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Effects of Sublethal Exposure to Diazinon on Longevity and Temporal Division of Labor in the Honey Bee (Hymenoptera: Apidae)

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ABSTRACT When worker honey bees, *Apis mellifera* L., were exposed to sublethal pesticide concentrations, the majority of tests revealed no significant differences between control and treatment groups in the ages when tasks were conducted. Longevity was the most consistently affected category studied, with division-of-labor tasks not consistently affected. Single exposures to various concentrations of diazinon reduced longevity in one case and altered task performance in three cases—"clean," "entrance," and "forage." In experiments that exposed workers once, twice, or three times to acetone or a dose of diazinon causing approximately 10% mortality, a number of adverse effects were seen; the majority were in the single-exposure groups. Longevity was reduced in two cases, and certain temporal division-of-labor tasks were adversely affected, especially nectar handling and foraging. Treatment age had a significant effect on the results, with workers treated at emergence being more sensitive to pesticide exposure than older workers (14 of the 20 significant results reported). Stress in the form of pesticide exposure and handling appears to be more harmful to newly emerged bees than any other age group. Longevity and foraging measures hold promise as potential methods of evaluating sublethal pesticide stress on the honey bee worker.

KEY WORDS Insecta, *Apis mellifera*, pesticides, foraging

THE USE OF PESTICIDES for pest control and honey bees (*Aphis mellifera* L.), for crop pollination have become essential components of modern agriculture. Unfortunately, these two practices are not always compatible, as honey bees are susceptible to many of the commonly used chemicals (Johansen 1977, National Research Council of Canada 1981). There has been a great deal of research on pesticide–pollinator interactions; with the majority of this work concentrated on acute mortality studies. However, pesticide-related problems such as disease, poor brood and honey production, queen supersedure, and winter colony loss have led researchers to examine the sublethal effects of pesticides on the honey bee (National Research Council of Canada 1981, Dixon & Fingler 1984, Melksham et al. 1985).

These studies have found a number of adverse effects associated with sublethal pesticide exposure. The chronic feeding of low amounts of such chemicals as parathion, methyl parathion, and methoprene (Barker & Waller 1978) and dimethoate (Waller & Barker 1979, Stoner et al. 1983) deleteriously affected such important colony characteristics as worker population size, honey production, and brood rearing. In addition, studies on the effects of pesticides on individual workers found that methyl parathion impaired the ability to communicate the location of food sources to other workers (Schricker & Stephen 1970), malathion and diazinon reduced worker longevity (Smirle et al. 1984), and permethrin altered foraging patterns (Cox & Wilson 1984).

Many of these effects may be involved in the regulation of an important aspect of honey bee colony functioning—temporal division of labor. Temporal division of labor can be defined as an ontogenetic sequence of activities performed throughout a worker's lifetime. Young workers generally perform hive activities, whereas older workers guard the entrance and forage (Lindauer 1953, Free 1965, Winston 1987). The factors that determine division of labor are only partially understood but seem to involve internal colony conditions such as the extent of brood rearing, food storage, adult population size, and age distribution (Ribbands 1952, Lindauer 1953, Free 1967, Winston et al. 1981), as well as external factors such as forage availability, weather conditions, and worker age (Winston 1987).

The purpose of this research was to examine the effects of sublethal pesticide exposure on temporal division of labor and longevity of worker honey bees. The objectives were threefold: to examine the effects of a single exposure, to examine the effects of repeated exposures, and to determine the importance of treatment age on these results.

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Materials and Methods

The Colonies. Studies were conducted at Simon Fraser University, Burnaby, B.C., from April to August 1983 and 1985. In each year, three plexiglass-sided four-frame observation hives were used. These hives were kept indoors and had plexiglass-covered entrance ramps (22 by 10 by 4 cm) leading from the base of the lowest frame to the outside. Angled plexiglass slabs were glued to the entrance ramp to force incoming marked workers to enter the colonies in a manner that permitted identification. Two of the hives in 1983 were "Dial-a-Bee" hives which had a moveable ring with portholes to allow the removal of older workers without dismantling the hive (Pickard 1980). In 1985, older workers were treated by dismantling the hives, removing workers, and returning the treated workers to the reassembled hives.

