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Geographic variation in prey preference in bark beetle predators

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Abstract. 1. Bark beetles and their predators are useful systems for addressing questions concerning diet breadth and prey preference in arthropod natural enemies. These predators use bark beetle pheromones to locate their prey, and the response to different pheromones is a measure of prey preference.

2. Trapping experiments were conducted to examine geographic variation in the response to prey pheromones by two bark beetle predators, *Thanasimus dubius* and *Temnochila virescens*. The experiments used pheromones for several *Dendroctonus* and *Ips* prey species (frontalin, ipsdienol, and ipsenol) and manipulated visual cues involved in prey location (black vs. white traps). The study sites included regions where the frontalin-emitter *Dendroctonus frontalis* was in outbreak vs. endemic or absent.

3. There was significant geographic variation in pheromone preference for *T. dubius*. This predator strongly preferred a pheromone (frontalin) associated with *D. frontalis* at outbreak sites, while preference was more even at endemic and absent sites. No geographic variation was found in the response by *T. virescens*. White traps caught fewer insects than black traps for both predators, suggesting that visual cues are also important in prey location.

4. The overall pattern for *T. dubius* is consistent with switching or optimal foraging theory, assuming *D. frontalis* is a higher quality prey than *Ips*. The two predator species partition the prey pheromones in areas where *D. frontalis* is abundant, possibly to minimise competition and intraguild predation.

Key words. Bark beetles, Cleridae, diet breadth, predators, switching, Trogositidae.

Introduction

Arthropod predators may be broad generalists that attack many different prey species or narrow specialists confined to a single species, a property known as diet breadth. Relatively little is known about the evolution of prey preference and diet breadth in these organisms, a fact noted in several reviews (Gilbert, 1990; Vet & Dicke, 1992; Hopper *et al.*, 1993). For example, a few studies indicate genetic variation in foraging behaviour and prey preference (e.g. Lesna & Sabelis, 1999), while a comparative study of lacewings illustrated how a specialist likely evolved from a generalist ancestor (Tauber *et al.*, 1993). Alternatively, predators might evolve behavioural mechanisms to deal with short-term variations in prey abundance. One possibility is switching behaviour, where the preference for a particular prey species depends on its relative abundance (Murdoch, 1969; Murdoch & Oaten, 1975). Predator learning is often proposed as a mechanism that may underlie switching behavior (Murdoch, 1969; Hassell, 2000). Optimal foraging theory also predicts changes in preference in response to prey abundance, with lower quality prey added to the diet only when higher quality ones are scarce (Stephens & Krebs, 1986; Křivan, 1996).

Bark beetles and their predators are tractable systems for addressing questions concerning diet breadth and prey preference. Bark beetles use pheromones to attract mates as well as conspecifics to help overwhelm the resistance of the host tree (Alcock,

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1982; Raffa *et al.*, 1993). Their predators, commonly clerid and trogositid beetles, also use these semiochemical signals to locate their prey (Vité & Williamson, 1970; Raffa, 2001). Adult predators attack adult bark beetles, while the larvae are predacious on bark beetle brood within the host tree (Thatcher & Pickard, 1966; Mignot & Anderson, 1969, 1970). As different bark beetles emit different pheromones, the response (or lack thereof) by predators to these pheromones is a potential measure of their preference for different prey species. These predators are also confronted with prey communities that vary dramatically in species composition and abundance both spatially and temporally, providing natural experiments where prey preference can be observed under varying conditions of prey availability (Futuyma & Moreno, 1988; Gilbert, 1990). The predator community also varies among locations, and competition among predators could promote specialisation (Gilbert, 1990).

One well-known system in eastern North America involves the predator *Thanasimus dubius* (Coleoptera: Cleridae) and its bark beetle prey. This predator has a broad geographic range, extending from the Gulf of Mexico to the Great Lakes within the eastern U.S.A. and northward into Canada, where it attacks bark beetles that infest pines. One common prey species in the southeastern U.S.A. is *Dendroctonus frontalis* (Coleoptera: Curculionidae: Scolytinae), the southern pine beetle. This bark beetle attacks and kills living pine trees and exhibits population outbreaks that result in significant tree mortality and economic losses (Price *et al.*, 1992), although densities can become vanishingly low between outbreaks (Reeve & Turchin, 2002). The northern range of *D. frontalis* appears limited by its low tolerance for winter temperature extremes (Ungerer *et al.*, 1999). Other bark beetles attacked by *T. dubius* include four *Ips* species, two with a southern distribution (*I. avulsus* and *I. calligraphus*), one with a more northern distribution (*I. pini*), and one with a broad range (*I. grandicollis*). These species are primarily associated with fallen or weakened trees (Baker, 1972), including those previously attacked by other bark beetles. The range of *T. dubius* can therefore be divided into two biotic regions; a southern one characterised by the presence of *D. frontalis* and the more southern *Ips* species, and a northern one where *D. frontalis* is absent and *Ips* are common prey. A third, boreal, region exists where the distribution of *T. dubius* overlaps another bark beetle species that exhibits outbreaks, the spruce beetle *Dendroctonus rufipennis*, beginning within the range of northern spruce species in the Great Lakes region and Canada (Haberkern *et al.*, 2002; Haberkern and Raffa, 2003; Maroja *et al.*, 2007). There are also reports of *T. dubius* in association with *D. rufipennis* from Alaska and Utah (Gara *et al.*, 1995; Bentz & Munson, 2000). In addition, the distribution of *T. dubius* overlaps with *Dendroctonus simplex*, *Dendroctonus terebrans*, and *Dendroctonus valens* at various points in its range (Baker, 1972; Wood, 1982). Although adult *T. dubius* would consume adults of these species, it is unclear whether they are suitable for larval development. We could find only one report of *T. dubius* larvae feeding on *D. simplex* (Seybold *et al.*, 2002), and none for *D. terebrans* or *D. valens.*

