

Responses to Aggregation Pheromones for Five *Carpophilus* Species (Coleoptera: Nitidulidae) in a California Date Garden

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ABSTRACT The nitidulid species, *Carpophilus mutilatus* Erichson, *C. hemipterus* (L.), *C. freemani* Dobson, and *C. obsoletus* Erichson, responded to their aggregation pheromones during a 17-mo study in a California date garden. The pheromones were dramatically synergized by volatiles from fermenting whole-wheat bread dough; pheromones alone attracted only 1.0–2.9% as many beetles as the combinations with dough, and dough alone attracted only 0–2.9% as many as the combinations. Unbaited controls caught no *Carpophilus*. *C. mutilatus* was the most abundant species, and individual trap catches were as high as 63,500 per week. Cross attraction was significant in some cases, especially for *C. mutilatus* responding to the pheromones of *C. hemipterus* and *C. obsoletus* but was minimal compared with responses to the species' own pheromones. The pheromone of *C. lugubris* Murray was also tested, but no *C. lugubris* were detected in the date garden. Two additional nitidulid species were caught consistently: *C. (Urophorus) humeralis* (F.) and *Haptoncus luteolus* (Erichson). *C. humeralis* responded significantly to all of the pheromones but especially to those for *C. hemipterus*, *C. lugubris*, and *C. obsoletus* in combination with dough. *H. luteolus* was attracted only to the dough. Adult beetles were present in the dates on the ground throughout the year, but flight activity, as measured by trap catch, occurred erratically. All species had an intense period of flight activity in April and May, following a winter with favorable rains and an abundant food supply. This flight terminated abruptly when dates spilled to the ground during harvest and were hydrated by a rain storm. Flights of *C. freemani*, *C. obsoletus*, *C. humeralis*, and *H. luteolus* were more frequent in summer than for *C. mutilatus* or *C. hemipterus*. Flight activity during December and January was low for all species, but there was great variability in patterns of flight activity. The use of these pheromones is discussed in relation to pest management.

KEY WORDS *Carpophilus*, pheromone, dates

NITIDULID BEETLES ARE abundant in the date-growing region of southern California and have the potential to infest a significant portion of each developing date crop. The dynamics of crop infestation have been understood for years. Beetle populations thrive throughout the year in the dates present on the ground under the trees, and the adults move from this population reservoir into the new crop as it ripens on the trees (Barnes & Lindgren 1947). Crop damage is worst during years with above-average rainfall (Lindgren & Vincent 1953; Warner et al. 1990a, b). Nitidulids are most attracted to dates that are soured, fer-

mented, or mechanically damaged (Lindgren et al. 1948) and are able to carry fruit-degrading microorganisms into the crop (Lindgren & Vincent 1953), leading to a cycle of ever-increasing damage. In 1945, for example, nitidulids and associated fungi caused a loss of between 50 and 75% of the date crop, depending on variety (Barnes & Lindgren 1946).

Today, malathion, sulfur, and ferbam dusts are applied to the date bunches for control of insects, mites, and fungi (see Warner et al. 1990a, b), and fumigation in the warehouse prevents buildup of beetle populations after harvest. These measures normally keep nitidulid damage within tolerable limits, and the carob moth, *Ectomyelois ceratoniae* (Zeller), is currently considered the most serious date pest (Warner et al. 1990b). In the future, alternative ways for managing both the nitidulids and the carob moth will be needed, given the current trend toward less pesticide use, the possibility of resistance of nitidulids to malathion (encountered in Israel; Kehat et al.

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1976), and the elimination of fumigants such as methyl bromide.

Four nitidulid species were associated with California dates in the earlier literature (e.g., Lindgren & Vincent 1953): *Carpophilus mutilatus* Erichson, *C. hemipterus* (L.), *C. (Urophorus) humeralis* (F.), and *Haptoncus luteolus* (Erichson). *C. mutilatus* was then mistakenly identified as *C. dimidiatus* (F.); the status of these sibling species was clarified by Dobson (1954). During our studies, these and two other species were consistently encountered: *C. obsoletus* Erichson, which was reported occasionally from California dates (Stickney et al. 1950), and *C. freemani* Dobson, which was not reported earlier from the date gardens but which was also confused with *C. dimidiatus*.

Male-produced aggregation pheromones have been identified for five *Carpophilus* species occurring in California: *C. mutilatus*, *C. hemipterus*, *C. freemani*, *C. obsoletus*, and *C. lugubris* Murray. *C. lugubris* is found most often in the northern part of the state (Okumura & Savage 1974). All of the pheromones are unsaturated hydrocarbons (Fig. 1), all attract adults of both sexes, and all are synergized by appropriate food odors (Bartelt et al. 1990a, b; 1991; 1992a, b; 1993; Petroski et al. 1994).

This article continues the study of responses of *C. hemipterus* to its pheromone throughout the year in a date garden (Bartelt et al. 1992a); expands that study to include the pheromones of *C. mutilatus*, *C. freemani*, *C. obsoletus*, and *C. lugubris*; and explores relationships between the responses to the pheromones and the abundance of beetles in their primary food source, dates on the ground. The objective was to develop baseline information that could lead to pest management strategies incorporating the pheromones.

