* (2013) Terpenoid emissions from fully grown east Siberian *Larix* cajanderi trees. *Biogeosciences*, **10**, 4705–4719.

Kenis, M. & Hilszczanski, J. (2004) Natural enemies of Cerambycidae and Buprestidae infesting living trees. *Bark and Wood Boring Insects in Living Trees in Europe, a Synthesis* (ed. by F. Lieutier, K. R. Day, A. Battisti, J.-C. Grégoire and H. F. Evans). Kluwer Academic Publishers, Dordrecht.

Lemay, M.A., Silk, P.J. & Sweeney, J. (2010) Calling behavior of *Tetropium fuscum* (Coleoptera: Cerambycidae: Spondylidinae). *Canadian Entomologist*, **142**, 256–260.

Lindelöw, Å., Isacsson, G., Ravn, H.P. & Schroeder, M. (2015) *Tetropium gabrieli* and *Ips cembrae* (Coleoptera; Cerambycidae and Curculionidae) – invasion of two potential pest species on larch in Sweden. *Entomologisk Tidskrift*, **136**, 103–112.

Lundberg, S. (1986) Några förklaringar till 1986 års skalbaggskatalog, med under 1984 och 1985 nytillkomna arter (notes to the 1986 Swedish Coleoptera catalogue, with species recorded for the first time during 1984 and 1985). *Entomologisk tidskrift*, **107**, 148–150 (in Swedish with English abstract).

Lundberg, S. (1988) Några intressanta skalbaggsfynd i till Norrbotten importerat barrvirke. (Records of Coleoptera from northern Sweden in timber imported from Central Europe). *Entomologisk Tidskrift*, **109**, 49–50 (in Swedish with English summary).

Lundberg, S. & Pettersson, R. (1997) Något om skalbaggsfaunan i ryskt virke vid en såg i Västerbotten. (Observations of the beetle fauna in Russian timber at a saw mill in Västerbotten, northern Sweden.). *Entomologisk Tidskrift*, **188**, 49–51 (in Swedish with English abstract).

Meier, L.R., Zou, Y., Millar, J.G., Mongold-Diers, J.A. & Hanks, L.M. (2016) Synergism between enantiomers creates species-specific pheromone blends and minimizes cross-attraction for two species of cerambycid beetles. *Journal of Chemical Ecology*, **42**, 1181–1192.

Meier, L.R., Zou, Y., Mongold-Diers, J.A., Millar, J.G. & Hanks, L.M. (2020) Pheromone composition and chemical ecology of six species of cerambycid beetles in the subfamily Lamiinae. *Journal of Chemical Ecology*, **46**, 30–39.

Mitchell, R.F., Graham, E.E., Wong, J.C.H. *et al.* (2011) Fuscumol and fuscumol acetate are general attractants for many species of cerambycid beetles in the subfamily Lamiinae. *Entomologia Experimentalis et Applicata*, **141**, 71–77.

Pfeffer, A. (1995) *Zentral- und westpaläarktische Borken und Kernkäfer*. Scolytidae, Platypodidae, Coleoptera Pro Entomologia, c/o Naturhistorisches Museum, Basel. 310 pp.

Rhainds, M., Heard, S.B., Sweeney, J.D., Silk, P. & Flaherty, L. (2010) Phenology and spatial distribution of native and exotic *Tetropium* longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology*, **39**, 1794–1800.

Ruuskanen, T.M., Hakola, H., Kajos, M.K., Hellen, H., Tarvainen, V. & Rinne, J. (2007) Volatile organic compound emissions from Siberian larch. *Atmospheric Environment*, **41**, 5807–5812.

Sama, G. & Löbl, I. (2010) Spondylinae. *Catalogue of Palearctic Coleoptera*, Vol. **6** (ed. by I. Löbl and A. Smetana), pp. 137–139. Apollo Books, Stenstrup 924 pp.

Schimitschek, E. (1929) *Tetropium gabrieli* Weise and *Tetropium fuscum* F. Ein Beitrag zu ihrer Lebensgeschichte and Lebensgemeinschaft. *Zeitschrift für Angewandte Entomologie*, **15**, 229–334.

Silk, P.J., Sweeney, J., Wu, J., Price, J., Gutowski, J.M. & Kettela, E.G. (2007) Evidence for a male-produced pheromone in *Tetropium fuscum* (F.) and *Tetropium cinnamopterum* (Kirby) (Coleoptera: Cerambycidae). *Naturwissenschaften*, **94**, 697–701.

Sweeney, J., Groot, P., Macdonald, L., Smith, S., Cocquempot, C., Kenis, M. & Gutowski, J.M. (2004) Host volatile attractants and traps for detection of *Tetropium fuscum* (F.), *Tetropium castaneum* L., and other longhorned beetles (Coleoptera: Cerambycidae). *Environmental Entomology*, **33**, 844–854.

Sweeney, J., Gutowski, J.M., Price, J. & De Groot, P. (2006) Effect of semiochemical release rate, killing agent, and trap design on detection of *Tetropium fuscum* (F.) and other longhorn beetles (Coleoptera: Cerambycidae). *Environmental Entomology*, **35**, 645–654.

Sweeney, J., Silk, P.J., Gutowski, J.M., Wu, J., Lemay, M.A., Mayo, P.D. & Magee, D.I. (2010) Effect of chirality, release rate, and host volatiles on response of *Tetropium fuscum* (F.), *Tetropium cinnamopterum* Kirby, and *Tetropium castaneum* (L.) to the aggregation pheromone, Fuscumol. *Journal of Chemical Ecology*, **36**, 1309–1321.

Von Rudloff, E. (1987) The volatile twig and leaf oil terpene composition of three western North American larches, *Larix laricina*, *Larix occidentalis*, and *Larix lyalli*. *Journal of Natural Products*, **50**, 317–321.

Yanega, D. (1996) Field Guide to Northeastern Longhorned Beetles (Coleoptera: Cerambycidae). Illinois Natural History Survey Manual 5. 184 pp.

Žunič-Kosi, A., Stritih-Peljhan, N., Zou, Y., McElfresh, J.S. & Millar, J.G. (2019) A male-produced aggregation-sex pheromone of the beetle *Arhopalus rusticus* (Coleoptera: Cerambycidae, Spondylidinae) may be useful in managing this invasive species. *Scientific Reports*, **9**, 19570.

Accepted 11 October 2020