The colonies were established with 0.9 kg of worker bees and a queen on two frames of drawn comb and two frames of foundation in 1983, and in 1985 with one frame each of honey, pollen, and brood and one empty frame; enough workers to cover the combs; and a laying queen. In 1985, three hives were found queenless, and each was requeened immediately. Colonies were manipulated only to treat workers at the desired ages, to introduce test workers, and to feed sugar syrup as necessary to prevent starvation.

Each year, workers to be treated were obtained from a single colony (not one of the observation hives) to minimize genetic variation. Combs containing emerging workers were placed overnight in an incubator at 34°C and 50–70% RH. Newly emerged workers were marked on the dorsal surface of the thorax with colored and numbered plastic labels (Opalithplattchen, Chr. Craze, KG, Endersbach, West Germany), and treated immediately or introduced into a test hive and removed and treated at the desired age.

Treatments. Honey bee workers were treated topically on the dorsal surface of their abdomens. A commercial 12.5% emulsifiable concentrate formulation of the organophosphorous insecticide diazinon (P.C.P. Act No. 11437; Later Chemicals Ltd., Rechmond, B.C.) was diluted in acetone to give the required concentrations. An S.M.I. Micro/Petter-A was used to dispense 1 μl of treatment solution to each insect. Workers were held by the hind leg with forceps while the insecticide was applied. A group of workers was treated with 1 μl of acetone as a control in all experiments. Previous work (Smirle et al. 1984, Robinson 1985) showed no significant differences in longevity or performance of division-of-labor tasks between acetone-treated and no-treatment controls. Therefore, only acetone-treated controls were used in this study. The bees were introduced into the test hive by placing the treated workers in a jar which was put over the feeding hole located at the base of the lowest frame opposite the entrance ramp.

Acute toxicity tests (LD_{50}) were conducted to choose the dose range for sublethal exposure for newly emerged bees in 1983 and for all treatments in 1985. Between 40 and 50 workers were treated at each of the four to seven doses in the mortality tests. Newly emerged workers (0 d) were treated and placed in holding cages, whereas the two older age groups (7 and 14 d) in 1985 were marked at emergence, placed into standard colonies, removed when they reached the appropriate ages (grasped by their hind legs with forceps and placed into cages), immobilized with carbon dioxide and treated, and placed in holding cages. Sugar syrup (50%) and water were supplied ad libitum via gravity feeding bottles. Mortality counts were taken at 24 h, and data were analyzed following the World Health Organization protocol for insecticide susceptibility tests (Swaroop 1966). The resulting regression lines were used to calculate doses corresponding to the desired mortality levels (Table 1). In 1983, the appropriate doses for treatment of older workers were the same as published in Smirle et al. (1984).

Single-Exposure Experiments. For experimental purposes, doses causing 5, 10, and 20% mortalities were used in 1983 (Table 1). In 1985, the highest dose was increased to 25% mortality. Single applications were given to bees at 0 and 6 d of age in both years (Table 2). One additional age group (15 d old) was added in 1985 because workers have been shown to begin foraging about this time (Ribbands 1952, Free 1965) and could be exposed to pesticides in the field.

Single- and Repeated-Exposure Experiments. Three repeated-exposure experiments were performed. There were six treatment groups in each study—workers treated either one, two, or three times with the concentration of diazinon causing approximately 10% mortality, and workers treated with 1 μl acetone one, two, or three times as controls (Table 2). In 1983, workers were treated at 0, 4, and 8 d of age, and in 1985, one group was treated at 0, 3, and 6 d of age and a second group at 10, 13, and 16 d of age. Treatments were closer together in 1985 because of differences in observation schedules—every second day in 1983 and every third day in 1985.

Observations. Observations of marked workers began the day after introduction to allow for any initial rejection (usually <5%, this study; Winston & Punnett [1982]). In 1983, hives were observed every second day for 3 h (1.5 h between 0800 and 1200 hours and 1.5 h between 1300 and 1700 hours) and in 1985, every third day for 2 h (between 1000 and 1700 hours). Each day's observation was evenly divided between entrance and within the hive. These continued until workers were 45 d old in single-exposure experiments in 1983, or until fewer than 10 bees remained alive for all other experiments.