The available evidence suggests there may be geographic differences in how *T. dubius* responds to prey pheromones. A number of studies have examined the response to three different prey pheromones: frontalin, ipsenol, and ipsdienol. Frontalin is associated with *D. frontalis*, *D. rufipennis*, *D. simplex*, *D. valens*, and *D. terebrans*; ipsenol with *I. grandicollis*, while ipsdienol is utilised by several *Ips* species (*I. avulsus*, *I. calligraphus*, and *I. pini*) (reviewed by Skillen *et al.*, 1997). In the northern and boreal biotic regions *T. dubius* responds to all three pheromones (Raffa & Klepzig, 1989; Herms *et al.*, 1991; Erbilgin & Raffa, 2001; Haberkern & Raffa, 2003; Aukema & Raffa, 2005), while in the southern region the response to *Ips* pheromones can be very weak (Billings & Cameron, 1984; Billings, 1985). Intriguingly, Billings and Cameron (1984) found that the response to *Ips* pheromones was much higher at a Texas site where *D. frontalis* was endemic relative to an outbreak site, suggesting a change in prey preference in response to prey abundance.

Studies in the southern biotic region have also examined the attraction of another common predator, *Temnochila virescens* (Coleoptera: Trogositidae), to these same pheromones (Billings & Cameron, 1984; Billings, 1985). The two predator species appear to partition the different prey pheromones, with *T. dubius* responding more strongly to frontalin and *T. virescens* only to *Ips* pheromones. When present on the same tree, they likely compete for prey, and *T. virescens* is also known to attack *T. dubius* (Mignot, 1966), a case of intraguild predation (Polis *et al.*, 1989).

Bark beetles often use visual cues in locating host trees (Gara *et al.*, 1965; Strom *et al.*, 1999; Strom & Goyer, 2001) and we would expect their predators to employ them as well. Certain visual cues may be associated with specific prey species. For example, *D. frontalis* attack living pines that provide a strong visual cue (a dark vertical silhouette) for approaching beetles and predators (Gara *et al.*, 1965). *Ips* beetles occur in both standing and fallen trees, however, and would not seem to be associated with consistent visual cues. A predator might therefore link certain visual cues with different prey pheromones, specialising on vertical silhouettes when *D. frontalis* and frontalin are detected, while exhibiting less or no visual preferences when *Ips* are detected. Trapping studies indicate that both *D. frontalis* and *T. dubius* are sensitive to visual cues (Strom *et al.*, 1999; Strom & Goyer, 2001), with far fewer insects trapped in white or yellow traps vs. black traps, while *Ips* are less influenced by visual cues (Goyer *et al.*, 2004). If *T. dubius* follows suit, we would expect visual cues to have less effect when combined with *Ips* pheromones than with frontalin. We might also expect a relatively weak response to manipulation of visual cues in *T. virescens*, given the pattern seen in the closely related species *T. chlorodia* and its prey *D. brevicomis* (Strom *et al.*, 2001).

The present paper reports on trapping studies that examine geographic variation in the response to prey pheromones by two bark beetle predators, *T. dubius* and *T. virescens.* The study sites span much of the range of these two predators, and include areas where *D. frontalis* populations were in outbreak vs. endemic, as well as areas where it is absent. For our purposes, outbreak means that *D. frontalis* is very abundant at a location, endemic that density is low (often below detection levels), while absent signifies an area outside its range. The present study also examines geographic variation in the response to visual cues in these two predators. The results of the present study are then

combined with those from previous studies to examine the response of *T. dubius* to prey pheromones in outbreak vs. endemic areas. The present study is a first step in determining whether regional variation in pheromone preference exists, and could be followed by more detailed behavioral studies that determine whether such variation is innate or learned.

Materials and methods

Two experiments were conducted to examine geographic variation in the response of *T. dubius* and *T. virescens* to bark beetle pheromones and visual cues. Experiment 1 spanned the distribution of *T. dubius* within the eastern U.S.A., but only examined variation in pheromone response. Study sites were pine forests, with four chosen from areas where *D. frontalis* or other frontalin-emitting species were absent or endemic [western Wisconsin (WI), central Michigan (MI), southern Illinois (IL), central Louisiana (LA)], and three from areas where *D. frontalis* was in outbreak [two adjacent sites in southern Kentucky (KYN, KYP), plus northern Alabama (AL)]. Outbreak status was confirmed by capture of *D. frontalis* during the experiment and by USDA Forest Service records of outbreak status (http://www.srs.fs.usda.gov/econ/data/spb/). Table 1 lists the locations, sampling times, and potential prey communities at each site, including their use of frontalin, ipsenol, and ipsdienol as pheromones.