Materials and Methods

Synthetic Pheromones. The seven synthetic compounds used in this study are shown in Fig. 1: (1) (3*E*,5*E*,7*E*)-5-ethyl-7-methyl-3,5,7-undecatriene; (2) (3*E*,5*E*,7*E*)-6-ethyl-4-methyl-3,5,7-decatriene; (3) (2*E*,4*E*,6*E*,8*E*)-3,5,7-trimethyl-2,4,6,8-decatetraene; (4) (2*E*,4*E*,6*E*,8*E*)-3,5,7-trimethyl-2,4,6,8-undecatetraene; (5) (2*E*,4*E*,6*E*,8*E*)-7-ethyl-3,5-dimethyl-2,4,6,8-decatetraene; (6) (2*E*,4*E*,6*E*,8*E*)-7-ethyl-3,5-dimethyl-2,4,6,8-undecatetraene; and (7) (2*E*,4*E*,6*E*)-5-ethyl-3-methyl-2,4,6-nonatriene. The proportions of these in the synthetic pheromones for the various species are given in Fig. 1. In each case there was a total of 500 μg of all-*E* isomers per septum. Blends were adjusted for experiment 2 so that proportions of components released from septa would more closely agree with those measured in the laboratory in emissions from beetles. Synthesis of the compounds and the preparation

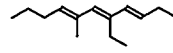
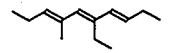
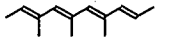
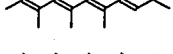
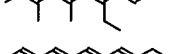
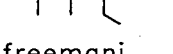
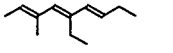
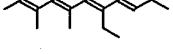
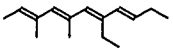
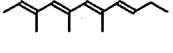
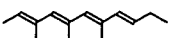
SPECIES AND STRUCTURES	RELATIVE AMOUNTS	
	(EXPT. 1)	(EXPT. 2)
<i>C. mutilatus</i>		
1 	100:	100:
2 	6	7
<i>C. hemipterus</i>		
3 	100:	100:
4 	11:	31:
5 	7:	11:
6 	3	8
<i>C. freemani</i>		
7 	100:	100:
6 	4	4
<i>C. lugubris</i>		
6 	100:	-
4 	10	-
<i>C. obsoletus</i>		
4 	-	100

Fig. 1. Structures of the pheromones for five *Carpophilus* species and the proportions of the synthetic compounds applied to rubber septa for the two experiments. Total pheromone per septum was always 500 μg .

method for the septa were described previously (Bartelt et al. 1990b, c; 1993; 1994).

Traps and Coattractant Baits. Wind-oriented funnel traps (Fig. 3 in Dowd et al. [1992], modified design) were used for all studies. Details of their use in the date garden were presented previously (Bartelt et al. 1994). Fermenting whole-wheat bread dough was used as the pheromone synergist in all cases (≈ 15 ml per trap) (Bartelt et al. 1994).

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 and were drip irrigated. The date palms were in rows, with ≈ 10 m between trees in a row and 10 m between rows. Redwood stakes were attached to tree trunks to serve as trap supports. Traps were hung from these by wires at a height of ≈ 1.5 m.

Experimental Design. The study consisted of two experiments, each having a complete block design (two blocks per experiment). Each block

