

## Exploitation of kairomones and synomones by *Medetera* spp. (Diptera: Dolichopodidae), predators of spruce bark beetles

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**Key words.** Dolichopodidae, *Medetera setiventris*, *Medetera melancholica*, predator, *Ips typographus*, *Pityogenes chalcographus*, *Picea abies*, volatiles, semiochemicals, kairomones, pheromones, monoterpenes

**Abstract.** The semiochemical relationships in a predator-prey-host plant system were studied by a series of multiple-choice field assays. The studied system included predatory flies of the genus *Medetera* (Diptera: Dolichopodidae), the bark beetles *Ips typographus* and *Pityogenes chalcographus* (Coleoptera: Curculionidae: Scolytinae) as prey and Norwegian spruce (*Picea abies*) as the host plant. Of the nine species of predators collected, only *M. setiventris* and *M. melancholica* provided sufficient data for statistical analysis. The response of the predators to monoterpene products of the host ( $\alpha$ -pinene, limonene, camphor), pheromone compounds of *I. typographus* (*S-cis*-verbenol and 2-methyl-3-buten-2-ol) and a mixture of the pheromones of *I. typographus* and *P. chalcographus* were investigated. Our field trials revealed that tree volatiles plus pheromones of the prey, and a pheromone mixture of both prey species were considerably more attractive to *M. setiventris* and *M. melancholica* than the individual chemicals. *Medetera* seem to respond to the stage of tree decay and the intensity of bark beetle infestation via the ratios of tree volatiles and/or prey pheromones.

### INTRODUCTION

Although few biological control programs have been successful in forestry (Berryman, 1967; Zondag, 1979; Lawson & Morgan, 1992; Fielding & Evans, 1997), several studies have explored the possibility of using natural predators as biocontrol agents of bark beetles (Coleoptera: Curculionidae: Scolytinae) (Berryman, 1967). Some authors suggest that the natural populations of predators might be manipulated by using semiochemicals (Aukema et al., 2000). However, this approach requires a thorough knowledge of the olfactory ecology of all the species involved, which is not yet available.

Several studies suggest that insects of the genus *Medetera* Fisher von Waldheim (Diptera: Dolichopodidae) are important predators of bark beetles worldwide (Nuorteva, 1956; Beaver, 1965; Bickel, 1987; Dippel et al., 1997; Hedgren & Schroeder, 2004). *Medetera* larvae inhabit galleries made by scolytid beetles in the bark of trees, and feed on scolytid eggs, larvae, pupae and emerging adults. Only rarely are *Medetera* reported to have little (Mills, 1985) or no impact on bark beetle populations (Kishi, 1969). In addition, some species of *Medetera* are efficient natural biocontrol agents even in spruce plantations (Weslien & Schroeder, 1999). Kolubajiv (1958) reported difficulties in rearing *M. signaticornis* in the laboratory.

Despite the potential significance of the genus *Medetera* in forestry, there are few studies on their

ecology and behavior. Ounap (2001) gives a summary of the current knowledge of the ecology of *M. signaticornis*, Nicolai (1995) and Dippel et al. (1997) of *M. dendrobaena* Kowarz, 1877; other authors focus on North American species (Schmidt, 1970, 1971; Williamson, 1971; Fitzgerald & Nagel, 1972, Aukema & Raffa, 2004). Despite these pioneer studies, many ecological features relevant to biological control, e.g. phenology, prey species range and olfactory orientation, have not been studied in most of the species of *Medetera*.

Olfactory communication plays an important role in predator-prey relationships, especially in the detection of particular species of prey (Foster & Harris, 1997). At present, little information is available on olfactory perception in *Medetera* species. Rudinsky et al. (1971) discovered that a solution of the primary attractants (synomones released by spruce)  $\alpha$ -pinene,  $\beta$ -pinene, camphene and limonene in ethanol is attractive to *M. signaticornis*. The North American species, *M. aldrichii* Wheeler, 1899, perceives  $\alpha$ -pinene as both an attractant and oviposition stimulus (Fitzgerald & Nagel, 1972). In another American species, *M. bistriata* Parent, 1929,  $\alpha$ -pinene alone does not elicit a response, but increases the attractiveness of bark beetle kairomones (Williamson, 1971). Although this species can also discriminate between individual compounds in its prey's pheromones, it does not respond to the individual compounds, but is strongly attracted by a mixture of the components. A mixture containing a prey

inhibitory compound is particularly attractive. There appear to be no similar studies on the response of European *Medetera* to bark beetle kairomones.

