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Influence of Pheromone Dose, Trap Height, and Septum Age on Effectiveness of Pheromones for *Carpophilus mutilatus* and *C. hemipterus* (Coleoptera: Nitidulidae) in a California Date Garden

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ABSTRACT Synthetic pheromones for *Carpophilus mutilatus* Erichson and *C. hemipterus* (L.) were field tested in a planting of 'Deglet Noor' dates in southern California to determine effects of pheromone dose, trap height, and age of pheromone formulation on trap catch. Fermenting whole-wheat bread dough was the pheromone synergist in all cases. *C. mutilatus* was the most abundant nitidulid in the date garden, and trap catches were as high as 114,000 beetles per trap per 3-d period. For *C. mutilatus*, pheromone doses from 50 to 15,000 μg were significantly more attractive than controls, and trap catch increased with pheromone dose. Catch of *C. mutilatus* to its pheromone (500 μg) was significantly greater at a 3-m trap height than at 0.3 m. *C. hemipterus* responded significantly to its pheromone at all doses (15 to 15,000 μg). In addition, *C. mutilatus*, *C. obsoletus* Erichson, and *C. (Urophorus) humeralis* (F.) responded to the *C. hemipterus* pheromone, and all four species responded best at the highest doses. With the *C. hemipterus* pheromone (500 μg) at trap heights between 0.3 and 3 m, captures of *C. hemipterus*, *C. mutilatus*, and *C. obsoletus* increased with trap height, but those for *C. humeralis* were greatest near the ground. Rubber septa with pheromone for either species became less effective over time. After 1 wk, septum activity ranged from 18% of its original value (*C. mutilatus* responding to the *C. mutilatus* pheromone) to 90% (*C. obsoletus* responding to the *C. hemipterus* pheromone). In all experiments and with all species, males and females responded similarly. Trap responses are influenced strongly by the availability of food; in one case, sudden appearance of an abundant food source on the ground decreased responses of *C. mutilatus* by 99% within 1 wk. Implications of the study for using the pheromones in practical pest management are discussed.

KEY WORDS *Carpophilus*, pheromone, dose

NITIDULID BEETLES of the genus *Carpophilus* attack a wide variety of fruits and grains worldwide. One frequently infested crop is dates, and these beetles, together with the carob moth, *Ectomyelois ceratoniae* (Zeller), cause serious losses in the date gardens of southern California (Warner et al. 1990). *Carpophilus mutilatus* Erichson was reported to be the most abundant nitidulid in the date gardens (Lindgren & Vincent 1953), although the driedfruit beetle, *C. hemipterus* (L.), can occur in large numbers also. At least four other nitidulid species also are found but less commonly: *C. obsoletus* Erichson, *C. freemani* Dobson, *C. (Urophorus) humeralis* (F.), and *Haptoncus luteolus* (Erichson). Beetle populations build up in dates that have fallen to the ground, and dates in the trees then become subject to infestation as they near maturity. Beetle damage often is associated with fungal infection of the dates, and both are more severe in years of above-avarage rainfall (Warner et al. 1990). The majority of the California dates (≈85%) are of the 'Deglet Noor' cultivar; nitidulid species composition and their economic impact can be different in other date cultivars (R.S.V., unpublished data).

Male-produced aggregation pheromones to which both sexes respond have been identified for a number of *Carpophilus* species, including *C. mutilatus* and *C. hemipterus*. Both of these pheromones were active under field conditions but were most effective when synergized by food volatiles (Bartelt et al. 1990a; 1992a,b; 1993a). Cross attraction of *C. mutilatus*, *C. obsoletus*, and *C. humeralis* to the *C. hemipterus* phero-

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mone also has been reported in the date gardens (Bartelt et al. 1992a).

The pheromones promise to be of value in the monitoring and control of nitidulid populations. However, successful practical use of these chemicals requires an understanding of parameters such as pheromone dose, trap height, and timing of bait replacement. Here, we report the results of dose and trap-height studies with both the *C. mutilatus* and *C. hemipterus* pheromones. All the experiments gave information about field longevity of rubber-septum pheromone formulations. The studies also provided further evidence about cross attraction of the date-garden nitidulids.