During within-hive observations, frames were scanned and marked workers were recorded as per-

Table 1. Doses of diazinon used to treat worker honey bees in sublethal pesticide-effect experiments

Year	Worker age (d)	Dose (μg/bee)[a]			
		LD_5	LD_{10}	LD_{20}	LD_{25}
1983	0	0.050	0.060	0.068	
1983	Adults[b]	0.075	0.100	0.125	
1985	0	0.035	0.040		0.045
1985	7	0.080	0.086		0.095
1985	14	0.085	0.090		0.100

[a] Determined using 24-h acute toxicity tests (LD_{50}'s) and analyzed by the World Health Organization's method for insecticide susceptibility tests (Swaroop 1966, Zar 1984).

[b] Approximate doses from Smirle et al. (1984) based on a random sample of adults of unknown age.

forming one or more of the following tasks. Clean: cleaning cells or removing cell cappings, dead larvae, pupae, or adults from the hive. Brood: feeding or inspecting larvae or eating pollen. Comb: constructing new cells, repairing old cells, or capping cells. Nectar: receiving, depositing, or eating nectar. Groom: cleaning other workers. Fan: fanning the winds. Drone: feeding or grooming drones. Queen: feeding, antennating, or grooming the queen. Dorsoventral abdominal vibrations (DVAV): vibrating the abdomen in a vertical direction directly on the comb or while grasping another worker. Dance: performing the round or waggle communication dance. Forage: pollen packing, carrying pollen or propolis in the corbiculae, or dancing. Inspect: moving through the hive inspecting cells. Rest: standing in hive or grooming self.

During entrance observations, the times of marked workers leaving and returning to the hive were recorded. Flights of <5 min were considered to be orientation flights, whereby young workers leave the hive, fly in circles in the immediate vicinity of the hive, and return to the colony. Those of ≥5 min were recorded as foraging flights, during which time workers collect nectar, pollen, propolis, or water (Winston & Katz 1982). Guarding and fanning by workers at the entrance were recorded and grouped together into the category of "entrance" for analysis purposes.

Data Analyses. Longevity in days (the last day a worker was seen), the total number of tasks performed, and (for each specific task) the first day and duration in days (the number of days between the first and last day a task was performed) were calculated from the observational data. Individual tasks were analyzed only where there were sufficient data (≥3 observations), and "inspect" and "rest" were not analyzed because these are tasks performed throughout a worker's life. However, all tasks were used to calculate the total number of tasks performed. The categories "longevity," "number of tasks," and "forage" were analyzed in all cases (17 cases), the categories "clean," "comb," and "nectar," in most cases (8–15 cases), and the categories "brood," "groom," "fan," "entrance," and "orient" when available (2–7 cases).

Table 2. Summary of single and repeated sublethal diazinon exposure experiments on longevity and temporal division of labor in the honey bee

Experiment	Date	Treatment age (d)[a]	Minimum no. workers per dose or treatment group
1	June, July 1983	0	30
2	May, June 1983	6	20
3	June–Aug. 1983	0, 4, 8	20
4	May–July 1985	0	50
5	May–July 1985	6	50
6	May–July 1985	15	50
7	July–Aug. 1985	0, 3, 6	20
8	July–Aug. 1985	10, 13, 16	20

[a] Treatment age is expressed as the number of days after emergence.

In single-exposure experiments, one-way analysis of variance and the Student-Newman-Keuls multiple comparison test (Zar 1984) were used. Only those workers seen the second observation day after treatment (72 h in 1983 and 96 h in 1985) were used in the analyses to ensure that only subacute results were included.

For repeated-exposure experiments, two statistical tests were done. Initially a comparison of diazinon-treated workers with controls (acetone-treated) for each number of treatments (one, two, or three) in each experiment was done by t test (Zar 1984). Workers seen the second observation day after the specific number of treatments were included in the analyses. This allowed the inclusion of those workers treated once or twice that began a task or died before the subsequent treatment date. Second, all six treatment groups were analyzed by two-way analysis of variance (i.e., control or diazinon and number of exposures) and the Student-Newman-Keuls multiple comparison test (Zar 1984). Only those workers seen the second observation day after the final treatment were included in this analysis.

Results

In this paper, only statistically significant differences are reported, but most tests revealed no significant differences between controls and treatments (150 of 170 comparisons). The nonsignificant results can be found in MacKenzie (1987). In the single-exposure experiments (Experiments 1, 2, 4, 5, and 6), 67 of the 71 comparisons were nonsignificant, while in the repeated-exposure experiments (Experiments 3, 7, and 8), 83 of the 99 comparisons were nonsignificant. When individual categories are considered, only three ("longevity," "nectar," and "forage") had more than one significant result.