Olfactory relationships between *I. typographus* and some of their coleopteran predators and hymenopteran parasitoids are better understood. The strongest attractant for *Thanasimus formicarius* L. (Coleoptera: Cleridae) appears to be the pheromone blend of its prey *I. typographus* (Hansen, 1983). *T. formicarius* is strongly attracted to the compounds that bark beetles use as intraspecific repellents and less to those acting as intraspecific attractants (Bakke & Kvamme, 1981). Also there is evidence that synomones produced by host tree attacked by the bark beetles play a role in the olfactory orientation of *T. formicarius*, and antennal receptors for  $\alpha$ -pinene are described for this species (Hansen, 1983). Moreover, *T. formicarius* also seems to respond to the pheromones of other bark beetle species as to kairomones (Tommeras, 1988; Zumr, 1988).

Hymenopteran parasitoids of *I. typographus* are attracted to oxidized monoterpenes such as camphor and isopinocampyon, which indicate advanced development of bark beetle brood (Pettersson, 2001, Pettersson & Boland, 2003). Since these parasitoids oviposit on bark beetle larvae in a late stage of development, their olfactory preferences correspond with factors that determine their reproductive success.

In an attempt to acquire more information on the semiochemical relationships between predators, prey and host plants, a survey was carried out in the Czech Republic of *Medetera*, the spruce bark beetle *I. typographus* and its host tree species, the Norwegian spruce *Picea abies* Karst.

## MATERIAL AND METHODS

### Chemical components

To investigate the olfactory preferences of the *Medetera* species associated with *I. typographus*, their responses to the volatiles emitted by Norwegian spruce attacked by *I. typographus* and/or *Pityogenes chalcographus* L. were tested. Substances produced by resisting, dying or deteriorating trees, and by the bark beetles at each stage of tree infestation were also included, as these chemicals are known to be olfactory cues for previously studied antagonists of the Spruce bark beetle.

Substances released by Norwegian spruce (primary attractants):

- Unoxidized monoterpenes: the most common are  $\alpha$ -pinene and limonene (Baier, 1999). They are part of the induced defense mechanisms of this tree (Paine et al., 1997), released predominantly at the beginning of an attack (Pettersson & Boland, 2003). *I. typographus* respond positively to the (–) isomer and negatively to the (+) isomer of  $\alpha$ -pinene (Reddemann & Schopf, 1996). In our assay, we tested both isomers as well as the racemic blend.

- Oxidized monoterpenes: one of the most common is camphor (Pettersson & Boland, 2003), produced as byproduct during the biodegradation of tree tissues.

Substances produced or modified by spruce bark beetles (secondary attractants):

- Pheromone blend of *I. typographus* (Birgersson et al., 1984; Byers, 1989):

- S-*cis*-verbenol: oxidized derivative of  $\alpha$ -pinene. The key attractive compound of the aggregation pheromone of *I. typographus*, produced by males arriving on the suitable trees. It is attractive to both sexes.

- 2-methyl-3-buten-2-ol: de novo product of *I. typographus*, with strong synergic effect on S-*cis*-verbenol. A mixture of 2-methyl-3-buten-2-ol and S-*cis*-verbenol forms the core of the aggregation pheromone of *I. typographus* and is referred to as the “pheromone” (or “kairomone”) in the following text.

- Pheromone blend of *P. chalcographus* L., a bark beetle species sympatric and often competing with *I. typographus* (Byers et al., 1988):

- Chalcogran (2-ethyl-1,6-dioxaspiro[4.4]nonane), a male produced pheromone

- methyl-2,4-decadienoate, a male produced synergistic compound.

### Field experiments

Fieldwork was carried out in the Šumava National Park and Protected Landscape Area in the Czech Republic, an area heavily affected by continuous outbreaks of bark beetles since the early 1990s. The experimental localities were distributed across an area of approximately 40 km<sup>2</sup>. Sampling sites were selected at random in representative spruce habitats.

