

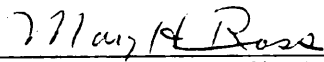
EFFECTS OF AN INSECTICIDE ON GERMAN COCKROACH BEHAVIOR

by

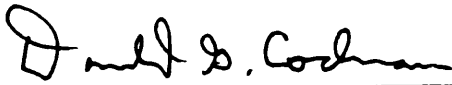
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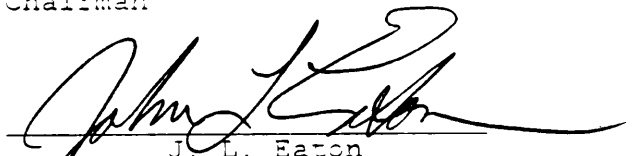
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THE EFFECTS OF AN INSECTICIDE ON GERMAN COCKROACH BEHAVIOR

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ABSTRACT

A quantitative and qualitative study of the behavioral effects of an insecticide on various life stages of the German cockroach, Blattella germanica (L.), was conducted. Comparisons between a susceptible laboratory strain (VPI) and a resistant field strain (BP) were made to examine the relationship between physiological resistance and behavioral resistance.

The effects of vapors from a formulation of 1% propoxur in oil were compared with vapors from a mineral oil control. Vapors from the control had little effect on cockroach behavior. Adult males, adult females, and middle instars were repelled from aquaria containing the insecticide vapors.

Early instars sought shelter in the pores of water sponges. No differences in behavior due to reproductive state were observed as females with oothecae and females without oothecae were equally repelled. Responses by adult males included increased movement, antennal grooming, and tarsal grooming. Electroantennogram studies showed that the vapors of the propoxur formulation were detected by the antennae.

Adults of the susceptible VPI strain responded more strongly to the insecticide vapors, relative to the controls, than did adults of the resistant BP strain. The negative correlation between physiological resistance and behavioral responses was not due to the development of behavioral resistance. Rather the resistance mechanism of the BP strain was probably responsible for inhibiting the behavioral response of that strain.

Responses to the propoxur insecticide may have been compounded by solvents in the formulation, but differences between the two strains were probably due to the propoxur. The oil base had no effect on cockroach behavior.

That wet sponges provided safe harborage for the early instars indicates the importance of even short range dispersal. Also, the use of repellent barriers to exclude cockroaches from sensitive areas may become less effective if physiological resistance in cockroach populations is accom-

panied by decreased avoidance responses. Knowledge of the levels of physiological resistance must be supplemented by an understanding of the behavioral characteristics of insect populations for the successful development of pest control programs.

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INTRODUCTION AND LITERATURE REVIEW

The German cockroach, Blattella germanica (L.), is a world-wide urban pest. The primary means of controlling cockroach infestations has been, and will probably continue to be, the use of insecticides. This dependence on chemical control has resulted in many changes in German cockroach populations. The best known and most studied change is the development of physiological resistance. German cockroaches have developed resistance to many compounds (Grayson 1966; Bennett and Spink 1968; Brown 1969; Cochran 1982). Cross-resistance has also become a major problem (Nelson and Wood 1982; Barson and Renn 1983). Genetic studies indicate that most resistance mechanisms in insects appear to be due to change in only a few loci rather than to multiple genetic mechanisms (Plapp 1984). For instance, the inheritance of DDT resistance in the German cockroach is due to one major locus (Cochran and Ross 1962a). DDT resistance has a Mendelian inheritance with an incompletely susceptible hybrid (Cochran and Ross 1962b). Resistance to pyrethrins (Cochran 1973a) exhibits a mono-factorial autosomal inheritance with partial dominance while malathion resistance is due to autosomal inheritance with complete dominance (Cochran 1973b).