Multiple-funnel traps (Lindgren, 1983) were baited with frontalin, ipsdienol, or ipsenol plus α-pinene, a host-produced volatile that synergises the responses of these predators (Billings, 1985; Erbilgin & Raffa, 2001). Baits were those considered standard devices for monitoring bark beetle and predator populations (Phero Tech Inc., Delta, Canada). Synthetic pheromones were racemic in optical composition with the following elution rates: frontalin at 5.2 mg day^{-1}, ipsdienol at 110 μg day^{-1}, and ipsenol at 230 μg day^{-1} (Phero Tech, Inc.). The host volatile α-pinene was released at approximately 1 g day^{-1} and was 95% (−)-α-pinene in optical composition. There were five treatments in the experiment: (1) blank or unbaited trap, (2) α-pinene, (3) frontalin + α-pinene, (4) ipsdienol + α-pinene, and (5) ipsenol + α-pinene. Treatment 3 is a combination associated with *D. frontalis* and *D. rufipennis*, although none of the latter was trapped at the sites. Treatment 5 is only associated with *I. grandicollis*. Treatment 4 was chosen because ipsdienol is a common pheromone used by *Ips* beetles, in particular *I. avulsus*, *I. calligraphus*, and *I. pini* (Skillen *et al.*, 1997).

At each of the seven sites, traps were deployed in a randomised block design with one replicate of each treatment per block and six total blocks. Traps were separated by 30 m within each block and blocks located 0.1–1 km apart. The traps were deployed for 3 weeks in each location during the spring or early summer (depending on local phenology) in either 2000 or 2001 (Table 1). The spring flowering of dogwood trees (*Cornus* spp.) was used as a signal to begin trapping (Thatcher & Barry, 1982).

The resulting data were analysed using methods for multiple randomised block experiments (McIntosh, 1983), treating sites and treatments as fixed effects. A log-transformation ($\log_{10}(Y + 1)$) equalised the variance across treatments. Treatments that caught few or no insects were excluded from the statistical analysis, because they could affect the validity of the analysis (Reeve & Strom, 2004). This involved the blank treatment and one or two other treatments in some cases (Table 2). Sites where *T. virescens* was absent or low in number were also excluded (Table 2). Of particular interest in these analyses was the treatment × site interaction – if present, it indicates that predators differ in their pheromone preference across sites. We were less interested in site or treatment effects, because differences of this type were expected (predator densities differ

Table 1. Locations, sampling times, and potential prey communities for the study sites in experiments 1 and 2. Prey are classified by aggregation pheromone, species, and density (O, outbreak; E, endemic and present in pine stands; N, endemic but not present in the pine stands; A, absent, lying outside the known range of a particular species). The prey species are *Dendroctonus frontalis* (Df), *D. rufipennis* (Dr), *D. simplex* (Ds), *D. terebrans* (Dt), *D. valens* (Dv), *Ips grandicollis* (Ig), *I. avulsus* (Ia), *I. calligraphus* (Ic), and *I. pini* (Ip). Sources for species distributions and aggregation pheromones include Baker (1972), Wood (1982), Skillen *et al.* (1997), and Luxova *et al.* (2007). Also shown are locations where *Thanasimus dubius* (Td) and *Temnochila virescens* (Tv) were present or absent (+ or −) based on observations made in the present study.

				Frontalin					Ipsenol	Ipsdienol				
Site	Lat.	Long.	Date	Df	Dr	Ds*	Dt*	Dv*	Ig	Ia	Ic	Ip	Td	Tv
Experiment 1 (pheromone)														
WI	45.03423	–91.83812	5/00	A	N	N	A	E	E	A	E	E	+	–
MI	42.39041	–85.35782	6/01	A	N	N	A	E	E	A	E	E	+	–
IL	37.54581	–88.69315	5/01	E	A	A	E	A	E	E	E	A	+	+
KYN	36.88050	–84.55624	5/00	O	A	A	E	A	E	E	E	E	+	+
KYP	36.87672	–84.54739	5/00	O	A	A	E	A	E	E	E	E	+	+
AL	32.95219	–87.17332	5/00	O	A	A	E	A	E	E	E	A	+	+
LA	31.93064	–92.64457	3/00	E	A	A	E	A	E	E	E	A	+	+
Experiment 2 (pheromone × colour)														
IL2	37.54581	–88.69315	5/02, 5/03	E	A	A	E	A	E	E	E	A	+	+
MS	31.48059	–90.86967	4/02	O	A	A	E	A	E	E	E	A	+	+
LA2	31.52614	–92.54501	4/02	E	A	A	E	A	E	E	E	A	+	+

*Limited or no evidence that *T. dubius* completes development on these species.

Table 2. Study sites and treatments excluded (vs. included) from the statistical analyses because of low trap catches of predators, in the two field experiments and for both predator species. Site codes are given in Table 1. Control, blank trap; AP, α -pinene; FR + AP, frontalin + α-pinene; ID + AP, ipsdienol + α-pinene; IS + AP, ipsenol + α-pinene; T, turpentine; FR + T, frontalin + turpentine; ID + T, ipsdienol + turpentine; IS + T, ipsenol + turpentine.