The different chemicals were tested in three experiments (Table 1). Each sampling site contained one complete set of baits of a particular experiment, arranged in the form of a multiple-choice design. Experiment I was replicated nine times, Experiment II ten times and Experiment III seven times, using a total of 133 traps at 26 sites. The traps, brown double-sided sticky boards 150 × 15 cm, were arranged in rows, the distance between the traps was 8 m, and their positions within a row randomized between sites. Each set of traps was exposed in the field for three weeks in June or July 2003, and was examined for specimens of *Medetera* at the end of this period. The traps were baited with dispensers consisting of a cellulose pad, impregnated with the chemical(s) and sealed within polyethylene foil. The evaporation rate of each chemical is comparable to that associated with injured or attacked Norwegian spruce (Ikeda et al., 1980; Kydonieus & Beroza, 1982; Charlwood et al., 1991; Borg-Karlson et al., 1996; Baier et al., 1999; Pettersson, 2001). The used evaporation rates were (mg/day):  $\alpha$ -pinene – 100; limonene – 60; camphor – 5; 2-methyl-3-buten-2-ol – 100; S-*cis*-verbenol – 5. The commercial dispenser Chalcoprax (BASF) was used for the *P. chalcographus* pheromone bait. The rates were achieved by selecting an appropriate thickness of the foil (0.1 or 0.5 mm) and restricting the evaporation area by impermeable Al-PET foil. The duration of evaporation (4 weeks, one week longer than the exposure period) was determined by the volume of the chemical.

### Statistical analysis

Individual trap catches were converted to the proportion of the total catch per group of traps to which the trap belonged, which decreased between-site variability and allowed for the integration of the data from sites with very different total catches (Table 3). These values were arcsin(square root(x)) transformed (Lepš, 1996). The null hypothesis that individuals were distributed randomly between traps regardless of the bait was tested using a Repeated measurements ANOVA. Catches of individual traps of each type were compared using a Tukey's HSD post-hoc comparison. Synergistic interactions between selected trap types were detected using a Factorial Two Way ANOVA. The synergistic effect was defined as “a joint effect of two substances, greater than the sum of effects of the individual substances” (Pennak, 1964). Only when more than 30 speci-

TABLE 1. The baits used in experiments I, II and III, with an indication of the natural occurrence of the chemicals, their role in the olfactory perception of the bark beetles, and sources and purity of the chemicals.

	Bait	Occurrence	Source, purity
EXPERIMENT I (primary attractants plus combinations with <i>I. typographus</i> pheromones). 9 replicates.	(+)- $\alpha$ -pinene	host tree monoterpene released following a bark beetle attack	Aldrich, Germany, >99%
	(-)- $\alpha$ -pinene	host tree monoterpene released following a bark beetle attack	Aldrich, Germany, >99%
	limonene	host tree monoterpene released following a bark beetle attack	Fluka, Germany, >95%
	camphor	host tree oxidized monoterpene, emitted by dying trees	Aldrich, Germany
	(S- <i>cis</i> -verbenol + 2-methyl-3-buten-2-ol) + ( $\pm$ )- $\alpha$ -pinene + limonene	<i>I. typographus</i> pheromone + unoxidized monoterpenes; simulates the beginning of an attack	
	(S- <i>cis</i> -verbenol + 2-methyl-3-buten-2-ol) + camphor	<i>I. typographus</i> pheromone + oxidised monoterpene; simulates a well developed bark beetle colony	
	S- <i>cis</i> -verbenol + 2-methyl-3-buten-2-ol	control bait plus <i>I. typographus</i> pheromone	
	blank control bait		
EXPERIMENT II (components of the aggregation pheromone of <i>I. typographus</i> in combination). 10 replicates.	S- <i>cis</i> -verbenol + 2-methyl-3-buten-2-ol	<i>I. typographus</i> pheromone	
	S- <i>cis</i> -verbenol		SH Chem, Slovakia, >95%
	2-methyl-3-buten-2-ol		Sigma-Aldrich, USA, 98%
	blank control bait		
EXPERIMENT III (multispecific preferences – pheromones of <i>I. typographus</i> , <i>P. chalcographus</i> , and of both species combined). 7 replicates.	S- <i>cis</i> -verbenol + 2-methyl-3-buten-2-ol	pheromone of <i>I. typographus</i>	
	chalcogran + methyl-2,4-decadienoate	pheromone of <i>P. chalcographus</i> ; Chalcoprax used as commercial dispenser	BASF, Germany
	(S- <i>cis</i> -verbenol + 2-methyl-3-buten-2-ol) + (chalcogran + methyl-2,4-decadienoate)	pheromones of both species	