Detectable biological changes have also occurred in populations due to selection pressure from pesticides. Those following laboratory selection of Blattella germanica were generally deleterious. Selection by exposure to DDT in the laboratory caused a significant decrease in egg case length and width (Grayson 1951) and fewer numbers of nymphs per egg case per resistant female and lower adult weights (Grayson 1953). The incubation period of eggs from German cockroaches selected for DDT resistance was shorter, the nymphal development was longer, and gravid female mortality was higher than for a non-selected susceptible strain (Perkins and Grayson 1961). Males and females from two laboratory selected strains resistant to either lindane or DDT and a field strain resistant to chlordane were significantly smaller than the susceptible parent strain (Mahan and Grayson 1956). The chlordane resistant field strain had fewer nymphs per egg case, lower adult weights, and smaller egg cases than a susceptible laboratory strain (Grayson 1954). However, morphological or developmental changes do not always occur. No change in adult weight or the number of nymphs per egg case occurred between unselected German cockroaches and cockroaches selected in the laboratory for resistance against benzene hexachloride (Grayson 1953). No significant difference occurred in the average weight, length of life cycle,

or time for 50% immobilization at different temperatures between a DDT-resistant field strain and susceptible laboratory strain of house flies (March and Lewallen 1950). No correlation was found between resistance and morphometric analysis of 16 characters in five resistant and four susceptible field strains of house flies (Sokal and Hunter 1955).

Another response to insecticides involves behavioral changes. Behavioral responses can occur to either repellents or irritants. Repellents have been described as eliciting a response from a distance while irritants elicit a response after direct contact (Pluthero and Singh 1984). These descriptions do not adequately reflect the true nature of those terms. Repellency can occur from a distance or upon direct contact (Dethier 1956). For example, Dethier and Yost (1952) showed no causal relationship between the vapor pressure of a chemical and its repellency to flies. The definitions as currently used have little operational difference. If insects respond to irritant pesticides before acquiring a lethal dose (Kennedy 1947) then the net result is the same: insects are not killed by the pesticide. The difference between repellency and irritancy is not a matter of the time at which they elicit a response, but rather in the type of response elicited. Insects move away from a stimulus source in response to its repellent nature (Dethier 1947). Repellency

can occur from a distance, in close proximity to, or upon contact with the source, as well as to a lethal, sub-lethal, or non-lethal stimulus (Dethier 1956). Irritancy is merely an exaggerated response to a stimulus. The type of response is not implied. Irritancy can result in increased movement rates, decreased movement rates (motionlessness), decreased landing rates of flying insects, and even repellency - dispersal away from the stimulus. A repellent is by definition an irritant, but an irritant can be, but need not be repellent. For instance, of 4 repellents studied, the most repellent, di-ethyl toluamide (deet), was the least irritating (Khan and Maibach 1972).

Most insects display protective behaviors when exposed to deleterious compounds. The odors of DDT repelled several dipteran species (Hocking and Lindsay 1958) while residues caused increased numbers of flights and decreased landing rates by mosquitoes (Muirhead-Thomson 1960). Contact with repellents disrupted the landing, probing, and feeding aspects of mosquito search behavior (Hocking and Khan 1966). Takeoff, flight, and approach of mosquitoes were inhibited 12 cm away from the source (Khan and Maibach 1972). Miticide-treated leaf surfaces elicited "walk-off" and "spin-down" escape responses in spider mites (Moon et al. 1972; Gemrich et al. 1976; Iftner and Hall 1983). Formosan ter-

mites sealed off galleys leading to insecticide treated areas (Su et al. 1982). German cockroaches responded to both liquid and vapor phases of the repellent MGK R-874, although responses to vapors were strongest (Reddy 1970a, 1970b). Many insecticides are very repellent to the cockroach, as shown by subsequent avoidance responses (Ebeling et al. 1966, 1967; Rust and Reiersen 1977). Insecticide treatments in the field increased inter-apartment movement of cockroaches (Ebeling et al. 1968; Owens and Bennett 1982). Inert components of insecticide formulations were also repellent (Bennett and Wright 1971; Sterling and Howell 1972).