Materials and Methods

Synthetic pheromones. The pheromone for *C. mutilatus* consisted of a blend of (3*E*,5*E*,7*E*)-5-ethyl-7-methyl-3,5,7-undecatriene and (3*E*,5*E*,7*E*)-6-ethyl-4-methyl-3,5,7-decatriene (Bartelt et al. 1993a). In 1991, the ratio of these components was 100:6. The pheromone for *C. hemipterus* consisted of a blend of (2*E*,4*E*,6*E*,8*E*)-3,5,7-trimethyl-2,4,6,8-decatetraene, (2*E*,4*E*,6*E*,8*E*)-3,5,7-trimethyl-2,4,6,8-undecatetraene, (2*E*,4*E*,6*E*,8*E*)-7-ethyl-3,5-dimethyl-2,4,6,8-decatetraene, and (2*E*,4*E*,6*E*,8*E*)-7-ethyl-3,5-dimethyl-2,4,6,8-undecatetraene (Bartelt et al. 1992b), and the 1991 porportions were 100:11:7:3, respectively. In 1992, blends were modified to 100:7 for *C. mutilatus* and to 100:31:11:8 for *C. hemipterus* so that emissions from freshly prepared septa more accurately reflected the proportions in emissions from beetles. (It was subsequently determined, however, that the modified formulations were not significantly better than the original ones in field effectiveness [R.J.B., unpublished data.]) The synthetic pheromones were purified only by distillation and open-column chromatography on silica gel. These procedures did not remove the small amounts of *Z* isomers produced in the syntheses (Bartelt et al. 1990b), but there is no evidence that these (currently unavoidable) impurities are detrimental to pheromonal activity (Bartelt et al. 1992b).

The pheromones were appropriately diluted with hexane and stored in a freezer until needed. Concentrations of components were determined by gas chromatography on diluted aliquots (instrumentation as described by Bartelt et al. [1990a]). Pheromone solutions (between 3 and 100 μl, depending on concentration and desired dose) were applied to rubber septa (11 by 20 mm, red rubber, Aldrich Chemical Co., Milwaukee, WI), followed by 300 μl of methylene chloride. After the liquid had soaked into the septa, they were aired in a fume hood for 1 h and stored in a freezer in tightly closed bottles until needed. For the dose studies, septa were prepared with 15, 50, 150, 500, 1,500, 5,000, and 15,000 μg of all-*E* isomers per septum (proportions as noted above). For the trap-height studies, only the 500-μg dose was used, which had been found to be effective in earlier field studies (Bartelt et al. 1992a; unpublished data).

Traps and Coattractant Baits. Wind-oriented funnel traps (Fig. 3 in Dowd et al. [1992], "modified" design) were used for all studies. Responding beetles become trapped in a collection bottle after passing through two funnels; no killing agent was used. One trap modification was that plastic bottles of ≈0.5-liter capacity were attached to the traps in some studies instead of the usual 20-ml glass vials to hold the large numbers of captured beetles. Fermenting whole wheat bread dough was used as the pheromone synergist in all cases (≈15 ml per trap); this was held in a 30-ml plastic cup, as described previously (Bartelt et al. 1992a). The dough was used as the control treatment in all experiments. Pheromone septa were pinned to the screens of the bait compartments of the traps. Responding beetles could not contact either the dough or the pheromone because of screens in the traps.

Study Location. The studies were conducted in a garden of 'Deglet Noor' dates at Rancho Eileen, near Oasis, CA. The trees were relatively short, with bunches of dates occurring between 1.5 and 5 m above the ground. Large numbers of fallen dates were present on the ground in various states of decay during the studies. Many of these were hydrated frequently by the drip irrigation system and were the major food source for the nitidulid populations. The date palms were in rows, with about 10 m between trees in a row and 10 m between rows. Redwood stakes were attached to tree trunks at appropriate locations and heights to serve as trap supports. Traps were hung from these by wires.

Temperatures during the studies were very warm. Mean daily maxima ranged from 32.7°C (during the trap-height studies, 27 April to 31 May 1991) to 39.2°C (during the second *C. hemipterus* dose experiment, 27 May to 29 September 1992). The respective mean daily minima were 16.4 and 21.0°C. The temperature patterns during this research followed closely those illustrated in Bartelt et al. (1992a).

Experimental Design of Dose Studies. During 1991, dose studies were done for both *C. mutilatus* and *C. hemipterus*. In each study there were six treatments: 15, 50, 150, 500, and 1,500 μg of pheromone, each with fermenting bread dough, and the dough by itself was the control. Each study had a randomized complete-block design. The six traps of each block were set out in a line, with 20 m between traps. Trap height was between 1 and 2 m. There were two blocks for each species. Traps were checked twice per week. The trap positions within the blocks were arranged randomly again, and the dough baits were replaced on each collection day. Pheromone septa were replaced every 2 wk, but the replacements were staggered so that the septa in the two blocks were changed in alternating weeks. Thus, after the first week, septa of two ages were always present, and information could be gained about septum aging. The study for *C. mutilatus* was conducted from 28 May to 28 June, and that for *C. hemipterus* from 7 June to 19 July. Based on earlier information (Bartelt et al. 1992a), the species were expected to be flying during the chosen test periods.