Single-Exposure Experiments. Four significant differences were found in the five single-exposure experiments (Fig. 1). Three of these occurred in

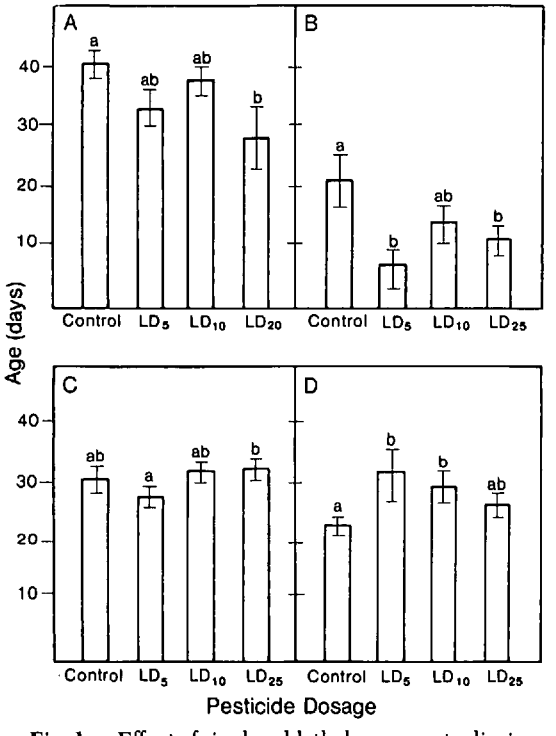

Fig. 1. Effect of single sublethal exposure to diazinon on honey bee workers. (A) Longevity, Experiment 1, 0 d, 1983 (P = 0.05). (B) Clean: first day, Experiment 4, 0 d, 1985 (P = 0.01). (C) Forage: first day, Experiment 4, 0 d, 1985 (P = 0.03). (D) Entrance: first day, Experiment 6, 15 d, 1985 (P = 0.01). Mean ± SE includes workers alive 72 h after treatment in 1983 and 96 h after treatment in 1985. Means followed by the same letter for each category and experiment are not significantly different at the P = 0.05 level (Student-Newman-Keuls multiple comparison test [Zar 1984]).

groups treated at 0 d of age. In Experiment 1 (newly emerged, 1983), longevity was reduced by pesticide treatment (Fig. 1A), and in Experiment 4 (newly emerged, 1985), bees exposed to diazinon began cleaning earlier than controls in two of the three dosages (Fig. 1B), and foraging began earlier in the LD_5 group than the LD_{25} group (Fig. 1C). For workers treated when 15 d old (Experiment 6), entrance activities began later in pesticide-treated bees (Fig. 1D).

Single- and Repeated-Exposure Experiments. When pesticide-treated workers were compared by t test with controls for each number of treatments, some significant differences were found (Table 3). Of these 12 differences, 8 were caused by single pesticide treatment and 2 each by two and three treatments of diazinon.

For workers treated once, seven of the eight significant differences were found in those groups treated at 0 d of age (Experiments 3 and 7). "Longevity" and "number of tasks" were reduced by pesticide treatment in Experiment 7. The initiation of some tasks—"nectar" in Experiment 3 and "brood" and "nectar" in Experiment 7—was reduced by pesticide treatment, whereas duration of "comb" was reduced in Experiment 7 and "nectar" duration increased in Experiment 3 because of pesticide treatment. Only one significant result was seen when older workers (Experiment 8, 10 d of age) were treated once; "clean" began later in pesticide-treated workers.

When workers were treated twice, the duration of "clean" was reduced by pesticide treatment in Experiment 7, and in Experiment 8 (analyzed when the workers were 13 d old), the initiation of "nectar" was delayed by pesticide treatment. When workers were treated three times, "longevity" was reduced in Experiment 8, and the onset of "forage"

Table 3. Comparison of control (acetone) and pesticide (diazinon, LD_{10}) treatments of one, two, and three exposures on longevity and temporal division of labor in the honey bee (Experiments 3, 7, and 8)