Experiment	Predator	Sites excluded (included)	Treatments excluded (included)
1	*T. dubius*	None (WI, MI, IL, KYN, KYP, AL, LA)	Blank, AP (FR + AP, ID + AP, IS + AP)
1	*T. virescens*	WI, MI, KYP (IL, KYN, AL, LA)	Blank (AP, FR + AP, ID + AP, IS + AP)
2	*T. dubius*	None (IL2, LA2, MS)	Blank, T (FR + T, ID + T, IS + T)
2	*T. virescens*	None (IL2, LA2, MS)	Blank, T, FR + T (ID + T, IS + T)

among sites, and certain treatments are more attractive than others). The analyses were conducted using PROC MIXED in SAS 9.1 (SAS Institute Inc., 2003). Contrast statements were used to examine the treatment × site interaction for each pair of sites. This resulted in 21 pairwise tests, and so we employed a sequential Bonferroni correction (Sokal & Rohlf, 1995) to judge significance.

Experiment 2 examined geographic variation in the response to pheromones and visual cues at two endemic sites [southern Illinois (IL2) and central Louisiana (LA2)) and one outbreak site (southwestern Mississippi (MS)]. The same bark beetle pheromones were used as in the first experiment, but in this study the release rates of the three pheromones were matched and the ratio of pheromone to host volatiles approximated natural values (Browne *et al.*, 1979; Seybold *et al.*, 1992). Baits containing racemic frontalin, ipsdienol, and ipsenol were chosen for release rates of approximately 0.5–1.0 mg day^{-1} (Phero Tech, Inc.). EZ Gum Turpentine was used (E. E. Zimmerman Co., Pittsburgh, PA) as the source of host volatiles in this study, released at a rate of 200 mg day^{-1} (J. D. Reeve, unpublished data) from two polyethylene transfer pipettes (No. 252, Samco Scientific, San Fernando, CA). A GC analysis found the turpentine was composed of 33% (+)-α-pinene, 36% (−)-α-pinene, 7% (−)-β-pinene, and smaller amounts of chemicals often found in the resin of host pines (Δ-3-carene, β-phellandrene, limonene, myrcene, and camphene). This turpentine was chosen, because it better matched the composition of pine volatiles than single component lures. Visual cues were manipulated by painting the traps white or black with Krylon spray paint (Sherwin-Williams Consumer Group, Cleveland, OH) (Strom *et al.*, 1999). There were 10 treatments in the experiment, trap colour crossed with five semiochemical treatments: (1) blank trap or control, (2) turpentine, (3) frontalin + turpentine (4) ipsdienol + turpentine, and (5) ipsenol + turpentine. The traps were deployed in a randomised block design with one replicate of each treatment per block and six blocks at each site. Trap and block spacing were the same as in the first experiment. At the MS and LA2 sites in 2002, three blocks of traps were deployed for a 3–week period, then the traps collected and three more blocks deployed for a second 3–week period. Predator densities were low at the southern Illinois site, however, and so the first three blocks of traps were left deployed for 2 months in 2002. The second three blocks were deployed in the following year, again for 2 months.

Data were analysed similarly to experiment 1, treating site, pheromone, and trap colour as fixed effects. Treatments that caught few or no insects were again excluded from the analysis (Table 2). We were primarily interested in testing the pheromone × site interaction (which examines differences in pheromone preference across sites) and the pheromone × colour interaction (differences in the response to visual cues across pheromones). The three-way pheromone × colour × site interaction then tests for differences among sites in the combined response to pheromones and colours. As there were only three sites in this study, we did not conduct pairwise tests of the interactions between sites.

We also compared the overall preference of *T. dubius* for frontalin vs. *Ips* pheromones in outbreak vs. endemic sites using the combined data from both experiments. For each experiment and study site, a preference index of the form

$$\rho = \log_{10}\left(\bar{Y}_{FR}\right) - \log_{10}([\bar{Y}_{IS} + \bar{Y}_{ID}]/2), \quad (1)$$

was calculated, where $\bar{Y}_{FR}, \bar{Y}_{ID}$ and $\bar{Y}_{IS}$ are the mean trap catches for treatments using frontalin, ipsdienol, and ipsenol. The second experiment involved both black and white traps, so to make it more comparable to the first, only the black trap means were used. Note that ρ is the log-transformed ratio of the trap catches for frontalin to the average for ipsdienol and ipsenol traps, and is similar in form to the log response ratio used in meta-analysis (Hedges *et al.*, 1999). Values of ρ are shown in Figs 1 and 2. In locations where more than one experiment was performed (IL and ILD, KYN and KYP, LA and LA2), the average value of ρ was used to avoid temporal pseudoreplication (Hurlbert, 1984). One-way ANOVA was used to compare ρ between the three outbreak vs. two endemic study sites within the range of *D. frontalis*, excluding the two northern sites (WI and MI). The analysis was then repeated adding the northern sites outside the range of *D. frontalis.*

Analogous ρ values were also calculated for three previous studies (Billings & Cameron, 1984; Billings, 1985; Aukema & Raffa, 2005). The frontalin baits in these studies were combined with host tree volatiles (α -pinene or turpentine), similar to our experiments. There were differences among studies in the baits involving *Ips* pheromones. Billings and Cameron (1984) used a bait that combined ipsdienol, ipsenol, and cis-verbenol; Billings (1985) added host volatiles to this bait, while Aukema and Raffa (2005) used ipsdienol alone. There were a total of four sites, with one endemic site for which $\rho = 0.38$ in Texas (Billings & Cameron, 1984), two epidemic sites in Texas where $\rho = 1.28$, 1.56 (Billings & Cameron, 1984; Billings, 1985), and one Wisconsin site outside the range of *D. frontalis* with $\rho = 1.10$ (Aukema & Raffa, 2005). These values of ρ were added to those