During 1992, the experiments were repeated, but the dose range was higher: 500, 1,500, 5,000, and 15,000 μg of pheromone per septum. As before, all pheromone-baited and control traps contained fermenting bread dough. For *C. mutilatus*, the experiment was conducted from 17 April to 22 May, and traps were checked and repositioned randomly twice weekly. The annual date harvest occurred while this experiment was being conducted (during the last week of April), which was unusually late. Many fully ripe dates dropped to the ground during harvest and then were wetted by a rain storm on 5 May. These provided an abundant new food source for the beetles midway through the study. For *C. hemipterus*, the study was conducted from 27 May to 29 September, and the traps were checked and repositioned randomly again once weekly. The *C. hemipterus* dose experiment ran longer in 1992 than in 1991 to compensate for lower numbers of flying *C. hemipterus* in 1992.

Trap Height Studies. For both species, the trap-height studies included four treatments: 0.3-, 1-, 2-, and 3-m trap heights. Each trap was baited with a 500-μg dose of pheromone and bread dough. As in the dose studies, treatments were organized into linear blocks, and there were two blocks per species. Traps were checked twice weekly, and the dough baits were replaced and the traps respositioned randomly at each collection time. (At each trap station, there were trap mounts available at all four heights, which facilitated random repositioning of treatments.) For *C. mutilatus*, the study was conducted from 30 April to 24 May 1991, and that for *C. hemipterus*, from 27 April to 31 May 1991.

Data Collection and Analysis. Captured beetles were killed by freezing and then were shipped to the National Center for Agricultural Utilization Research at Peoria for analysis. Beetles were sorted by species and sex for trap catches of up to ≈4,000 insects. For larger trap catches, which occurred only with the *C. mutilatus* pheromone, the whole collection was weighed, and then two aliquots of ≈200 beetles were taken out, also weighed, and carefully counted by sex. Total trap catches and overall sex ratios were calculated from these subsamples. These large trap catches were homogeneous; no species except *C. mutilatus* was attracted in numbers to the *C. mutilatus* pheromone.

Analysis of covariance was used for the trap catch data. Trap counts were transformed to the $\log(X + 1)$ scale before analysis to stabilize variance; graphs of residuals indicated that the transformation was effective. It is interesting that the residual standard deviations for the 15 analyzed data sets were remarkably similar (between 0.123 and 0.397), despite the wide range of total beetles in these data sets (25 to 1,650,000). In all analyses, fitted factors were treatments, collection days, and blocks. The treatment × collection-day interactions also were modeled so that any changes over time in relationships among treatments could be detected. Septum age (in weeks) at the beginning of the trapping period was the covariate in the analyses. Initially, one parameter was fitted for each septum dose, but the slopes were generally homogeneous and a single slope for all doses gave an adequate description of the data. (Aging parameters were never fitted for controls.)

The 2 yr of dose data for each species were combined later so that relationships among all seven pheromone doses could be evaluated. A multiple regression program was used for this analysis because of the unbalanced nature of treatments and replications between the years. By coding the factors with dummy variables, differences among treatments, collection days, and blocks were fitted. The septum-age covariate also was included, but treatment × collection-day interactions were not fitted. Further statistical details are presented with *Results*.

Results

Dose Study for the *C. mutilatus* Pheromone. During both years, *C. mutilatus* responded well to its synthetic pheromone (Table 1). The lowest dose that was significantly more attractive than the dough control was 50 μg. In both years, mean trap catch always increased with dose. No antagonistic effect was evident, even with 15,000 μg per septum, although the response did appear to level off at that dose. In 1991, 52% of the captured beetles were females; this percentage was similar for all doses (range was 48 to 53% females). Beetles were not identified by sex for the 1992 experiment.