No. treatments	Experiment[a]	Category[b]	Mean ± SE[c]		Significance[d]
			Control	Diazinon	
1	3	Nectar—first day	8.1 ± 1.3	4.5 ± 0.8	0.02
		Nectar—duration	9.6 ± 1.7	19.4 ± 2.8	0.01
	7	Longevity	31.6 ± 2.1	22.7 ± 2.0	0.01
		Number of tasks	6.1 ± 0.4	5.0 ± 0.3	0.02
		Brood—first day	6.6 ± 1.3	3.9 ± 0.6	0.05
		Comb—duration	12.5 ± 2.0	5.4 ± 1.8	0.01
		Nectar—first day	15.8 ± 2.2	10.3 ± 1.6	0.05
	8	Clean—first day	17.0 ± 2.0	23.0 ± 0.7	0.02
2	7	Clean—duration	12.5 ± 2.0	5.4 ± 1.8	0.01
	8	Nectar—first day	19.1 ± 1.7	26.0 ± 2.3	0.03
3	3	Forage—first day	16.7 ± 0.5	18.4 ± 0.7	0.04
	8	Longevity	28.6 ± 1.1	15.6 ± 1.1	0.05

[a] Experiment no. from Table 2; treatment schedule as follows: Experiment 3 (1983), 0, 4, and 8 d old; Experiment 7 (1985), 0, 3, and 6 d old; Experiment 8 (1985), 10, 13, and 16 d old.

[b] Analysis performed only where the number of observations ≥3.

[c] For each category and number of treatments, mean includes workers alive 72 h after treatment for Experiment 3 and 96 h after treatment for Experiment 7 and Experiment 8. Longevity expressed in days is the last day a bee was seen. Number of tasks, total number of tasks performed; Task—first day, first day a task was seen performed; Task—duration (expressed in days), time between the first and last performance of a task.

[d] Probabilities from t test (Zar 1984).