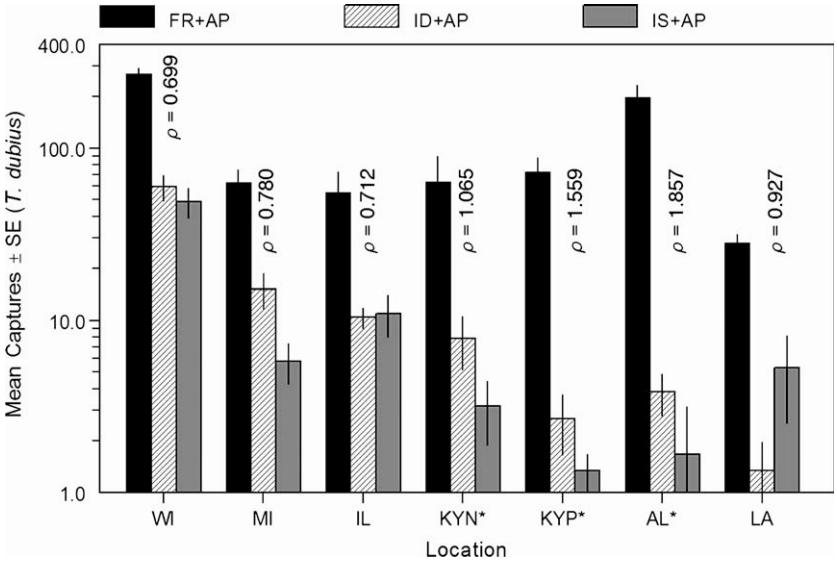

Fig. 1. Mean trap catches (±SE) of *Thanasimus dubius* for different pheromone treatments (experiment 1) across seven sites (*site in *Dendroctonus frontalis* outbreak). Treatments that caught few or no insects are not shown. FR + AP, frontalin + α -pinene; ID + AP, ipsdienol + α -pinene; IS + AP, ipsenol + α -pinene. Estimates of the preference index ρ are given above the bars for each site.

from experiments 1 and 2, and again tested for differences between outbreak and endemic sites.

Results

Outbreak status and prey abundance

Trap catches $\left(\bar{Y} \pm \mathrm{SE}\right)$ of *D. frontalis* confirmed its outbreak or endemic status at the study sites. In experiment 1, none were found at the four endemic (or absent) sites, while large numbers were captured at the three outbreak sites, ranging from 108.6 ± 47.0 per trap (AL) to 10445.8 ± 2679.3 (KYP). In experiment 2, none were captured at the two endemic sites while 39.5 ± 36.8 (MS) were captured at the outbreak site. *Ips* species were observed at all study sites. For example, *I. grandicollis* densities ranged from 1.8 ± 0.5 (IL) to 121.3 ± 33.8 (AL) in experiment 1, and 163.5 ± 24.8 (MS) to 259.7 ± 30.6 (LA2) in experiment 2.

Thanasimus dubius

Pheromone response – experiment 1. There was a highly significant effect of site ($F_{6,33.2} = 16.20$, $P < 0.0001$) and treatment ($F_{2,66} = 251.11$, $P < 0.0001$) on the number of *T. dubius* captured (Fig. 1), reflecting variation among sites in overall abundance, and also demonstrating that the frontalin + α-pinene treatment was the most attractive treatment. The treatment × site interaction was highly significant ($F_{12,66} = 7.62$, $P < 0.0001$),

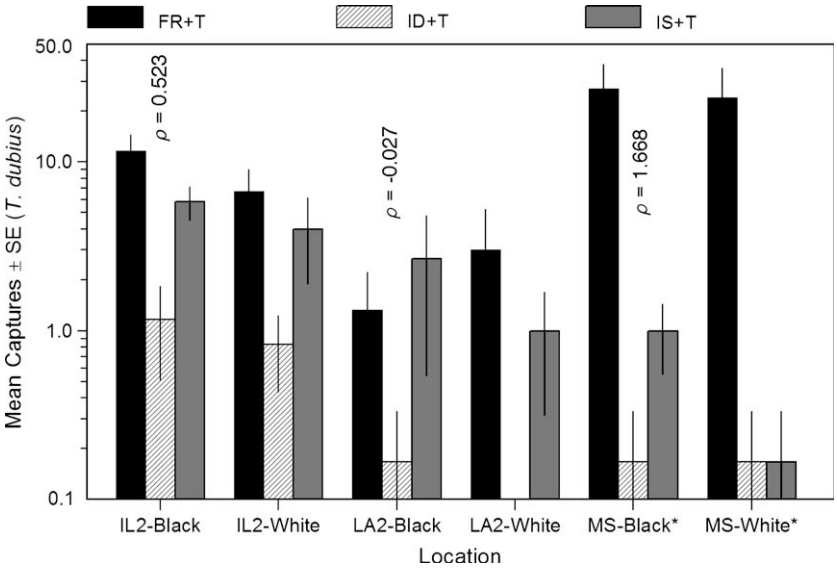

Fig. 2. Mean trap catches (±SE) of *Thanasimus dubius* for different pheromone and visual treatments (experiment 2) across three sites (*site in *Dendroctonus frontalis* outbreak). Treatments that caught few or no insects are not shown. FR + T, frontalin + turpentine; ID + T, ipsdienol + turpentine; IS + T, ipsenol + turpentine. No insects were caught for the ID + T–white colour treatment in Louisiana (LA2). Estimates of the preference index ρ are given above the bars for each site (black traps only).

indicating that there were differences among sites in preference for the three bark beetle pheromones. Two of the three outbreak sites, AL and KYP (but not KYN), showed a strong preference for frontalin over ipsdienol and ipsenol (Fig. 1). The pairwise tests for the pheromone treatment × site interaction support this pattern (Table 3), with AL showing a significant pairwise interaction with every site except KYP, while KYP showed a significant interaction with the three sites where *D. frontalis* was absent or rare (WI, MI, IL). Predators trapped at these three sites showed the least preference for frontalin.