The data for the 1992 experiment are presented in two portions in Table 1: 17 April to 5 May was before the date harvest and subsequent rain storm, and 5 May to 22 May was after the storm. The trap catches before the storm for the highest dose were dramatic, with as many as 114,000 beetles being captured in one trap in a 3-day period. Average trap catches after the storm were <1% of those before it, and the transition occurred within several days. Many ripe dates were spilled to the ground during the harvest and wetted by the rain storm, and the de-

Table 1. Response of *C. mutilatus* to seven doses of synthetic *C. mutilatus* pheromone

Dose (μ)[a]	1991[b]		1992, before harvest[c]		1992, after harvest[d]		Relative activity[e]
	Mean	(Range)	Mean	(Range)	Mean	(Range)	
15	60.7	(21– 433)	—		—		1.0×
50	133.9*	(28– 1,539)	—		—		2.2×
150	561.3***	(36– 6,258)	—		—		9.1×
500	999.0***	(94– 7,968)	7,943***	(178– 52,100)	26.5***	(4– 959)	17.×
1,500	4,785.3***	(213–20,340)	21,379***	(6,600– 62,900)	39.7***	(10–1,120)	50.×
5,000	—		42,657***	(11,900–113,000)	228.1***	(31–1,000)	110.×
15,000	—		58,883***	(28,300–114,000)	222.9***	(42–1,996)	130.×
Control	59.3	(32– 206)	645	(64– 5,360)	3.4	(0– 12)	0.49×[f]

Analysis in $\log(x + 1)$ scale; means converted back to numerical scale for presentation. Within each column, significant differences from control denoted by * ($P < 0.05$) or *** ($P < 0.001$).

[a] All traps (pheromone and control) also contained fermenting whole-wheat bread dough

[b] 28 May to 28 June 1991; $n = 18$; collected twice per week.

[c] 17 April to 5 May 1992; $n = 10$; collected twice per week.

[d] 5 May to 22 May 1992; $n = 10$; collected twice per week.

[e] Regression analysis using all data was employed to calculate relationships among all eight treatments. Relative activity for the 15-μg dose was set arbitrarily at 1.0; for other doses, relative activity is ratio of fitted catch to that for 15 μg. Linear contrast of log(trap catch + 1) on log dose: $F = 307$; df = 1, 180; $P \ll 0.0001$. Curvature: $F = 2.57$; df = 5, 180; $P = 0.021$.

[f] Activity of control was relative to fresh septa.

crease in flying beetles coincided with the rapid colonization of the newly fallen dates.

In all three analyses in Table 1, the differences among treatments were consistent over time (treatment × collection day interactions were not significant). This remained true when both portions of the 1992 data set were recombined.

Dose Study for the *C. hemipterus* Pheromone. *C. hemipterus* responded to all doses (15–15,000 μg) at well above the control level ($P < 0.001$) (Table 2). During both study periods, however, beetle flight activity was concentrated into periodic peaks of several weeks duration (e.g., see Bartelt et al. [1992a]). The trap-catch ranges in Table 2 are broad because they include both the activity peaks and the periods of reduced flight activity between the peaks. For both years, the dose × collection day interaction was highly significant ($P < 0.01$); this occurred because the dough controls were always essentially zero, whereas pheromone trap catches varied widely over time. The interaction was no longer significant when the dough control was not analyzed with the other treatments. For all treatments, both sexes always responded similarly. In 1991, 55% of the captures were females, and 44% were females in 1992. In both years, sex ratios were very similar for all doses.

Three other species also responded to the pheromone of *C. hemipterus*; these were *C. mutilatus*, *C. obsoletus*, and *C. humeralis* (Table 2). For *C. mutilatus* in 1991, only the response to the 1,500-μg dose was clearly greater than that to controls. In 1992, all four of the doses were consistently above the control level. As with *C. hemipterus*, the sex ratio was always nearly 1:1; beetle captures were 48% females in both 1991 and 1992. *C. obsoletus* and *C. humeralis* were less common, but both responded significantly to doses of *C. hemipterus* pheromone of 500 μg or above. Overall, the *C. obsoletus* captured were 58 and 56% females in 1991 and 1992, respectively. For *C. humeralis*, the corresponding values were 47 and 44%.

Insufficient *C. freemani* were captured in this or in any other of the experiments for meaningful conclusions to be drawn about treatments. Small numbers of *H. luteolus* were caught, but, as before (Bartelt et al. 1992a), they responded only to the dough and ignored the synthetic pheromones.

Trap-Height Study with *C. mutilatus* Pheromone. The trap-height study for *C. mutilatus* was conducted during a period of intense flight activity (Table 3). Beetles were caught at all levels between 0.3 and 3 m, but traps at 2 and 3 m caught significantly more. The interaction of trap height and collection day was not significant. Overall, captured beetles were 55% females, and this percentage was similar for all heights (range was 53 to 59%).

Trap-Height Study with *C. hemipterus* Pheromone. *C. hemipterus* responded to its pheromone at all trap heights, but, as with *C. mutilatus*, higher traps tended to have greater capture rates (Table 3). The trap-height × collection day interaction was not significant. Sex ratio was similar at all heights; overall, 59% of the captured *C. hemipterus* were females.