mens of a *Medetera* species was collected in an experiment and at more than 3 sampling sites was the catch analyzed. All statistical analyses were performed using Statistica 5 package (StatSoft, 1995).

## RESULTS

A total of 3,678 specimens of 9 *Medetera* species were collected (Table 2). The most abundant species was *M. setiventris* Thunberg, 1955 with 2,565 specimens. *M. setiventris* and *M. melancholica* Lundbeck, 1912 were the only species that were abundant enough for statistical analyses in all three experiments. In Experiment I, also *M. adjaniae* Gosseries, 1988, *M. abstrusa* Thunberg, 1955, *M. infumata* Loew, 1857 and *M. pinicola* Kowarz, 1877 were caught in sufficient numbers, but the catches of these species by the baited traps didn't differ significantly from those of the control traps (Table 2). In Experiment III more than 30 specimens of each of *M. abstrusa* and *M. nitida* Macquart, 1834 were caught, but not analyzed as almost all of them were caught at a single site. *M. dendrobaena* Macquart, 1834 and *M. signaticornis* were always collected in low numbers or at fewer than 4 localities per

experiment. Thus, the following analyses are only for *M. setiventris* and *M. melancholica*. *M. adjaniae*, *M. melancholica* and *M. setiventris* are newly recorded species for the Czech Republic (see Chvála, 1997).

In Experiment I (primary attractants), both *M. setiventris* and *M. melancholica* were nonrandomly distributed among the trap types (Fig. 1). Both species were attracted most to the blend of kairomone and unoxidized monoterpenes, imitating a freshly attacked tree. Adding  $\alpha$ -pinene and limonene to the pheromones increased the catch of *M. setiventris* by an average of 298%. The kairomone alone was significantly less attractive than the kairomone/monoterpene blend, and the addition of camphor did not affect the level of attractiveness. *M. melancholica* was also significantly more attracted to a combination of  $\alpha$ -pinene, limonene and kairomone compared to the kairomone on its own, but in contrast to *M. setiventris*, it was not attracted by kairomone plus camphor. Camphor on its own and the control bait were the only baits significantly less successful than the mixture of unoxidized monoterpenes and kairomone. The high absolute number of individuals caught by the kairo-

TABLE 2. Summary of total catch (numbers of specimens) of each *Medetera* species in experiments I, II and III. ANOVA test of the hypothesis that the specimens are distributed randomly among the baits. Only species for which more than 30 specimens were collected per experiment were analyzed.

	Experiment I		Experiment II		Experiment III		Total
	Primary attractants (df = 56)		<i>I. typographus</i> pheromone (df = 24)		Multispecific preferences (df = 12)		
<i>M. setiventris</i>	1852	F = 17.57; p < 0.01	229	F = 5.36; p < 0.01	484	F = 4.25; p = 0.04	2565
<i>M. melancholica</i>	168	F = 2.58; p = 0.02	43	F = 0.89; p = 0.46	42	F = 0.89; p = 0.45	253
<i>M. adjaniae</i>	34	F = 0.56; p = 0.78	12		6		52
<i>M. dendrobaena</i>	20		3		21		44
<i>M. abstrusa</i>	48	F = 0.59; p = 0.78	12		37*		97
<i>M. infumata</i>	40	F = 1.21; p = 0.31	2		9		51
<i>M. nitida</i>	23		3		31*		57
<i>M. pinicola</i>	49	F = 0.97; p = 0.46	11		9		69
<i>M. signaticornis</i>	48		5		8		61
undetermined	251		124		54		429

\* *M. abstrusa* and *M. nitida* in Experiment III were collected in sufficient numbers, but not analyzed (see text).

more plus camphor bait (Table 3) was due to a single exceptional catch at one site. Except for limonene in the case of *M. setiventris*, no monoterpene was significantly attractive.