EXPERIMENT 1

EXPERIMENT 2

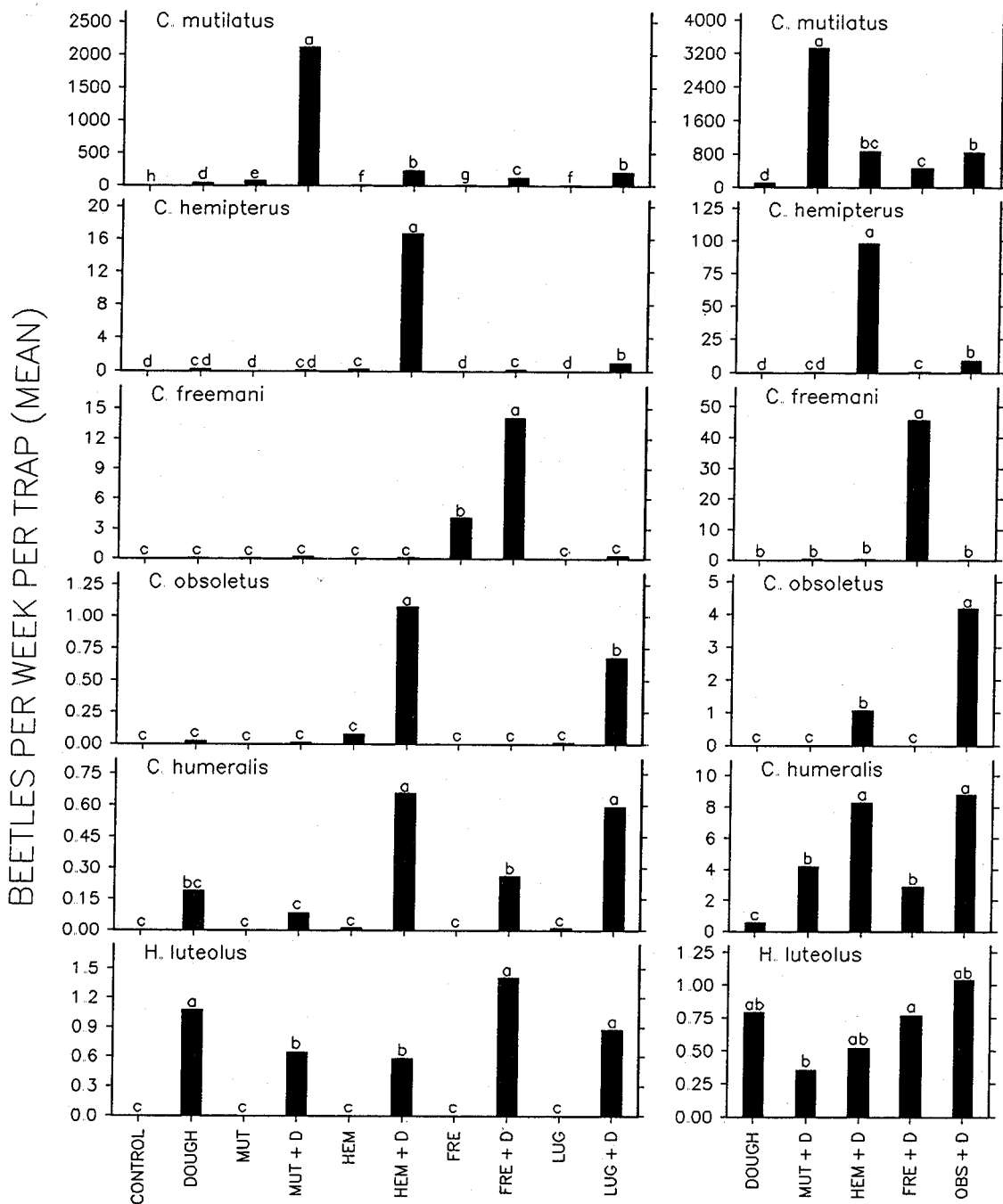


Fig. 2. Mean trap catches for six nitidulid species by the 10 treatments of experiment 1 ($n = 96$) and by the five treatments of experiment 2 ($n = 48$). Pheromones of *C. mutilatus*, *C. hemipterus*, *C. freemani*, *C. lugubris*, and *C. obsoletus* are denoted along the horizontal axis by "MUT", "HEM", "FRE", "LUG", and "OBS", respectively. Dough is represented by "D" in the combination baits. Within each panel, different letters above bars indicate significant differences between treatments (least significant differences, $P < 0.05$; analysis in $\log[x + 1]$ scale). Experiment 1 ran from 30 April 1991 to 14 April 1992, and experiment 2, from 14 April 1992 to 29 September 1992.

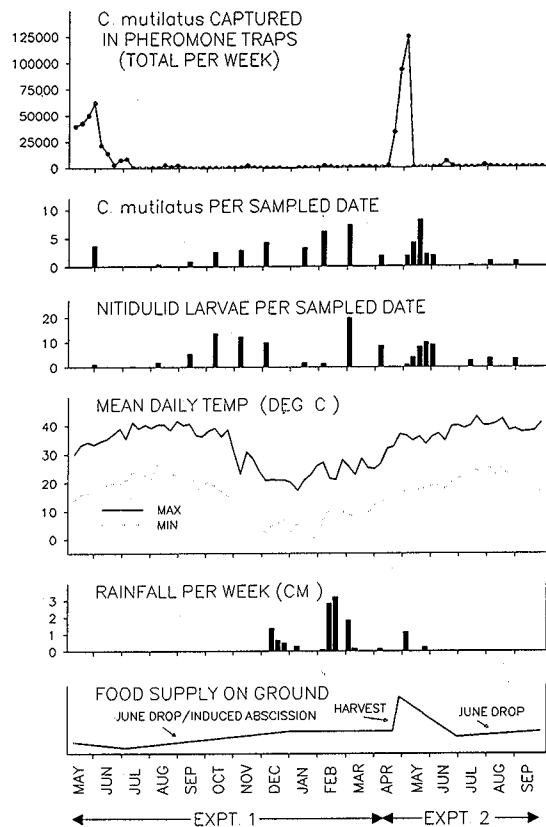


Fig. 3. Relationships among trap catch, abundance in date samples, temperature, rainfall, and food supply over time for *C. mutilatus* and nitidulid larvae (mostly *C. mutilatus*). Trap catches are weekly totals over all treatments but reflect primarily the *C. mutilatus* pheromone plus dough. Weather data were taken from the *Los Angeles Times* for Thermal, CA; both Thermal and the date garden are in the Coachella Valley. Food supply is shown diagrammatically; trends over time, but not actual quantities of dates, are represented.

was a line of trees, and the traps were attached to alternate trees along it (trap spacing was 20 m). For experiment 1 (30 April 1991–14 April 1992), the treatments included the pheromones of *C. mutilatus*, *C. hemipterus*, *C. freemani*, and *C. lugubris*, each being used alone and in combination with the dough co attractant. In addition, there was an unbaited control and a treatment containing just dough (a total of 10 traps per block). For experiment 2 (14 April 1992–29 September 1992), the treatments again included the pheromones of *C. mutilatus*, *C. hemipterus*, and *C. freemani*, but that for *C. obsoletus* replaced the *C. lugubris* pheromone. Each of the pheromones was used in combination with dough, and dough alone was the final treatment (a total of five traps per block). Captured beetles were removed from the traps weekly. Treatments were rerandomized within the blocks and the dough baits were replaced at each trap check.