C. mutilatus again responded to the *C. hemipterus* pheromone, but the captures increased dramatically with trap height (Table 3). The beetles were 51% females, and the sex ratio was similar for all trap heights. More *C. mutilatus* than *C. hemipterus* responded to the *C. hemipterus* pheromone (Table 3), but this (unexpected) situation was merely a result of greater abundance of *C. mutilatus*. In fact, *C. mutilatus*

Table 2. Responses of four *Carpophilus* species to seven doses of synthetic *C. hemipterus* pheromone

Responding species	Dose, μg[a]	1991[b]		1992[c]		Relative activity[d]
		Mean	(Range)	Mean	(Range)	
C. hemipterus	15	2.3***	(0– 35)	—		1.0×[e]
	50	4.8***	(0– 55)	—		1.8×
	150	7.2***	(0– 107)	—		2.5×
	500	10.4***	(0– 153)	4.4***	(0– 51)	3.9×
	1,500	15.0***	(0– 316)	4.2***	(0– 61)	4.4×
	5,000	—		4.5***	(0–106)	4.3×
	15,000	—		9.0***	(0–253)	7.8×
	Control	0.03	(0– 1)	0.03	(0– 1)	—
C. mutilatus	15	18.6	(1– 106)	—		1.0×[f]
	50	20.1	(0– 104)	—		1.1×
	150	21.7	(0– 228)	—		1.2×
	500	22.1	(0– 311)	17.4***	(3– 85)	1.5×
	1,500	44.0***	(0–1,012)	21.8***	(2–114)	2.2×
	5,000	—		33.4***	(0–134)	3.1×
	15,000	—		40.2***	(5–436)	3.7×
	Control	14.7	(0– 79)	5.5	(0– 61)	0.55×
C. obsoletus	15	0.06	(0– 1)	—		1.0×[g]
	50	0.12	(0– 1)	—		1.1×
	150	0.09	(0– 1)	—		1.0×
	500	0.36***	(0– 3)	1.4***	(0– 5)	1.3×
	1,500	0.57***	(0– 2)	1.4***	(0– 10)	1.4×
	5,000	—		2.4***	(0– 11)	2.0×
	15,000	—		4.0***	(0– 36)	2.9×
	Control	0.00		0.02	(0– 1)	—
C. humeralis	15	0.11	(0– 2)	—		1.0×[h]
	50	0.14	(0– 2)	—		1.0×
	150	0.21	(0– 3)	—		1.1×
	500	0.18	(0– 2)	0.52**	(0– 5)	1.1×
	1,500	0.32*	(0– 5)	0.71***	(0– 5)	1.2×
	5,000	—		1.01***	(0– 9)	1.4×
	15,000	—		1.69***	(0– 30)	1.9×
	Control	0.05	(0– 2)	0.08	(0– 1)	—

Analysis in $\log(x + 1)$ scale; means converted back to numerical scale for presentation. Within each column and species, significant differences from control denoted by * ($P < 0.05$), ** ($P < 0.01$), or *** ($P < 0.001$).

[a] All traps (pheromone and control) also contained fermenting whole-wheat bread dough.

[b] 7 June to 19 July 1991; $n = 24$; collected twice per week.

[c] 27 May to 29 September 1992; $n = 36$; collected once per week.

[d] For each species, regression analysis using all data was employed to calculate relationships among all seven doses (and also the dough control for *C. mutilatus*, the only species consistently caught in control traps). Relative activity for the 15-μg dose was set arbitrarily at 1.0; for other doses, relative activity is ratio of fitted catch to that for 15 μg.

[e] Linear contrast of log(trap catch + 1) on log dose: $F = 81.7$; df = 1, 225; $P \ll 0.0001$. Curvature: $F = 3.27$; df = 5, 225; $P = 0.007$.

[f] Linear contrast of log(trap catch + 1) on log dose: $F = 78.3$; df = 1, 284; $P \ll 0.0001$. Curvature: $F = 1.90$; df = 5, 284; $P = 0.09$.

[g] Linear contrast of log(trap catch + 1) on log dose: $F = 44.8$; df = 1, 225; $P \ll 0.0001$. Curvature: $F = 3.61$; df = 5, 225; $P = 0.004$.

[h] Linear contrast of log(trap catch + 1) on log dose: $F = 17.6$; df = 1, 225; $P < 0.0001$. Curvature: $F = 2.15$; df = 5, 225; $P = 0.06$.

responded still better to its own pheromone. For example, 302,000 *C. mutilatus* were caught by the *C. mutilatus* pheromone, but only 32,000 *C. mutilatus* were caught by the *C. hemipterus* pheromone, comparing the trap-height studies (Table 3) when both were in place in the same area and at the same time (30 April to 24 May).