In Experiment II, only the kairomone of *I. typographus* (blend of *S-cis*-verbenol and 2-methyl-3-buten-2-ol) was significantly more attractive for *M. setiventris* than the control (Table 3, Fig. 2). *S-cis*-verbenol on its own was also more attractive than the control (see Fig. 2), but not statistically so. Factorial ANOVA did not reveal any synergistic interaction between *S-cis*-verbenol and 2-methyl-3-buten-2-ol ( $F = 0.377$ ;  $p = 0.543$ ; df of groups = 1; df total = 32). The preference for the complete blend showed by *M. melancholica* was not statistically significant.

In experiment III, only *M. setiventris* showed any significant preferences. *M. setiventris* was most attracted to the pheromone of both prey species, less to the kairomone of *I. typographus*, and even less to the pheromone of *P. chalcographus* (Fig. 3). The majority of the specimens of *M. melancholica* were caught by the trap baited with

the pheromone of *I. typographus*, while the other two baits containing the pheromone of *P. chalcographus* were less successful. These results are not statistically significant.

## DISCUSSION

The traps caught mainly the rarely studied *M. setiventris*. Only Nuorteva (1956) records this species, mainly on spruce (*Picea excelsa*). He reared adults from pupae collected in galleries of *Hylurgops palliatus* and *Pityogenes chalcographus* (Coleoptera: Scolytidae) and collected adult flies on trunks of spruce containing galleries of the scolytids *Hylurgops palliatus*, *Pityogenes chalcographus*, *Ips typographus* and *Polygraphus* sp. *M. setiventris* was also collected on a pine tree infested by *Ips amitinus*. The most frequently reported *Medetera* predator of *I. typographus* in Europe, *M. signaticornis* (Ounap, 2001; Wermelinger, 2002), occurred much less frequently in our survey. Despite its abundance in our experiment and the fact that *M. setiventris* is a common predator of *I. typographus* in the study area (Hulcr & Zelený, unpubl. data), it may not be the most abundant, as different species are known to respond differently to pheromone trap-

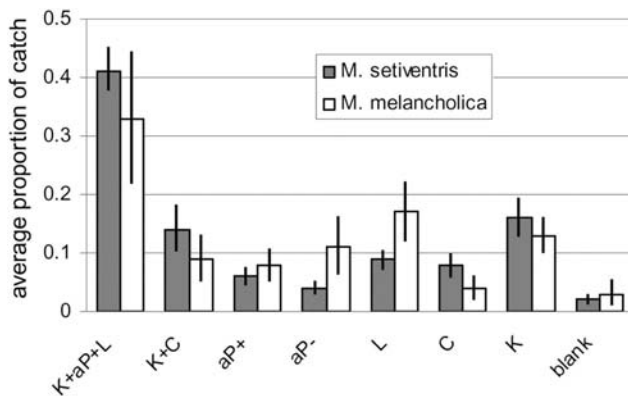


Fig. 1. Experiment I, trap catches of *M. setiventris* and *M. melancholica*, expressed as the average proportion of total catch per blocks. Vertical lines – SE of mean. aP – (+)- $\alpha$ -pinene and (-)- $\alpha$ -pinene; aP+ – (+)- $\alpha$ -pinene; blank – blank control bait; C – camphor; K – kairomone (cV – *S-cis*-verbenol and MB – 2-methyl-3-buten-2-ol); L – limonene.

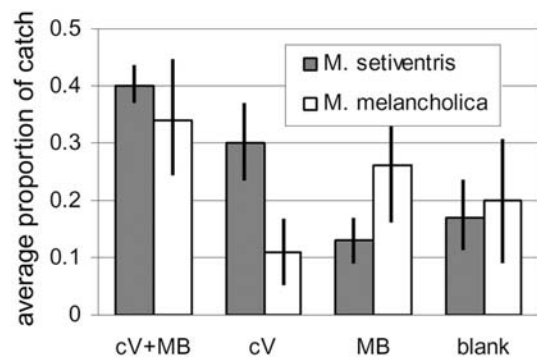


Fig. 2. Experiment II, trap catches of *M. setiventris* and *M. melancholica*, expressed as the average proportion of total catch per block. Vertical lines – SE of mean. blank – control bait; cV – *S-cis*-verbenol; MB – 2-methyl-3-buten-2-ol.