Septa remained in the field for 2 wk, but replacement was staggered so that those in only one of the blocks were replaced each week. Thus, after the 1st wk, septa of two ages (0–1 wk and 1–2 wk) were always present simultaneously for each pheromone treatment. This allowed degradation of septa over time to be measured without being confounded with changes in beetle flight activity.

Data Collection and Analysis of Trap Catches. Trapped beetles were frozen and shipped to the National Center for Agricultural Utilization Research (NCAUR) at Peoria, IL, for analysis. Beetles were sorted by species and sex for trap catches of up to $\approx 4,000$ insects. For larger trap catches, which occurred only with the *C. mutilatus* pheromone, the whole collection was weighed, and two aliquots of ≈ 200 beetles were taken out, weighed, and counted by sex. Total trap catches and overall sex ratios were calculated from these subsamples. The entire samples were examined, however, for species other than *C. mutilatus*. Characteristics described by Okumura & Savage (1974) and Connell (1991) were used to identify species.

Trap counts were transformed to the $\log(x + 1)$ scale and subjected to analysis of covariance. The model included treatments, weeks, and blocks as main effects and the treatment-by-week interaction. Septum ages for the four types of pheromone were the covariates. Treatment means were compared by *t*-tests (least significant difference, $P < 0.05$) for when the covariates were at their overall means.

Date Samples. At intervals of ≈ 1 mo, samples of between 39 and 131 dates were collected off the ground from under trees in the date garden. These were frozen and subsequently dissected at NCAUR. Numbers of adults for each of the species and numbers of nitidulid larvae were recorded for each date. (Larvae could not be reliably determined to species because of poor condition.) The general condition of each date was also recorded (e.g., extent of deterioration, presence of mold). Date samples were collected weekly during May 1992 to monitor the colonization of dates dropped during the harvest.

Chi-square tests were used to determine whether certain species tended to associate with, or avoid, other species in the sampled dates. For each date sample, a table (2 by 2) was constructed for each possible pair of species; cells contained the numbers of dates in which both species were present, only one was present, only the other was present, and neither was present.

Results

Pheromone Treatments. *C. mutilatus* was the major species caught in pheromone traps (Fig. 2), representing 98.4% of the total nitidulid catch in experiment 1 and 96.7% in experiment 2. This

species responded best to the combination of its own pheromone plus fermenting whole-wheat bread dough, and catches to this treatment were as high as 63,500 in 1 wk in one trap. In experiment 1, the pheromone alone attracted only 3.4% as many *C. mutilatus* as the combination bait and dough attracted only 1.9% as many. The unbaited control caught no *Carpophilus* beetles of any species. In experiment 2, the dough caught 2.9% as many *C. mutilatus* as the combination.

Carpophilus hemipterus and *C. freemani* represented 0.6 and 0.7%, respectively, of the total trap catch in experiment 1 and 1.9 and 0.8% in experiment 2. The *C. hemipterus* pheromone alone caught only 1.3% as many *C. hemipterus* as the combination, and the dough alone, 1.0% in experiment 1. In experiment 2, the dough treatment attracted 0.2% as many *C. hemipterus* as the pheromone-dough combination. The *C. freemani* pheromone worked relatively well by itself in experiment 1, catching 29% as many beetles as the combination with dough. The dough by itself caught only 0.1% as many *C. freemani* as the combination in experiment 1 and 0.05% as many in experiment 2. Cross attraction among these three species was fairly low.

In experiment 1, *C. obsoletus* responded clearly to the pheromones of *C. hemipterus* and *C. lugubris* when combined with dough. For experiment 2, the pheromone of *C. obsoletus* was substituted for that of *C. lugubris* because the pheromone for the former species had just been identified and it was clear that the latter species was not present in the date garden. In experiment 2, *C. obsoletus* responded significantly better to its own pheromone (with dough) than to that of *C. hemipterus*. *C. obsoletus* was a minor species, accounting for only 0.07% and 0.09% of the total trap catch in experiments 1 and 2, respectively. *C. obsoletus* did not respond to dough alone. The data for *C. obsoletus* responding to its own pheromone plus dough and to dough alone were presented earlier (Petroski et al. 1994) but are included here also for completeness.

Carpophilus humeralis, for which a pheromone is not known, nevertheless responded consistently to the pheromone of *C. hemipterus* plus dough. In addition, the pheromones of *C. lugubris* (experiment 1) and *C. obsoletus* (experiment 2) plus dough were attractive. In 1992, when larger populations were present, *C. humeralis* was also trapped by the pheromones of *C. mutilatus* and *C. freemani* plus dough significantly more often than by dough alone. *C. humeralis* represented 0.06% of the total trap catch in experiment 1, but increased to 0.4% in experiment 2. *H. luteolus* responded to all treatments containing dough. There was no evidence of attraction to the pheromones, and those of *C. mutilatus* and *C. hemipterus* even appeared to be somewhat repellent (significantly so in experi-

ment 1). *H. luteolus* accounted for 0.16% and 0.06% of the total trap catch in experiments 1 and 2, respectively.