C. obsoletus responded in trend much like *C. hemipterus*, with more beetles being captured at the highest trap location. *C. humeralis*, on the other hand, was captured most frequently near the ground, and catches diminished with increasing height. Overall, captures of *C. obsoletus* were 66% females, and the *C. humeralis* were 36% females.

Regression Analysis. Relative activities of treatments are summarized in Tables 1–3. For each species, the dose experiments of 1991 and 1992 were combined into one model so that all seven dose levels could be compared. Differences were expressed in a relative scale so that the large variations in overall trap catch at different times of the year would not obscure relationships among treatments. The multiplicative relationships result from analysis in the $\log(X + 1)$ scale. The lowest dose was assigned arbitrarily a relative activity of one.

The six degrees of freedom for differences among doses also were modeled into a linear effect (1 df) and lack of fit from the straight line

Table 3. Responses of five *Carpophilus* species to synthetic pheromones at four trap heights

Pheromone type[a]	Responding species	Trap ht, m	Mean catch	(Range)	Relative activity[b]
C. mutilatus[c]	*C. mutilatus*	0.3	2,90a	(865– 5,665)	1.0×[d]
		1	3,547b	(921– 6,819)	1.6×
		2	6,456c	(3,747–13,470)	2.8×
		3	6,606c	(1,718–15,060)	2.9×
C. hemipterus[e]	*C. hemipterus*	0.3	6.1a	(0– 30)	1.0×[f]
		1	10.0b	(1– 40)	1.6×
		2	9.0ab	(0– 51)	1.4×
		3	23.0c	(7– 67)	3.8×
	C. mutilatus	0.3	44.7a	(12– 108)	1.0×[g]
		1	140.3b	(24– 1,343)	3.1×
		2	370.5c	(25– 2,159)	8.1×
		3	1,095.5d	(81– 4,032)	24.0×
	C. obsoletus	0.3	0.28a	(0– 2)	1.0×[h]
		1	1.00b	(0– 4)	3.3×
		2	1.08b	(0– 3)	3.3×
		3	1.78b	(0– 9)	6.3×
	C. humeralis	0.3	0.50a	(0– 5)	1.0×[i]
		1	0.17b	(0– 2)	0.31×
		2	0.11b	(0– 1)	0.19×
		3	0.04b	(0– 1)	0.06×

Analysis in $\log(x + 1)$ scale; mean trap catches converted back to numerical scale for presentation. For each pheromone/species combination, means followed by the same letter are not significantly different (least significant difference, $P = 0.05$). Ranges in trap catch given in parentheses.

[a] All traps had fermenting whole-wheat bread dough in addition to pheromone.

[b] Relative activity for 0.3-m height was arbitrarily set at 1.0; for other heights, relative activity is ratio of mean catch to that at 0.3 m.

[c] 30 April to 24 May 1991; $n = 14$; collected twice per week; 500 μg per septum.

[d] Linear contrast of log(trap catch + 1) on trap height: $F = 66.7$; df = 1, 26; $P \ll 0.0001$. Curvature: $F = 4.82$; df = 2, 26; $P = 0.017$.

[e] 27 April to 31 May 1991; $n = 20$; collected twice per week; 500 μg per septum.

[f] Linear contrast of log(trap catch + 1) on trap height: $F = 29.3$; df = 1,38; $P = <F = 3.42$; df = 2, 38; $P = 0.043$.

[g] Linear contrast of log(trap catch + 1) on trap height: $F = 204$; df = 1, 38; $P \ll 0.0001$. Curvature: P 1.30; df = 2, 38; $P = 0.28$.

[h] Linear contrast of log(trap catch + 1) on trap height: $F = 16.2$; df = 1, 38; $P = 0.0003$. Curvature: $F = 1.28$; df = 2, 38; P 0.29.

[i] Linear contrast of log(trap catch + 1) on trap height: $F = 15.3$; df = 1, 38; $P = 0.0004$. Curvature: $F = 1.86$; df = 2, 38; $P = 0.17$.

(*curvature*, 5 df), where the response variable was log(trap catch + 1) and the independent variable was log(dose). In each case, the linear increase in trap catch with dose was overwhelmingly significant, but three of the five regressions also showed significant curvature. For *C. mutilatus* responding to its pheromone, the lack of fit to the linear trend was because the response flattened out at the higher doses. For *C. hemipterus*, the lack of fit was primarily the result of the 5,000-μg dose, which had an irregularly low response, for unknown reasons. For *C. obsoletus*, the departure from linearity was because the response was essentially constant at the control level for the lowest three doses and then increased abruptly.