Visual cues and pheromone response – experiment 2. There were significant main effects of site ($F_{2,15} = 4.19$, $P = 0.0358$), colour ($F_{1,15} = 5.98$, $P = 0.0273$), and pheromone treatments ($F_{2,30} = 25.88$, $P < 0.0001$) on *T. dubius* trap catches (Fig. 2). Fewer predators were trapped in white vs. black traps (a 36% overall reduction), while traps baited with frontalin and turpentine caught more than those baited with ipsdienol or ipsenol and turpentine. The preference for frontalin was much stronger at the MS outbreak site (Fig. 2). Reflecting this pattern, the pheromone treatment × site interaction was highly significant ($F_{4,30} = 4.99$, $P = 0.0033$). The colour × site, pheromone × colour, and pheromone × colour × site interactions were all non-significant.

Preference for frontalin vs. Ips pheromones in Thanasimus dubius – combined analysis. For study sites within the range of *D. frontalis*, the preference index for frontalin vs. *Ips* pheromones was significantly higher in outbreak vs. endemic sites [$\rho = 1.61 \pm 0.16$ (SE) vs. 0.53 ± 0.08, $F_{1,3} = 25.05$, $P = 0.0153$, $R^2 = 0.89$]. The results were little changed by the inclusion of the two northern sites (WI and MI) where *D. frontalis* is absent ($\rho = 1.61 \pm 0.16$ vs. 0.64 ± 0.07, $F_{1,5} = 38.36$, $P = 0.0016$, $R^2 = 0.88$), nor the values of ρ from previous studies (Billings & Cameron, 1984; Billings, 1985; Aukema & Raffa, 2005) ($\rho = 1.54 \pm 0.11$ for outbreak vs. 0.67 ± 0.11 for endemic and absent sites, $F_{1,9} = 32.23$, $P < 0.0003$, $R^2 = 0.78$). Although these studies used different baits involving *Ips* pheromones than in our experiments, their values of ρ did not appear to be outliers.

Temnochila virescens

Pheromone response – experiment 1. Four sites in experiment 1 caught sufficient *T. virescens* for statistical analysis (see Table 2). The effects of site ($F_{3,18.8} = 12.94$, $P < 0.0001$) and treatment ($F_{3,57.7} = 20.72$, $P < 0.0001$) were highly significant. Ipsdienol + α-pinene and ipsenol + α-pinene traps were more attractive than the remaining treatments (Fig. 3), while frontalin + α-pinene was no more attractive than α-pinene alone. In contrast to *T. dubius*, the pheromone treatment × site effect was non-significant ($F_{9,57.6} = 1.60$, $P = 0.1378$) for *T. virescens*, suggesting pheromone preference was similar among sites.

Visual cues and pheromone response – experiment 2. There was a highly significant effect of colour ($F_{1,15} = 25.18$, $P = 0.0002$) and pheromone ($F_{1,30} = 8.72$, $P = 0.0061$) on trap catches of *T. virescens* (the site effect was non-significant). White traps caught fewer insects than black traps (a 77% overall reduction), while ipsenol + turpentine caught somewhat more insects than ipsdienol + turpentine traps (Fig. 4). No interactions were significant.

Discussion

The findings for *T. dubius* indicate there is geographic variation in preference for prey pheromones, as evidenced by a significant pheromone treatment × site interaction in both experiments. The pattern appears to involve a reduced response to *Ips* pheromones relative to frontalin at sites where a frontalin emitter, *D. frontalis*, was at outbreak levels. An exception to this pattern was the KYN site (see Table 3). This could be an indication of local variation in the response, or it may simply represent sampling error in the estimates of preference. The results of the analysis combining the data from both experiments (using ρ values) also provided support for a change in preference in outbreak vs. endemic sites. This pattern held after including other studies on pheromone preference in *T. dubius* (Billings & Cameron, 1984; Billings, 1985; Aukema & Raffa, 2005), although the baits involving *Ips* pheromones were different in formulation from the experiments in the present study.

The change in response by *T. dubius* is consistent with switching (Murdoch, 1969; Murdoch & Oaten, 1975), because the response to frontalin was higher relative to *Ips* pheromones when *D. frontalis* was abundant, although *T. dubius* seems to prefer frontalin under all circumstances. The pattern agrees with the predictions of optimal foraging theory as well, provided *D. frontalis* is a higher quality prey than *Ips* species. There is little information on whether *T. dubius* adults or immatures perform better using *D. frontalis* vs. *Ips* species as prey, although both prey types have been used to rear them (Thatcher & Pickard,

Table 3. Pairwise tests of the pheromone treatment × site interaction for *Thanasimus dubius* for the seven sample sites (see Table 1 for site abbreviations).