For all species, both sexes were caught in similar numbers, and no effect of treatment on sex ratio was indicated.

Longevity of Pheromone Baits. From covariance analysis of experiment 1, the *C. mutilatus* pheromone septa were 39% as attractive during their second week in the field as they were during the 1st wk. The value for experiment 2 was 36%. For *C. hemipterus*, the percentages for experiments 1 and 2 were 66% and 54%, respectively. For *C. freemani*, the 2nd-wk pheromone activity was 13% of the 1st wk in experiment 1 and 8.5% in experiment 2. The *C. obsoletus* pheromone, which was tested only in experiment 2, was 96% as active during the 2nd wk as during the 1st wk; this value was not significantly different from 100%. All other percentages listed above were significantly <100% ($P < 0.05$).

Patterns in Time for *C. mutilatus*. *C. mutilatus* was captured in traps primarily during the months of April and May (Fig. 3, top panel); beetles were captured during all other months of the year as well, but numbers were much lower. The graph of total trap catch versus time includes all treatments but reflects primarily the *C. mutilatus* pheromone plus dough (see Fig. 2).

The major food source for *C. mutilatus* in the date garden was dates that had fallen to the ground. The size of this food supply throughout the year is shown diagrammatically in Fig. 3, bottom panel. Dates on the ground slowly decomposed, resulting in a steady decline in available food. However, superimposed on this trend were increases caused by the *June drop* (a natural thinning of the ripening crop in early summer) and to a further abscission of maturing dates caused by fungal or insect infestation. Finally, the late-April harvest increased the food supply because many dates from the bunches were left on the ground. Based on the condition of dissected dates from the first sample in May (intact new dates versus badly decomposed, old dates) the number of dates on the ground more than doubled during the harvest (all dates in the last sample before harvest were badly decomposed). The date harvest was very late at the study site; normally it occurs in early winter.

Adult *C. mutilatus* were found in the fallen dates throughout the year, and during autumn and winter, many dates had five or more individuals (Fig. 3, second panel). The numbers were lowest during summer (July–September). The progressive infestation of the dates dropped during harvest was evident from the more frequent sampling during May. By late May, however, the numbers of adult *C. mutilatus* in the dates decreased toward summer levels.

Nitidulid larvae (assumed to be primarily *C. mutilatus* because of the great abundance of this

species) showed a pattern over time similar to that of the adults (Fig. 3, third panel). Unlike the adults, however, larval numbers were very low during the months of January and February. The numbers of larvae in the dates clearly increased in the weeks following the date harvest.

The fourth and fifth panels of Fig. 3 summarize weather data for the region of the date garden. Daily maximum temperatures frequently exceeded 40°C during the summer and usually recovered to 20°C or higher even in winter. Freezing temperatures were not recorded during the study. The weather was fairly wet, with frequent rains between December 1991 and March 1992. Another storm in early May, shortly after the date harvest, was particularly significant because it coincided with the termination of the spring beetle flight (discussed below).

Trap-Catch Patterns Over Time. The trap catch patterns for all six species are shown in Fig. 4; the pattern for *C. mutilatus* is included again for comparison.

Relationships Among Species in Date Samples. *C. mutilatus* was the most abundant species in the date samples, representing 65% of the adult nitidulids found. Overall, *C. hemipterus*, *C. freemani*, *C. humeralis*, and *H. luteolus* accounted for 8.8, 2.7, 4.9, and 18.3%, respectively, of the sampled nitidulids. No *C. obsoletus* were found. *C. mutilatus* were found in 57% of the sampled dates, and the mean per date was 3.87 (± 4.46 SD, 46 was the maximum). The percentage of occurrence and mean abundance per date (\pm SD, maximum) for *C. hemipterus* were 19% and 0.34 (± 0.93 , 13); for *C. freemani*, 7.8% and 0.11 (± 0.44 , 7); for *C. humeralis*, 11% and 0.19 (± 0.81 , 12); and for *H. luteolus*, 20% and 0.71 (± 3.11 , 42). Nitidulid larvae were found in 60% of the sampled dates, and the mean number per date was 5.99 (± 11.9 SD, the maximum was 116).

The patterns over time for infestation in the sampled dates are shown in Fig. 5 for the five nitidulid species. *C. mutilatus* and the nitidulid larvae were included again, for comparison. As with the pheromone trap catches, the sex ratios of beetles in the date samples were close to 1:1 for all detected species.