The dough control was omitted from the analyses for *C. hemipterus*, *C. obsoletus*, and *C. humeralis* because it was virtually zero throughout, regardless of the size of captures in the other treatments.

For the trap-height study, regression analysis was applied to the relationship between log (trap catch + 1) and trap height (Table 3). Except with *C. humeralis*, there was always a significant increase in the response variable with trap height; this was most dramatic for *C. mutilatus* when responding to the pheromone of *C. hemipterus*. For *C. humeralis*, response decreased significantly as trap height increased. Lack of fit to the linear trend was also significant for two of the five regressions: for *C. hemipterus*, the increase was not "smooth" over the middle two trap heights, and for *C. mutilatus* responding to its own pheromone, there was no further increase in response beyond 2 m.

Septum Aging Effect. The experimental procedure (replacing half of the pheromone septa each week) allowed information to be obtained about the effect of septum age on attractiveness. Septum age, in weeks, was incorporated into the analysis model as a covariate. In each case, there was a significant ($P < 0.05$) decrease in log(trap catch + 1) as septa aged. This effect is summarized in Table 4 as activity of week-old septa, which expresses the mean catch (+ 1) for a week-old septum as a percentage of the corresponding value for a fresh septum. (The logarithm of the week-old septum activity is the slope from the covariance analysis.)

For the *C. mutilatus* pheromone, activity after 1 wk was between 18 and 44% of the original activity. For *C. hemipterus* responding to its pheromone, the activity after 1 wk was between

Table 4. Activity of week-old septa as percentage of original activity

Pheromone type	Responding species	Experiment		
		Dose, 1991	Dose, 1992	Trap ht
C. mutilatus	*C. mutilatus*	44%	18%, 35%[a]	40%
C. hemipterus	*C. hemipterus*	49%	56%	54%
	C. mutilatus	71%	71%	62%
	C. obsoletus	90%	74%	73%
	C. humeralis	86%	81%	85%

Activity of week-old septum is defined as the mean trap catch (+1) for a 1-wk-old septum, divided by the corresponding quantity for a fresh septum. The activity was calculated from analysis of covariance (see text). The dose and trap-height experiments are summarized in Tables 1–3.

[a] Values are for periods before and after harvest, respectively

49 and 56% of the original. For *C. mutilatus* responding to the *C. hemipterus* pheromone, the septa were between 62 and 71% as active after 1 wk as originally. For *C. obsoletus* and *C. humeralis*, the values were between 73 and 90%.

Discussion

Dose Response Studies. The threshold dose for *C. mutilatus* responding to its pheromone was about 50 μg per septum. The threshold for *C. hemipterus* to its pheromone was below 15 μg because even the lowest experimental dose was clearly active. In the laboratory, *C. mutilatus* was found to produce more pheromone than *C. hemipterus* (Bartelt et al. 1990a, 1993a). *C. mutilatus* may simply be adapted to respond to higher pheromone levels than *C. hemipterus*. For the cases of cross attraction to the *C. hemipterus* pheromone (Table 2), the thresholds were higher (usually $\approx$500 μg), as one might expect for interspecific attraction.

Increase in pheromone dose affected some species more strongly than others (Tables 1 and 2). *C. mutilatus* responded 130 times better to its pheromone at 15,000 μg than at 15 μg, but *C. humeralis* responded only 1.9 times better to the 15,000-μg dose of the *C. hemipterus* pheromone than to the 15-μg dose. Some of this variability may be explained in terms of the shape of a typical dose–response curve. A sigmoid curve, having a nearly flat region at the lowest doses (which perform much as controls), a sharply rising middle section, and a plateau at the highest doses (among which responses change very little), would be expected. For *C. mutilatus* responding to its pheromone, the experimental dose range spanned all three sections of the dose response curve, starting out at essentially the control level and ending as a plateau was approached. For *C. hemipterus* responding to its pheromone, the experimental doses contained only the upper portion of the expected dose–response curve because the lowest tested dose was already much more active than the control. Thus, the maximum possible range of responses to doses was not seen in the experiment. In the cases of cross attraction (Table 2), the data corresponded to the lower portion of the expected dose–response curve; about half of the lower doses were as controls, and inclusion of doses far higher than 15,000 μg would have been required to determine the full range of possible responses.