TABLE 3. Tukey post-hoc comparison of the results for selected species and bait comparisons. Mean proportion – mean proportion of the total catches per block, K – kairomone, aP – ( $\pm$ )- $\alpha$ -pinene, aP- – (-)- $\alpha$ -pinene, aP+ – (+)- $\alpha$ -pinene, L – limonene, C – camphor, blank – blank control bait, cV – S-cis-verbenol, MB – 2-methyl-3-buten-2-ol, I.t. – kairomone of *I. typographus*, P.c. – kairomone of *P. chalcographus*, both – pheromones of both prey species. No test for *M. melancholica* response to *I. typographus* pheromone and to pheromones of both species (ANOVA results insignificant).

<i>M. setiventris</i> , Primary attractants								
	blank	C	L	aP-	aP+	K	K+C	K+aP+L
no. specimens	49	149	103	142	107	273	453	576
mean proportion	0.02	0.08	0.09	0.04	0.6	0.16	0.14	0.41
K+aP+L	0.000	0.000	0.000	0.000	0.000	0.000	0.000	
K+C	0.001	0.899	0.962	0.162	0.392	0.995		
K	0.000	0.459	0.610	0.025	0.089			
aP+	0.368	0.988	0.955	1.000				
aP-	0.680	0.873	0.757					
L	0.034	1.000						
C	0.062							
<i>M. melancholica</i> , Primary attractants								
	blank	C	L	aP-	aP+	K	K+C	K+aP+L
no. specimens	9	20	9	25	19	26	27	33
mean proportion	0.03	0.06	0.10	0.11	0.10	0.13	0.10	0.36
K+aP+L	0.015	0.023	0.442	0.146	0.081	0.403	0.095	
K+C	0.996	0.999	0.992	1.000	1.000	0.995		
K	0.826	0.893	1.000	0.999	0.992			
aP+	0.998	1.000	0.987	1.000				
aP-	0.985	0.995	0.999					
L	0.793	0.867						
C	1.000							
<i>M. setiventris</i> , <i>I. typographus</i> pheromone					<i>M. setiventris</i> , Multispecific preferences			
	blank	MB	cV	cV+MB		both	P.c.	I.t.
no. specimens	23	27	70	109		197	107	180
mean proportion	0.17	0.13	0.30	0.40		0.49	0.21	0.30
cV+MB	0.013	0.025	0.798		I.t.	0.219	0.524	
cV	0.098	0.163			P.c.	0.034		
MB	0.993							
<i>M. melancholica</i> , <i>I. typographus</i> pheromone					<i>M. melancholica</i> , Multispecific preferences			
	blank	MB	cV	cV+MB		both	P.c.	I.t.
no. specimens	9	7	11	16		7	10	25
mean proportion	0.22	0.29	0.12	0.37		0.19	0.21	0.60

ping (Murlis et al., 1992). Ounap (1999) reared *M. adjaniae*, *M. nitida*, *M. setiventris* and *M. signaticornis* from trees colonized by both *I. typographus* and *P. chalcographus* and observed adults of *M. abstrusa*, *M. infumata* and *M. melancholica* on these trees. Nicolai (1995) confirmed that *M. dendrobaena* feeds on *P. chalcographus*. Of the species collected in this study, only *M. pinicola* is not yet recorded as a predator of the two bark beetles studied. Nevertheless, Bickel (1985) lists no less than 7 scolytid species of prey of *M. pinicola* in the Nearctic.

## Experiment I

The results for *M. setiventris* indicate that this species prefers trees freshly attacked by bark beetles, which produce mainly unoxidized monoterpenes. The species is probably attracted even to later stages of infestation, since the volatile associated with these stages, camphor, has no effect on the attractiveness of the kairomone.