Sampled dates commonly contained two or more of the above species, and 4 of the 1,327 dissected dates contained all five. Chi-square analyses indicated that the occurrence of each species in the dates was typically independent of each other species. In a few instances, positive associations were suggested by the statistics, but there was no evidence for one species excluding another from the dates. The few cases of calculated positive association between species may have been artifacts of heterogeneous date samples: some of the dates may have been uninfestable (e.g., too dry from full exposure to the sun), and counting these in the sample may have made it appear that two beetle species occurred

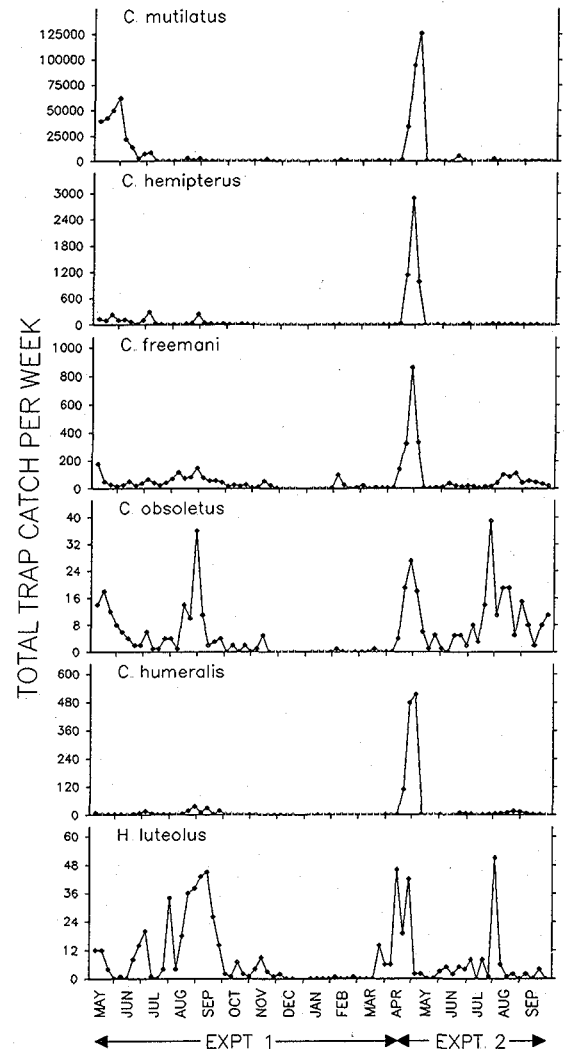


Fig. 4. Comparison of flight activity patterns for six nitidulid species. Each point is a weekly total over all experimental treatments.

together more often than expected by chance in the remaining, infestable dates. There were numerous dates containing both adult beetles and larvae; thus, the presence of one did not preclude the other.

Discussion

Effects of Pheromones. The study further demonstrated the effectiveness of the synthetic pheromones for *C. mutilatus*, *C. hemipterus*, and *C. freemani*. As before (e.g., Bartelt et al. 1990b, 1992a, 1993), the synergistic effect of pheromone and food-type coactractant was dramatic. The pheromone for *C. freemani* was the most effective of the three in the absence of a coactractant (Fig. 2); relatively good performance of this pheromone without a coactractant had been re-

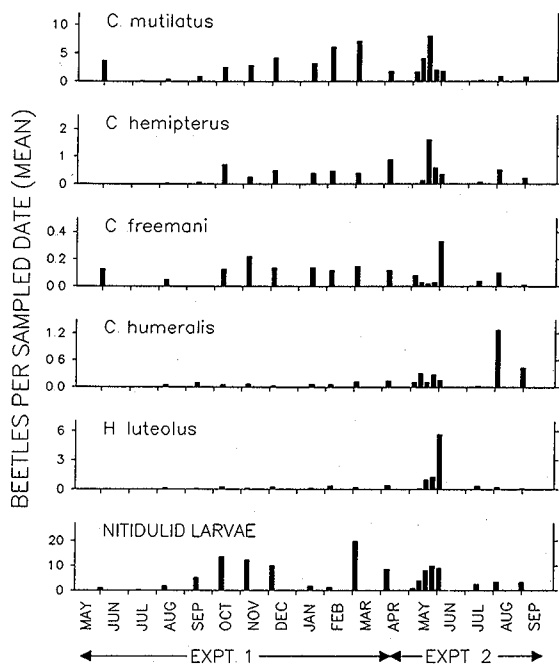


Fig. 5. Comparison of infestation levels of dates on the ground by adults of five nitidulid species and by nitidulid larvae (mostly *C. mutilatus*) over time. Each bar is a mean count per sampled date.

ported previously in a peach orchard (Bartelt et al. 1990b).

There was relatively little cross attraction among these three species. There was essentially no response by *C. hemipterus* or *C. freemani* to the pheromone of the other or to that of *C. mutilatus*. Only for *C. mutilatus* was the response to the pheromones of other two species significant; this was more apparent in experiment 2 than in experiment 1. The trends of synergistic responses and preference for the species' own pheromones were similar to those reported in other parts of the world: Israel (Blumberg et al. 1993), Australia (James et al. 1993), and Ohio (Williams et al., 1993).

The presence of *C. freemani* in the date gardens of California was not documented previously, probably because of its similarity to the more abundant *C. mutilatus* and because it was not recognized as a distinct species until 1956 (Dobson 1956). Nevertheless, the species was easily detected by using the appropriate pheromone.

In experiment 1, *C. obsoletus* responded clearly to the pheromones of *C. hemipterus* and *C. lugubris*. These two pheromones have one minor component in common, compound 4 (Fig. 1), which was later determined to be the pheromone of *C. obsoletus* (Petroski et al. 1994). In experiment 2, the *C. obsoletus* pheromone (100% compound 4) replaced that of *C. lugubris*

(9% compound 4) and became the most attractive treatment for *C. obsoletus*.