Procedures used to evaluate repellency or irritancy are often quite different and frequently make comparisons between experiments difficult to assess (Schreck 1977). Several factors influence behavioral responses to chemicals (Travis 1950). For example, the species and physiological state of the insect are of certain importance. Compounds repellent to Aedes aegypti were less effective against Anopheles quadrimaculatus (King 1951). Protection time of mosquito repellents did not differ significantly between patches of the same population, but was different between separate populations (Khan et al. 1975). Age also influenced the outcome of tests. Biting rates of A. aegypti on repellent treated subjects increased rapidly for the first 6 days after eclo-

sion, then stabilized (Gouck and Smith 1962). Another study showed a similar pattern but did not show statistical significance, perhaps due to low biting rates (Kashin and Kardatzke 1975). Size and vigor, as influenced by larval density, did not affect adult behavior. However, high adult densities resulted in significantly lower protection times (Khan et al. 1975).

The nature of the chemical also influences the behavioral response. Studies with the sheep blowfly have indicated a positive correlation between toxicity and repellency (Virgona et al. 1976). Additional studies on the housefly showed that a highly toxic substance such as DDT was not necessarily a strong repellent, but the strongest repellents were invariably highly toxic (Virgona et al. 1983). Similarly, although no correlation between DDT susceptibility and repellency occurred in three species of mosquitoes, the most susceptible species, Anopheles albimanus, was also the most irritated (Hecht et al. 1960).

Chemical and physical properties of compounds also influence repellency (Johnson et al. 1967; Piper et al. 1951; Garson and Winnike 1968). Amides have been found to be the largest class of compounds effective as repellents. Of 59 vapors repellent to mosquitoes, 36% were amides (Travis et al. 1949). Cyclic amides in particular, were successful re-

pellents against cockroaches (McGovern et al. 1974a, 1974b) and mosquitoes (Johnson et al. 1967). One of the most effective insect repellents is N,N-diethyl-m-toluamide, more commonly known as deet. Alcohols and phenols also exhibit good repellency. Of the 59 repellent vapors discussed above, 17% were alcohols or phenols (Travis et al. 1949). Aldehydes and ketones were generally ineffective as mosquito repellents (Roadhouse 1953).

Vapor pressure is another characteristic that can affect a chemical's repellency. Although some studies found no correlation between vapor pressure and repellency (Dethier and Yost 1952), others found a positive correlation between repellency and volatility (Johnson et al. 1967). Most likely, vapor pressure only influences the distance from which a compound is active and the duration of its activity. A compound with too low a vapor pressure cannot be detected at a distance by olfactory receptors on the antennae, but at low concentrations, may be detected at short distances by contact chemoreceptors (Bar-Zeev and Schmidt 1959). On the other hand, rapid evaporation from too high a vapor pressure will result in a short half-life of the chemical.

Muirhead-Thompson (1960) suggested that natural, preselected protective responses be called protective avoidance. He reserved the term behavioristic resistance for instances

where continued pesticide exposure selected for changes in the behavioral responses of the population. Because behaviors can be genetically controlled, they can be selected for in the same sense as morphological and physiological traits (Ehrman and Parsons 1981). For instance, exposure of Anophe-line mosquitoes to Risella Oil, DDT, and even dry filter papers increased escape rates after 10 generations of selection (Gerold and Laarman 1964). Insensitivity to diethyl-toluamide (deet) was increased after 12 generations of selection in Drosophila melanogaster. The genes responsible for insensitivity appeared to be partially dominant (Becker 1970).

The relationship between physiological resistance and behavioral avoidance is poorly understood. Selection of avoidance behaviors has been positively correlated with physiological resistance by several investigators. More DDT-resistant than susceptible flies avoided treated surfaces (Silverman and Mer 1952) and displayed a greater irritability (Drobozina et al. 1977; Gaaboub and Dawood 1974). Laboratory selected and wild populations of malathion-resistant flies avoided baits more than non-selected, susceptible strains (Fay et al. 1958; Kilpatrick and Schoof 1958; Schmidt and LaBrecque 1959).