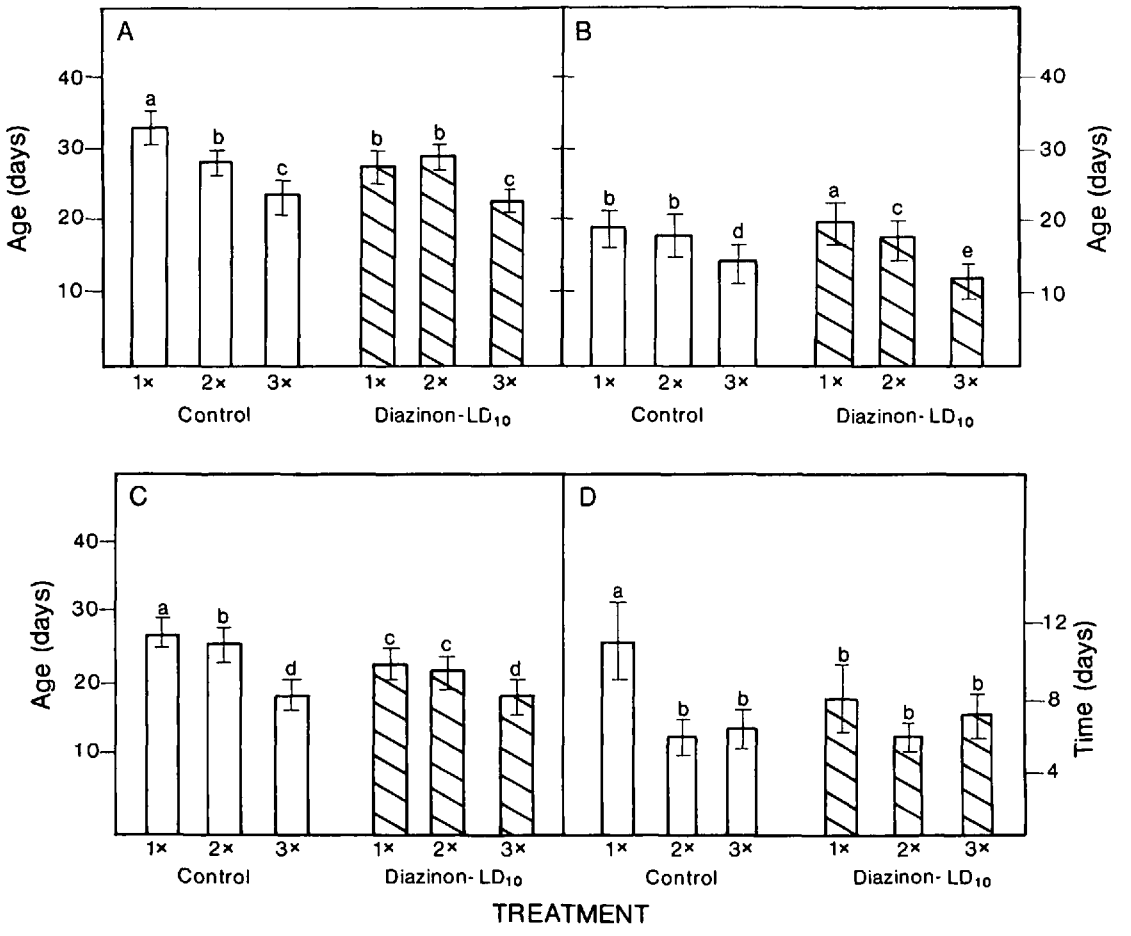

Fig. 2. Effect of one, two, and three exposures to diazinon at a dose causing 10% mortality or to acetone control on the honey bee worker treated at 0, 3, and 6 d of age (Experiment 7, 1985). (A) Longevity ($P = 0.01$). (B) Comb: first day ($P = 0.03$). (C) Forage: first day ($P = 0.01$). (D) Forage: duration ($P = 0.01$). Mean ± SE includes workers alive 96 h after final treatment. Means followed by the same letter for each category are not significantly different at the $P = 0.05$ level (Student-Newman-Keuls multiple comparison test [Zar 1984]).

was delayed by pesticide treatment in Experiment 3 (analyzed when these workers were 8 d old).

Four significant results were found in the analysis of variance tests (Fig. 2). These were all in Experiment 7, 1985, where workers were treated at 0, 3, and 6 d of age. "Longevity" was reduced as a function of the number of treatments in the three control groups, and the control treated once lived longer than any other group (Fig. 2A). In the diazinon treatments, there was a progression to an earlier onset of the task "comb" as the number of treatments increased. Workers treated with diazinon three times began this task the earliest (Fig. 2B). Groups treated once and twice with acetone began the task "forage" the latest, whereas those treated three times with acetone or diazinon began the earliest (Fig. 2C). The control treated once continued foraging the longest (Fig. 2D).

Discussion

The most pronounced effect of sublethal pesticide exposure was the reduction of worker life span; approximately 25% of the comparisons showed this effect. The impact of sublethal pesticide exposure on temporal division of labor was infrequent and inconsistent, with only 10% of comparisons showing significant differences from controls. In those cases where pesticide exposure did influence division of labor, the effects were usually related to foraging, particularly the onset or duration of foraging and the handling of nectar. Further, these effects were not dependent on the dosage level and probably not on the number of treatments, although the age of the worker when exposed was an important factor. However, perhaps most important was that there were so few significant results (only 12% overall), especially concerning the performance of division-of-labor tasks.

Longevity was the most consistently affected trait studied, being reduced by both single and repeated sublethal exposures of various-aged workers. In a similar study, Smirle et al. (1984) found reduced longevity when workers in field colonies were treated at emergence with diazinon, and when workers

held in cages in the laboratory were treated at 2 wk of age with malathion or with diazinon. Significant results occurred in about half of their experiments. Pesticide-related reductions in worker life span have also been shown in field colonies (MacKenzie 1987).

The performance of temporal division-of-labor tasks was not affected as consistently as longevity. The initiation of "nectar" and "forage" showed reductions in some cases and increases in others. Other tasks were only significantly affected once.

The large number of factors influencing temporal division of labor may explain the lack of consistent, if any, impact of pesticides on worker caste ontogeny. Sequencing and timing of tasks and the initiation of new behaviors are only partially understood, although changes in glandular development seem to be followed by ontogenetic changes (Winston 1987). Colony population, worker age distribution, amount of brood rearing, availability of nectar and pollen in the field, and general activity levels in addition to colony history have all been suggested as stimuli for foraging and as influences on temporal division of labor and longevity (Maurizio 1950; Lindauer 1953; Free 1965; Sekiguchi & Sakagami 1966; Winston & Katz 1981, 1982; Winston & Punnett 1982). In addition, environmental conditions also are important and may alter behavior and activity (Free 1965, Sekiguchi & Sakagami 1966, Kolmes 1985). Thus, the regulation of temporal division of labor in the honey bee is complex and flexible.