Kairomonal Use of Nitidulid Pheromones. The clear response of *C. mutilatus* to the pheromone of *C. hemipterus* may reflect a kairomonal use of the pheromone under natural conditions. *C. mutilatus* could co-colonize or take over feeding–breeding sites first discovered by *C. hemipterus*. (However, this ability would probably be of little benefit to *C. mutilatus* in the situation reported here because *C. hemipterus* was relatively rare.) A similar kairomonal relationship was documented for *C. antiquus* Melsheimer responding to the pheromone of *C. lugubris* Murray (Bartelt et al. 1993b).

The response of *C. obsoletus* to the *C. hemipterus* pheromone probably is caused by sharing of pheromone components rather than by a kairomonal relationship (R. J. Petroski, personal communication). The situation is unclear with respect to *C. humeralis*, however, because its pheromone remains unknown.

Trap-Height Studies. Both *C. mutilatus* and *C. hemipterus* responded well to their respective pheromones placed anywhere between 0.3 and 3 m above the ground. The beetles feed primarily in dates that have fallen to the ground, but they are not restricted to flying at that level; they ascend readily to the level at which the new date crop is subject to infestation by the beetles.

The traps at the greatest heights usually caught the largest numbers of beetles, but we believe that this result was at least partly a result of competition from natural pheromone sources being greatest near the ground rather than merely a tendency for the beetles to fly at higher levels. This suggestion is based on the response pattern of *C. mutilatus* toward the pheromone of *C. hemipterus*, compared with the pattern toward its own pheromone (Table 3). Specifically, the catches of *C. mutilatus* by the *C. hemipterus* pheromone were very low near the ground. The *C. hemipterus* pheromone is a relatively weak attractant for *C. mutilatus*, and one would expect this pheromone to compete poorly for *C. mutilatus* when placed near natural pheromone sources (dates on the ground infested with *C. mutilatus*).

The trend for *C. obsoletus* responding to the *C. hemipterus* pheromone was similar to that for *C. mutilatus*, but *C. humeralis* was quite different (Table 3). *C. humeralis* responded best to the *C. hemipterus* pheromone when it was close to the ground, despite probable colonization of dates and pheromone emission by *C. humeralis* near those traps. This result suggests a far stronger preference of *C. humeralis* to fly near the ground than that shown by the other species. Williams et al. (1993) showed corresponding differences in height preferences within a different complex of nitidulid species.

Longevity of Pheromone Septa. In all experiments, there was significant degradation of septum performance over the 2 wk that each was in the field. This is not surprising, given the first-order release characteristics of rubber septa (release rates decrease over time and are proportional to the amount of pheromone remaining in the septum [reviewed by McDonough 1991]). Perhaps it is more surprising that the pheromone formulation works at all, given the relative lability of these highly unsaturated hydrocarbons and the high desert temperatures (as high as 46°C during these studies). If change in attractiveness after 1 wk is used as the criterion for comparison, the septa with *C. mutilatus* pheromone showed the greatest reduction in activity over time (Table 4). This decrease probably reflects the declining release rate, coupled with the steep dose–response relationship for *C. mutilatus*. The observed decrease in activity of *C. hemipterus* septa (Table 4) was greatest for *C. hemipterus*, which had the steepest dose–response relationship among the four responding species (Table 2).

It is likely that additional factors such as changing component ratios and pheromone degradation also are involved in the decreasing septum activity, but the net effects on activity are apt to be complex. There is clearly room for improvement of the *Carpophilus* pheromone formulation, but the current system will provide a good basis for comparison as new formulations are developed. Chemical emissions from septa from the field need to be measured in addition to field activity to understand what is happening to the amount and quality of emitted pheromone.

Implications for Pest Management. For both *C. hemipterus* and *C. mutilatus*, the results of the dose–response studies were very favorable for use of the pheromones in practical pest management (e.g., monitoring or mass trapping). There was never evidence for antogonistic behavioral effects at high doses, despite pheromone amounts that were almost certainly far above physiological levels and despite the presence of unwanted geometrical isomers of the pheromones in the technical-grade synthetic mixtures. Response increased dramatically with dose even to the point at which traps were inundated with tens of thousands of beetles per day. For the major species, trap catch was not affected greatly by trap height, but the studies suggest using the highest practical trap locations for greatest effectiveness. Finally, female beetles of both species were attracted in large numbers to the pheromones, and it is of great benefit to be able to attract the egg-laying sex. However, the reduction in trap response after the date harvest and rain storm demonstrated in a dramatic way that the pheromones do not perform well in the presence of abundant, high-quality food. From the earliest stages of this work (Bartelt et al. 1990a), it was evident that well-fed beetles do not fly readily. Thus, the availability of food needs to be taken into account when using pheromone-trap catch data to evaluate damage potential. Sanitation would provide the double benefit of lowering beetle populations while increasing the effectiveness of the population monitoring method.

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