Negative correlations, where resistant strains showed less response than susceptible strains, have also been found. Irritability of DDT-resistant mosquitoes exposed to DDT was less than that of susceptible mosquitoes (DeZulueta 1959; Brown 1964; Busvine 1964). Spotted root maggots selected for DDT-resistance were less irritable than unselected maggots (Hooper and Brown 1965a, 1965b). Development of malathion resistance in the fruit fly, Drosophila melanogaster was correlated with decreased avoidance responses (Pluthero and Threlkeld 1984).

Rust and Reiersen (1978) reported no relationship between diazinon and bendiocarb resistance and repellency in German cockroaches. No correlation between behavioral and physiological responses to malathion was seen in eight field strains of Drosophila melanogaster (Pluthero and Threlkeld 1981). Laboratory selection for increased resistance to malathion did not change avoidance behavior of D. melanogaster (Pluthero et al. 1982). Clearly, little is known or understood about relationships between physiological resistance and behavioral responses of insects. In some cases, mechanisms responsible for physiological resistance are also responsible for behavioral responses. A strain of spotted root maggot with increased susceptibility and irritability to malathion also had a reduced ability to detoxify it (Hooper

and Brown 1965b). Houseflies with Kdr (knockdown) and pen (penetration) forms of resistance were less repelled by pesticides (Virgona et al. 1983).

Historically, little attention has been paid to the behavioral responses of insects to insecticides as they were thought to be inconsequential to control efforts. Decreases in insect populations were assumed to result from mortality, with little regard to the effects of repellency or dispersal from the treated surfaces (Buxton 1945; Gahan et al. 1945; Metcalf et al. 1945). Other investigators realized that reduced population size may not be due to mortality alone, but also a departure from the immediate vicinity (Kennedy 1947). It is now realized that survival of a population can be due to both factors (Georghiou 1972), or even a combination of the two (Gould 1984; Lockwood et al. 1984).

The sensillae by which insects detect noxious compounds are located on several parts of the body. Those of cockroaches are on the cerci, labial and maxillary palps, tarsi, and antennae. Cercal receptors serve primarily as wind detectors (Camhi and Tom 1978, Camhi et al. 1978) and are ineffective for chemical detection (Reddy 1970a, 1970b). Some thick-walled contact chemoreceptors (sensilla chaeticae B) occur on all maxillary and labial palp segments, and thin-walled olfactory chemoreceptors (sensilla trichodea) only

occur on the most distal segment of the palps (Ramaswamy and Gupta 1981a, 1981b). Consequently, labial palps of the German cockroach are ineffective for detection of vapors and detect liquids only weakly (Reddy 1970a, 1970b). Tarsi of the American cockroach contain two types of receptors which appear to function primarily as contact chemoreceptors, sensilla basiconica and sensilla trichodea (Brousse-Gaury 1981). Tarsi of American and German cockroaches also carry olfactory receptors which respond to both liquids and vapors (Reddy 1970a, 1970b). Antennae are the primary sites of chemoreception. They play a major role in mating and aggregation (Ishii 1971; 1972). Antennae of adult German cockroaches have over 5,000 sensilla (Ramaswamy and Gupta 1981a, 1981b). Although most sensilla are non-contact chemoreceptors, many are contact chemoreceptors. Thus, antennae can respond to both liquids and vapors (Reddy 1970a, 1970b). Dethier (1972) has suggested that contact chemoreceptors over the entire body may serve as a "common chemical sense" to detect general, noxious odors.

The objective of the following studies was to examine the behavioral response of the German cockroach to vapors of a propoxur formulation. Differences between age/sex classes were studied with respect to dispersal from a simulated harborage. Other behaviors quantified were the rate of move-

ment, number of antennal cleanings, and number of tarsal cleanings of adult males. An additional objective was to compare the responses of a susceptible laboratory strain and a resistant field strain. This was done to detect any behavioral changes that may have developed in a "field" strain. Of particular interest was whether any changes observed were of a type likely to impart "behavioristic resistance" and thereby increase chances of the insect's survival.