Foraging may be a useful task to investigate in further work, particularly because foraging and longevity are correlated. The age at first foraging was important in determining longevity of two honey bee races (Winston & Katz 1981, 1982), and increased worker activity (Free & Spencer-Booth 1959, Sekiguchi & Sakagami 1966) and early foraging (Winston & Fergusson 1985) resulted in reduced longevity. In addition, the switch to foraging from hive activities has a distinct demarcation (Kolmes 1985). Hive bees often undertake a number of tasks within a day, and the switch from task to task is, in most cases, hard to delineate (Lindauer 1953, Kolmes 1985). Foraging is normally the last task a worker undertakes, and only in unusual situations such as altered colony age structure will a forager return to hive duties (Lindauer 1953, Free 1965). Thus, it is probably easier to see alterations in foraging performance than in other tasks. For these reasons and because of the difficulty of data collection, the task of "nectar," although affected by sublethal diazinon exposure in this study, is probably not very useful for further assessment of sublethal pesticide exposure.

Newly emerged workers were particularly susceptible to sublethal pesticide exposure. The greatest number of significant results were found in this age group in both single and repeated diazinon exposure experiments. Newly emerged, pesticide-treated workers began tasks earlier than the controls, whereas older workers delayed task performance in those cases where effects were found. This is especially apparent in Table 3 for the task "nectar." Susceptibilities to pesticides such as toxaphene and DDT (Koch 1958–1959), malathion and diazinon (Mayland & Burkhardt 1970, Smirle et al. 1984), and carbaryl and resmethrin (MacKenzie 1987) also are greater in newly emerged workers. The reasons for these differences in sublethal and acute pesticide sensitivity are likely similar, involving differences in enzymes that are concerned with the metabolism of pesticides. Newly emerged workers have lower glutathione S-transferase and polysubstrate monooxygenase (enzymes involved in detoxification) levels and activities than any other age group studied (Smirle & Winston 1988).

One other important factor in this study may have been the response of workers to stress. Honey bees have been shown to be sensitive to stress in many forms, including narcosis (Ribbands 1950, Beckmann 1974, Ebadi et al. 1980), sublethal pesticide exposure (Schricker & Stephen 1970, Cox & Wilson 1984, Smirle et al. 1984), and increased activity (Lindauer 1953, Free & Spencer-Booth 1959, Sekiguchi & Sakagami 1966). Smirle et al. (1984) found newly emerged workers treated with either insecticide or acetone always had shorter life spans than older workers, regardless of the conditions. He believed the stress of handling was more deleterious to newly emerged workers. In our study, newly emerged workers appeared to be more sensitive to stress in the form of both sublethal pesticide exposure and handling.

Neural function has been shown to be adversely affected by stress in the forms of exposure to low temperatures and carbon dioxide, captivity (Beckmann 1974), and parathion (Stephen & Schricker 1970). The production of hormones that regulate temporal division of labor such as the juvenile hormone, particularly during the preforaging phase (Jaycox et al. 1974, Robinson 1985), can be influenced by neural changes. Changes in neural function caused by stress such as pesticide exposure or handling may be more deleterious to newly emerged workers just beginning their nest activity than to older workers.

To our knowledge, this study is the first time the effect of repeated topical applications of insecticides to individual workers has been studied. Although there were some indications of deleterious effects because of repeated exposure in Experiment 7 (Fig. 2), these were confounded by the adverse effects of repeated handling as seen in both control and pesticide-treated groups. Because recurrent pesticide exposure is probably more common than single episodes in agricultural areas, future studies of this kind should be carried out, but a better handling method that reduces the stress on the workers would have to be devised.

This study has shown that sublethal pesticide exposure may have deleterious effects on the work-

er honey bee. Both reduction in longevity and occasional alteration of task performance of temporal division of labor were seen. Colony problems often associated with pesticide spray programs, such as poor overwintering and honey production (National Research Council of Canada 1981, Dixon & Fingler 1984, Melksham et al. 1985), are likely a result of reduced longevity and altered foraging of workers that have received sublethal exposure to chemicals. Future work might investigate the relationships between pesticide effects on individual workers and on the whole colony. In addition, the interaction of the various factors involved in both pesticide susceptibility and temporal division of labor needs to be explored. This type of research will allow us better to evaluate the chemicals used in pest control and their effects on the honey bee, an important crop pollinator.

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