	WI	MI	IL	KYN	KYP	AL	LA
WI	–	–	–	–	–	–	–
MI	0.4743	–	–	–	–	–	–
IL	0.7763	0.1975	–	–	–	–	–
KYN	0.3314	0.8691	0.0981	–	–	–	–
KYP	0.0008*	0.0019*	0.0001*	0.0085	–	–	–
AL	<0.0001*	<0.0001*	<0.0001*	<0.0001*	0.0142	–	–
LA	0.0582	0.0094	0.0459	0.0154	0.0162	<0.0001*	–

*Significant after sequential Bonferroni correction (Sokal & Rohlf, 1995).

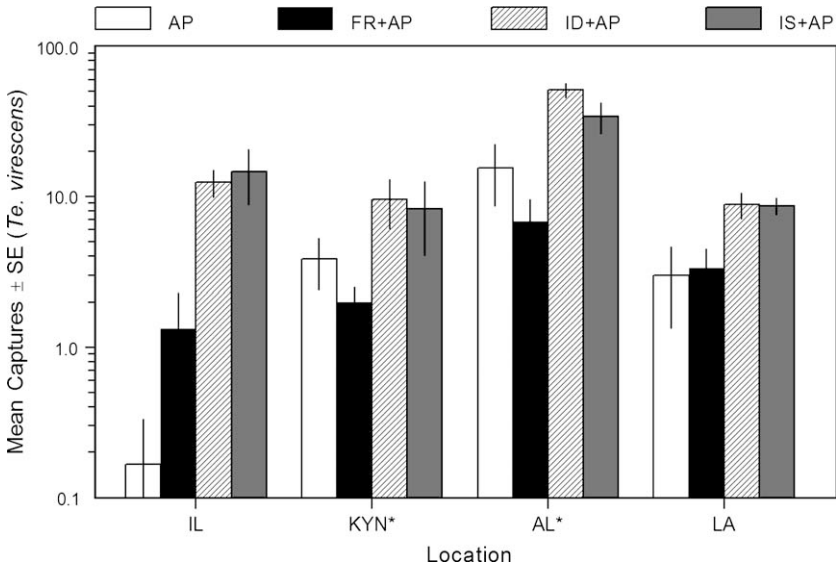

Fig. 3. Mean trap catches (±SE) of *Temnochila virescens* for different pheromone treatments (experiment 1) across four sites (*site in *Dendroctonus frontalis* outbreak). Treatments that caught few or no insects are not shown. AP α -pinene alone, FR + AP frontalin + α -pinene; ID + AP ipsdienol + α -pinene; IS + AP ipsenol + α -pinene.

1966; Nebeker *et al.*, 1982; Lawson & Morgan, 1992). However, we suspect that *D. frontalis* is higher quality prey than *Ips* species, because adult *D. frontalis* are higher in nitrogen content than at least one *Ips* species, *I. grandicollis* (Ayres *et al.*, 2000), although differences in size (*I. grandicollis* is larger than *D. frontalis*) could offset this to some extent. Another advantage is the tendency of *D. frontalis* to form large multiple-tree infestations, whereas *Ips* infestations are smaller. Therefore, a predator locating a *D. frontalis* infestation would likely find a higher quality and more abundant source of prey. Another advantage of switching behavior in *T. dubius* could be lower densities of *T. virescens*, a likely intraguild predator (see below).

The two predator species in this study neatly partition the major prey pheromones in areas where *D. frontalis* is abundant, with *T. dubius* responding to frontalin and *T. virescens* to ipsenol and ipsdienol. The results from the present study as well as previous work (Billings & Cameron, 1984; Billings, 1985) indicate that *T. virescens* is a specialist on *Ips* pheromones, although there is some response to host volatiles (α-pinene) that are more associated with *D. frontalis* attacks on host pines. Another explanation for the partitioning could be avoidance of competition with *T. dubius*, although studies by Mignot (1966) suggest that competition would favour *T. virescens.* However, Mignot and Anderson (1969, 1970) reported that *T. virescens* performed worse under dry conditions than *T. dubius*, and rapid drying of the host tree is associated with attack by *D. frontalis* (Webb & Franklin, 1978). Thus, trees attacked by *D. frontalis* may provide poorer conditions for *T. virescens*, because of competition with *T. dubius*, as well as a dryer environment. A similar partitioning of the same three pheromones occurs between