PART I. INSECTICIDE-INDUCED DISPERSAL

INTRODUCTION

Many studies have been conducted on movement patterns of the German cockroach, Blattella germanica (L.). Laboratory studies of the exploratory behavior of the German cockroach have shown an increase in movement due to food and water deprivation (Darchen 1952; Ballard et al. 1984). Darchen (1952) reported that the novelty of the environment increased movement, but Ballard et al. (1984) showed the opposite, environmental familiarity resulted in increased movement. Population density has an inverse effect on movement (Ebeling and Reiersen 1970; Ballard et al. 1984; Bret and Ross 1985).

Several investigators have shown that cockroaches can move between adjacent apartments (Akers and Robinson 1981; Owens and Bennett 1982). However, movement seemed to be greater within apartments than between apartments (Owens and Bennett 1982; Zungoli 1982). A particular concern within the pest control industry is the possibility that insecticide treatments stimulate an increase in movement. Pyrethrin treatments significantly increased interapartment movement (Owens and Bennett 1982; Runstrom and Bennett 1984). Caulking of cracks and crevices between apartments did not pre-

vent movement after a pyrethrins treatment (Farmer and Robinson 1985).

Increased movement results from the repellent nature of many insecticides. German cockroaches responded to both liquid and vapor phases of the repellent MGK R-874, although response to vapors was stronger (Reddy 1970a, 1970b). Many insecticides are highly repellent to cockroaches, as shown in laboratory and field studies (Ebeling et al. 1966, 1967, 1968; Rust and Reiersen 1977). Even the inert components of insecticide formulations can be repellent (Hocking and Lindsay 1958; Bennett and Wright 1971; Sterling and Howell 1972).

Changes in behavioral responses to insecticides have been studied in relation to the development of resistance. An increased avoidance of insecticides has been positively correlated with physiological resistance in several species (Fay et al. 1958; Kilpatrick and Schoof 1958; Schmidt and LaBrecque 1959). Negative correlations have also been found. In these cases, resistant insect strains showed less irritability, movement, and/or dispersal than susceptible strains (DeZulueta 1959; Brown 1964; Busvine 1964; Hooper and Brown 1965a, 1965b; Pluthero and Threlkeld 1984). In other cases, such as in the German cockroach, no relationship was found between insecticide repellency and resistance

(Rust and Reiersen 1978). Pluthero and Threlkeld (1981) reported no correlation between behavioral and physiological responses to malathion in eight wild-type strains of Drosophila melanogaster. Laboratory selection for increased resistance to malathion did not change the avoidance behavior of D. melanogaster (Pluthero et al. 1982).

The objectives of the present study were 1) to examine behavioral responses of German cockroaches to a carbamate insecticide formulation, 2) to compare insecticide-induced dispersal behavior of a susceptible and a resistant strain, 3) to determine if differences exist in the response of different age/sex classes to vapors from an insecticide formulation, and 4) to determine the effect of reproductive state on the response of females to insecticides.

MATERIALS AND METHODS

Strains: Two strains of German cockroaches were used: VPI normal and Bowling Park. The VPI strain has never been exposed to pesticides, and is the standard susceptible strain used in our laboratory and many others throughout the country. The Bowling Park (BP) strain was collected from the Bowling Park Redevelopment and Housing Authority in Norfolk, VA., in 1981. It had been exposed routinely to insecticides.