*M. melancholica* was also attracted mostly to unoxidized monoterpenes and kairomone, volatiles signalling early stages of tree attack. But, unlike *M. setiventris*, it seems to be repelled by the presence of camphor (indica-

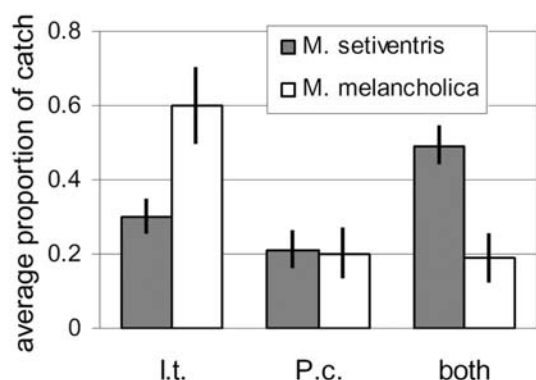


Fig. 3. Experiment III, trap catch of *M. setiventris* and *M. melancholica*, expressed as the average proportions of total catch per block. Vertical lines – SE of mean. I.t. – pheromone of *I. typographus*, P.c. – pheromone of *P. chalcographus*, both – both pheromones.

tive of the later stages of attack), which possibly inhibits the attractiveness of the pheromone to a certain extent.

For *Medetera* species preying on bark beetles, a preference for the early stages of the prey population establishment is not unexpected, since late oviposition and hatching results in poor survival of the first instar larvae of *Medetera*, which feed on the eggs and young larvae of bark beetles, but are killed by the final instar larvae of bark beetles (Ounap, 2001). Surprisingly, Ounap (1999) observed first *Medetera* larvae in the galleries as late as 19 days after a bark beetle infestation started. The opposite, a preference for trees in later stages of attack and bark beetle larval development, when the trees produce oxidized monoterpenes – is found in hymenopteran parasitoids (Pettersson, 2001), whose hosts are the late larval instars.

*M. setiventris* and *M. melancholica* were only slightly attracted by individual monoterpenes or not at all, which might be related to the fact that in natural conditions, this signal possibly only indicates a tree injury not necessarily caused by bark beetle infestation. Furthermore, the monoterpenes are commonly produced by any coniferous trees. In terms of the “reliability-detectability” gradient (Feener & Brown, 1997), such a signal is at the “unreliable” end of the gradient. On the other hand, Lawson et al. (1997) mention that *M. signaticornis* arrive on injured trees even before they are colonized by bark beetles.

According to Williamson (1971), Nearctic *M. bistriata* are attracted to a mixture of kairomone and synomones, but do not respond significantly to the kairomone or synomone components on their own. The most attractive bait for this species was a naturally infested log. Our results and those of Williamson (1971) indicate that natural sets of chemical cues, rather than individual substances, are the most attractive for *Medetera*.

Although *M. adjaniae* is a predator of the bark beetles in question, and *M. abstrusa* and *M. infumata* were observed to arrive on bark beetle infested trees (Ounap, 1999), they showed no preference for any of the tested chemicals. Therefore, these species either use a different

means of locating their prey, or the numbers of specimens caught in this study were too few to determine any pattern in their preferences.

### Experiment II

Of the two compounds in the *I. typographus* pheromone, only (S)-*cis*-verbenol is clearly attractive to *M. setiventris*. The same is the case for other predators of *I. typographus* of the genus *Thanasimus* (Hansen, 1983). *M. melancholica* was most attracted by the complete pheromone, but contrary to *M. setiventris*, S-*cis*-verbenol failed to attract more individuals than the control bait. The presence of both compounds appears to be necessary to elicit a response.

### Experiment III

*P. chalcographus* and *I. typographus* regularly colonize the same tree. Their galleries often overlap, which allows subcortical predators to exploit both species. However, larvae of *P. chalcographus* are much smaller and a poorer food resource for predators and often colonize parts of the tree (tree top, branches) with an inferior phloem quality than does *I. typographus*. This seems to be reflected in the olfactory responses of *M. setiventris*, which shows a preference for traps baited with attractants of both prey species, and for traps with the *I. typographus* pheromone if the two pheromones are offered separately. The behavior of *M. melancholica* seems to be different, as the majority of individuals chose traps baited with pure pheromone of *I. typographus* over traps baited with the pheromones of both prey species, indicating a strong preference for *I. typographus*. Again, mixtures of chemicals apparently inform the species about the suitability of the habitat for oviposition.

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