Carpophilus humeralis responded significantly to pheromone treatments in both experiments (Fig. 2), but there was no simple explanation for the pattern of responses as there was for *C. obsoletus*. In experiment 1, *C. humeralis* responded about equally to two pheromones composed of tetraenes (3–6, Fig. 1). In experiment 2, when *C. humeralis* was more abundant, it also responded significantly to pheromones composed primarily or entirely of trienes (1, 2, and 7, Fig. 1). The species is, therefore, responsive to at least some of the pheromones of its relatives, but we don't believe the present set of test compounds (Fig. 1) includes the pheromone of *C. humeralis*. This belief is reinforced by the very low trap captures of *C. humeralis* relative to the numbers encountered in the date samples, especially late in 1992. The response of *C. humeralis* to other *Carpophilus* pheromones was noted in earlier reports (Bartelt et al. 1992a, 1994; Blumberg et al. 1993; James et al. 1993).

Haptoncus luteolus was attracted to fermenting dough but not to the synthetic compounds. The lack of response of *H. luteolus* to *Carpophilus* pheromones was reported in other studies (Bartelt et al. 1992a, Blumberg et al. 1993) and is not surprising, given its distant relationship to *Carpophilus*.

Pheromone degradation over time was evident, especially for the *C. freemani* pheromone. This bait lost $\approx 90\%$ of its activity after 1 wk; the major component of the *C. freemani* pheromone (compound 7) is the most volatile of the synthetic compounds. For the *C. obsoletus* bait, activity remained essentially constant during the 2-wk period; bait degradation undoubtedly occurred, but even during the 2nd wk, the baits must have emitted enough pheromone for a maximal response (see Bartelt et al. 1994, Petroski et al. 1994). The pheromones for *C. mutilatus* and *C. hemipterus* showed intermediate decreases. Pheromone formulations can certainly be improved, and additional attention should be paid to this aspect before the pheromones are used in applied beetle management.

Relationships Among Trap Catch, Food Supply, and Weather for *C. mutilatus*. The pheromone traps and the date samples indicated that *C. mutilatus* was the most abundant species in the date garden. Yet it is clear from Fig. 3 that during much of the year, trap catches did not reflect the beetle population present in the date garden. Pheromone traps monitor flight activity, but the beetles are often present in large numbers without flying and are, therefore, not always detected by the traps.

Beetle flights are probably related to dispersal and location of new food resources and, perhaps, to escape from high temperatures or other unfavorable environmental factors. Responsiveness

to the pheromone/bread dough baits during these flights indicates a tendency to aggregate at new food sites, and aggregation would be followed by reproduction. However, flight is not an absolute prerequisite of reproduction, and the date samples during winter provided evidence for this; the presence of nitidulid larvae throughout September to early December suggested that much oviposition had occurred during this period because larval development normally requires only 1–2 wk. Few larvae were found during January and February, but large numbers appeared again in March and April, indicating that successful oviposition occurred in late winter. The numbers of adults in the dates generally increased from September to March, further indicating beetle reproduction during the winter. While some of the adults alive in autumn probably survived into spring, the population in the dates in March was likely to have been a mixture of old and newly emerged beetles. Beetle reproduction during winter in southern California was also suggested by Barnes & Lindgren (1947).

It is not clear what triggered the major beetle flight in April 1992. The beetles probably came from the floor of the date garden rather than through immigration, judging from the numbers in the winter date samples. It is unknown whether the flight included only newly emerged adults or if older individuals also flew. The flight coincided with daily maximum temperatures beginning to exceed 30°C, but the flight peak of April 1991 occurred after maximum temperatures had been steady at ≈30°C for ≈4 wks (see Bartelt et al. 1992a). Furthermore, while high desert temperatures (>45°C) can be lethal rapidly to the beetles (Lindgren & Vincent 1953), the 30°C temperatures of mid-April seem unlikely to drive the beetles from the dates. Some date samples taken when temperatures were >35°C (e.g., October 1991 and mid-May 1992) contained large numbers of *C. mutilatus* adults. Curiously, the 1991 and 1992 spring flights began in the same calendar week, suggesting photoperiod may be important.

Regardless of what triggered the spring flight of *C. mutilatus*, we believe the sudden appearance of an abundant new food supply terminated it abruptly. The spring flight of 1992 declined from its maximum to <1% of the maximum in just 1 wk, whereas the decline in 1991 was very gradual (Fig. 3). The 1992 date harvest occurred during the last week of April, and many dates were dropped. The increased date supply on the ground did not by itself terminate the beetle flight, and numbers of trapped beetles continued to rise into early May (Fig. 3). However, on 5 May, 1.1 cm of rain fell. This rehydrated the fallen dates, making them highly acceptable for beetle colonization, and the flight terminated quickly. The fruit sample taken on 5 May had a mean of 1.8 *C. mutilatus* per date; by 19 May,

this had risen to 8.1 per date, indicating that the flying beetles had colonized the fruit on the ground rather than dispersing to other areas. The appearance of larvae followed closely the colonization by adults (Fig. 3), indicating successful oviposition. By late May, however, the number of adult *C. mutilatus* in the dates again dropped toward typical summer levels. It is unknown what happened to the beetles after departing the dates, whether they died or dispersed. If they dispersed by flight, they were not intercepted by the pheromone traps. A huge population of *C. mutilatus* was present early in 1992, but the beetles were hardly in evidence by the end of the study. Despite the high fecundity of nitidulids, conditions (especially summer temperatures) in the date gardens frequently approach tolerance limits (Lindgren & Vincent 1953); when the limits are exceeded, populations can apparently decrease rapidly.