LC-50 studies were conducted on the two strains to determine the difference in susceptibility to propoxur. Appropriate amounts of technical grade propoxur (2-(1-Methylethoxy)phenol methylcarbamate, Mobay Chemicals, Inc.) were dissolved in 2 ml of trichloro-ethylene (TCE) and 1 ml of Risella Oil (Shell Chemical Co.) The solution was distributed evenly over the surface of a 20 X 20 cm piece of Whatman No. 1 filter paper, and allowed to dry until the TCE evaporated. Ten medium-sized nymphs (3-4th instar) were placed on the paper and enclosed by a glass chimney 15 cm diameter. The walls of the chimney had been greased with petroleum jelly to prevent escape. The number of cockroaches moribund or on their backs was counted after 3 h of exposure to provide comparisons of knockdown. This test was designed to assess resistance, but knockdown data gave an additional comparison. All cockroaches were removed from the filter papers and placed in clean recovery jars. Final mortality counts were taken 48 h from the start of the experiment. Six replicates at each concentration were conducted for each strain. Mean percentage knockdown and mortality were plotted on logarithmic-probability paper and concentrations at which 50% mortality (LC-50) occurred were estimated. Fifty percent knockdown was calculated for the BP strain nymphs.

Chemicals: The experimental chemical used in the dispersal experiment was a formulation of 1.0% propoxur in oil (Octagon Roach Spray, Octagon Process Inc.). Propoxur is one of the more repellent blatticides (Rust and Reiersen 1977). Risella Oil (Shell Oil Co.), a mineral oil, was the control chemical. The composition of the oil base in Octagon Roach Spray is similar to the oil used in Risella Oil (Octagon Process Inc., personal communication). The insecticide formulation may contain other chemicals such as solvents. Further references to the propoxur insecticide are meant to include the propoxur plus any additional solvents.

Dispersal of mixed age groups: Forty-eight experiments were conducted as follow: 12 each of exposures to the propoxur formulation and the control using VPI strain cockroaches and a like number of BP strain cockroaches. The response of mixed age/sex groups was tested. Each replicate consisted of 40 cockroaches, as follows: 10 adult females without egg cases, 10 adult males, 10 mid-instar nymphs (3rd-4th instar), and 10 early instar nymphs (1st instar). No cockroaches were reused.

Two 18.9 liter aquaria were connected by means of Tygon tubing (2.5 cm ID x 3.2 cm. OD) centered 2.5 cm above the floor. The first aquarium was wrapped with brown paper and supplied with dog food pellets, a 1 dram vial of water with

a sponge wick, and 3 folded pieces of 15x4 cm filter paper. The second aquarium had no brown paper, food, water, or filter papers. A thin film of petroleum jelly was spread on the inside of the aquaria (top and bottom) to prevent cockroaches from escaping. Each aquarium was covered with a 20x46 cm glass pane. A dark cover was placed on top of the first aquarium to further decrease the amount of light inside. Six or eight sets of adjoining aquaria were used simultaneously, 3 or 4 for controls and 3 or 4 for the propoxur treatments. Aquaria and tubing were washed thoroughly with soap and water and rinsed with acetone after each experiment.

Cockroaches were placed in the first aquarium in the late afternoon the day before exposure to either the propoxur formulation or the control oil. The tube leading to the second aquarium was plugged. On the following morning, 5 ml of Risella Oil or 1.0% propoxur in oil (Octagon Roach Spray) were placed in a 57 mm aluminum weight pan. A 5x5 cm piece of wire screen was placed over each weight pan to prevent direct contact with the liquid. Cockroaches were exposed only to the vapors. The pan was placed in the first aquarium at the end opposite the tubing and the tubing unplugged. The number of each age/sex class dispersing from the first aquarium was recorded at the following time intervals: 15,

30, 45, and 60 min, 1.5, 2, 3, 6, 12, and 24 hours. The number dispersed was subtracted from the original number, to give the percentage remaining in the first aquarium after each time interval. The log of the percentage remaining was used for plotting the data. Slopes were calculated using a generalized linear regression (SAS 1982). A generalized linear model (GLM) was used on the means of the log percent remaining and the time in order to compare the slopes of the lines. Slopes represent the rate of movement through time from the first aquarium.