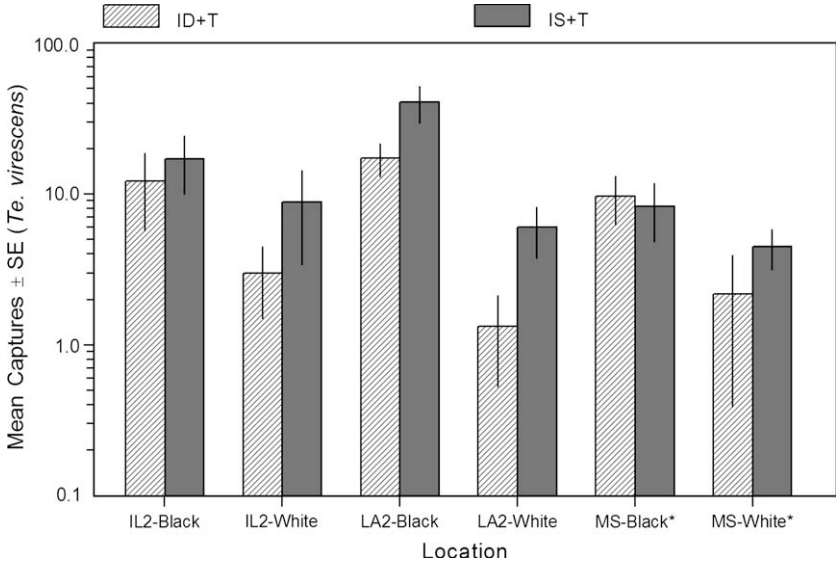

Fig. 4. Mean trap catches (±SE) of *Temnochila virescens* for pheromone and visual treatments (experiment 2) across three sites (*site in *Dendroctonus frontalis* outbreak). Treatments that caught few or no insects are not shown. ID + T, ipsdienol + turpentine; IS + T, ipsenol + turpentine.

T. dubius and the histerid predator *Platysoma cylindrica*, which also competes with *T. dubius* (Aukema & Raffa, 2002; Haberkern & Raffa, 2003; Aukema *et al.*, 2004; Raffa *et al.*, 2007). Given the tendency of these predators to attack one another, partitioning of prey pheromones may be a common strategy to reduce competition and intraguild predation.

The results of the present study indicate that visual cues are important in prey location by *T. dubius*, as found in previous work (Strom *et al.*, 1999; Strom & Goyer, 2001). However, the response to black vs. white traps appears similar among the three study sites (outbreak vs. two endemic sites) and across different prey pheromones, as none of the interactions were statistically significant. This suggests that geographic variation in the response by *T. dubius* is confined to the prey pheromones rather than the visual cues that may be associated with different prey species (a dark vertical silhouette for *D. frontalis* vs. no consistent pattern for *Ips*). Trap catches of *T. virescens* were also affected by trap colour, and so the responses of both predators appear modulated by visual cues (Prokopy & Owens, 1978). We speculate that the consistency of the response, regardless of prey pheromone, could indicate some desirable property of standing host trees irrespective of prey species.

There are locations within the range of *T. dubius* where frontalin-emitting prey, such as *D. frontalis* or potentially, *D. rufipennis* are low in density or absent, such as our more northern study sites. It is interesting that *T. dubius* maintains a strong response to frontalin in such locations where its utility appears questionable. One explanation could be gene flow among *T. dubius* populations. Phylogeographic studies and direct estimates of dispersal indicate that relatively high levels of gene flow may occur (Cronin *et al.*, 2000; Schrey *et al.*, 2005). Another possibility is that low levels of frontalin emitters are present in trees primarily colonised by *Ips* or other bark beetles, and by responding to frontalin, *T. dubius* may locate these alternate prey species, deriving an indirect benefit in this way. The frontalin emitters could be prey species (*D. frontalis*, *D. rufipennis*) as well as other *Dendroctonus* that may not be suitable prey (such as *D. simplex*, *D. terebrans*, or *D. valens*), because all commonly inhabit trees attacked by *Ips* and other bark beetles (Baker, 1972; Wood, 1982; Pajares & Lanier, 1990; Haberkern *et al.*, 2002; Bryant *et al.*, 2006).

Thanasimus dubius appears to be an important source of mortality for its prey (Reeve, 1997; Aukema & Raffa, 2002), possibly contributing to outbreak collapse in *D. frontalis* (Turchin *et al.*, 1999). What are the implications of switching behavior for the population dynamics of *T. dubius* and its prey? Switching can be stabilising or at least persistence-enhancing in simple predator–prey models (Murdoch & Oaten, 1975; Křivan, 1996), although destabilising factors such as prolonged development in *T. dubius* could offset this effect (Reeve, 2000; Reeve & Turchin, 2002). At a minimum, though, we would expect switching to enhance the persistence of *T. dubius* populations when *D. frontalis* is endemic, because their attraction to alternative prey (*Ips* species) would be increased under these circumstances. In fact, this predator remained at detectable levels during a long endemic period following the collapse of a *D. frontalis* outbreak, likely persisting on *Ips* prey (Reeve & Turchin, 2002).

What underlying mechanisms could explain the patterns of pheromone preference for *T. dubius*? One explanation could be an evolved change in preference in response to the prevalence of *D. frontalis* during outbreaks. This could involve selection for individuals that respond more strongly to frontalin during outbreaks and to *Ips* pheromones in endemic periods. However, selection would have to occur quite rapidly, because outbreaks are brief relative to the generation time of this predator (Reeve, 2000). Learning provides another potential explanation for these differences in pheromone preference. Learning would most likely occur during the adult stage, given the patterns seen in other natural enemies (Turlings *et al.*, 1993; Barron, 2001). Adult *T. dubius* might increase their response to a particular pheromone after exposure to the pheromone alone or in combination with a prey reward (Vet & Dicke, 1992). Learning has been demonstrated in parasitic wasps (see Turlings *et al.*, 1993), but evidence is scarce for other groups of predatory arthropods (De Boer & Dicke, 2006), although a few studies suggest learning in coleopteran predators (e.g. De Jean *et al.*, 2003). We are currently investigating the ability of adult *T. dubius* to learn different prey pheromones using wind tunnel experiments.

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