Comparisons in Trends over Time for Trap Catches. All six species had a peak of flight activity during April of 1992 and all stopped flying after the early May rainstorm, as described above for *C. mutilatus* (Fig. 4). This sort of synchrony was not observed by us previously. We believe the conditions preceding this flight were extremely favorable for nitidulids (abundant food, good moisture, and mild temperatures) and may have helped to trigger the spring flight activity. Except for the single spring peak, the patterns over time were similar to those reported earlier (Bartelt et al., 1992a). *C. freemani*, *C. obsoletus*, *C. humeralis*, and *H. luteolus* tended to fly more readily in summer than *C. mutilatus* or *C. hemipterus*. Few beetles were caught in the traps during winter. Kehat et al. (1983) reported flight patterns over time for *C. mutilatus*, *C. hemipterus*, *C. humeralis*, and *H. luteolus* in Israel to food baits, and they also found *C. mutilatus* to be primarily a spring flier and *C. humeralis* and *H. luteolus* to be captured most often in summer. In their study, *C. hemipterus* tended to fly slightly later in the season than *C. mutilatus*. (In our experience, responses to food baits and pheromone/food baits are very similar in pattern and differ only in magnitude). In the flight data from Israel and from California, great variability was evident in the timing and intensity of flight peaks. This variability must have a complex set of causes, which probably include interactions involving weather and food supply, the great longevity of adult beetles, their potentially short generation times, high fecundity, and strong powers of flight (leading to dispersal or immigration).

Date Samples. The numbers of beetles in individual dates could be very large, and the apparent tolerance among adults of the various species was striking. While the numbers of nitidulid larvae in dates were also large, they seemed well below the egg-laying potential of the adults.

Intra- and interspecific competition among immature nitidulids or between adults and immatures must affect the population sizes and species profiles. The present study provided little information along these lines because the poor condition of sampled larvae prevented determination to species.

The numbers of *C. mutilatus*, *C. hemipterus*, and *C. freemani* adults in the dates were relatively lower during the summer than during the cooler months. Although we did not sample the soil beneath the fallen dates, Barnes & Lindgren (1947) indicated that the soil beneath waste dates was essentially devoid of nitidulids during July. Therefore, the lower numbers of these species in the dates during early summer probably reflected changes in population size rather than a movement to cooler, damp soil beneath the dates.

Carpophilus humeralis and *H. luteolus* were found in greater numbers in the dates late in the study. We believe this reflected a real (if temporary) shift in the nitidulid species profile in response to the previous winter weather and abundant food supply. Apparently, the large April 1992 flight of *C. humeralis* (Fig. 4) did presage the subsequent higher infestations of this species in the dates on the ground. However, the trap catches of *H. luteolus* seemed unrelated to infestation levels in the dates, suggesting the need for a more sensitive monitoring method for this species.

Infestation of the Date Crop in the Trees. Growers are obviously only concerned with the quality of their date crop in the trees. The beetles in the population reservoir on the ground must fly to the fruit in the trees to infest it. Curiously, the flights of *C. mutilatus*, which are primarily in the spring, are poorly synchronized with the presence of infestable fruit in the trees (typically July through November or December). However, the beetle flights in summer and autumn must still involve enough individuals to cause serious crop damage; these later-flying beetles are more successful, more abundant, or both, in years with above-average rainfall. It seems likely that, in normal years, the vast majority of the beetles in the spring flight disperse from date gardens, perhaps infesting other crops but probably experiencing very high mortality. Removal of fallen dates would enhance dispersal from the date garden and would reduce the population reservoir from which the crop-damaging flights would be made. The early literature (e.g., Lindgren et al. 1948, Stickney et al. 1950) made a strong plea for thorough sanitation, and this advice is sound today, if frequently unheeded.

Date crops in the trees are normally protected with applications of pesticides (e.g., malathion dusts and sulfur), and fumigation in the warehouse after harvest (e.g., with methyl bromide) kills remaining pests. As environmental con-

cerns mount, as insects become resistant to insecticides, and as consumers demand less use of pesticides, new strategies of insect control will be necessary. Clearly, the pheromones have a profound effect on beetle behavior at certain times of the year and could be used to advantage in beetle control. We suggest the pheromones (particularly that for *C. mutilatus*) would be especially useful during two time periods: first, during the months of April and May to mass trap much of the local beetle population and second, between July and early winter to protect the ripening fruit from the surviving local beetles and from immigrants. Obviously, sanitation would be a crucial accompanying step. If the other major date pest, the carob moth, can be controlled with its pheromone through the male-confusion technique as suggested by Baker et al. (1991), then growing dates without prophylactic reliance on insecticides could be accomplished.

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