At the end of the study (24 h), the effect of vapors from the propoxur formulation or the oil on the distribution of cockroaches that remained in the first aquarium was examined. The number and location of each age/sex class in the first aquarium was recorded for nine replicates of the BP strain. The three locations were the filter papers, the floor of the aquaria, and around the sponges of the water vials.

Dispersal of females of different reproductive states:
An additional experiment was done to determine whether reproductive state affected insecticide-induced dispersal of females. The experiment was like the above, except that only adult females were used. Ten females with and ten females without oothecae were placed in the dark aquarium and

provided with resources. After exposure to the test chemical, the number of non-oothecae and oothecae-bearing females leaving the first aquarium was recorded at the same time intervals as the previous experiment. Eight replicates were conducted for each strain exposed to each chemical. Statistical analysis was the same as before.

RESULTS

Figure 1 shows the results of the toxicity test. The VPI strain showed 100% knockdown at all but the lowest concentration. The concentration causing 50% knockdown was not determined but was less than 1 mg/ml. KC-50 for the BP strain was about 6 mg/ml. At 10 mg/ml, knockdown of the VPI strain nymphs was 100%. This sensitivity contrasts sharply with that of the BP strain whose knockdown was incomplete (90%) even at 500 mg/ml. Forty eight hour mortality data show LC-50 values of about 15 mg/ml for the VPI nymphs and 115 mg/ml for the BP nymphs. This represents a 7-8 fold resistance of the BP strain.

The combined dispersal data from both strains showed that 95% of the cockroaches exposed to control oil remained in the first aquarium after 15 min (Figure 2). This increased to 99% within 45 min as more returned to the first aquarium. In contrast, only 84% remained after 15 min of exposure to

the insecticide vapors and, unlike the controls, cockroaches continued to disperse from the first aquarium, especially during the first 2 hours.

Movement in the first 15 min was apparently due to disturbance as indicated by the initial activity in the controls. Most of the movement in the experiments with insecticide vapors occurred in the first two hours. Approximately 30% of the cockroaches left the first aquarium in the first 2 h, or 15% per hour. Only 10% more left the first aquarium during the remaining 22 h, less than 0.5% per hour. Therefore, analyses were based on the results from 15 min to 2 hours.

Figure 3 shows the dispersal of each strain. Regression lines and slopes showed no significant difference ($p > 0.12$) in the overall rate of movement of BP and VPI strain cockroaches in the control experiments. The rates of movement of BP females, males, middle instars, and early instars did not differ significantly from their VPI counterparts.

A significant difference ($F=19.34$, $p < 0.003$) did occur in the rate of movement of BP and VPI cockroaches leaving the first aquarium after exposure to vapors of the insecticide formulation (Figure 3). Cockroaches of the VPI strain dispersed faster than those of the BP strain, but this was not true for all age/sex classes (Figure 4). Regression lines

and slopes calculated for each age/sex class of both strains showed no significant difference between the rate of movement of BP and VPI early instars ($p > 0.50$) or BP and VPI middle instars ($p > 0.24$). The difference between the two strains was due entirely to the adults. The dispersal response of VPI adult females and males exposed to the insecticide vapors was significantly faster than the BP adult females ($F = 21.48$, $p < 0.002$) and males ($F = 33.49$, $p < 0.001$), respectively.

Very few early instars of either strain dispersed from the first aquarium (Figure 4). The dispersal rate for BP age/sex classes, as represented by the slopes of the lines, was in the following order: adult females ($b = -0.14$), middle instars ($b = -0.16$), and adult males ($b = -0.21$). These slopes were not statistically different ($p > 0.29$). The corresponding rates for the VPI strain were in the order of middle instars ($b = -0.10$), adult females ($b = -0.32$), and adult males ($b = -0.46$). The rate of adult male movement was significantly greater than adult female movement ($F = 9.94$, $p < 0.014$) which in turn was significantly greater than middle instars ($F = 23.99$, $p < 0.002$).

The distribution of BP cockroaches that remained in the first aquarium after 24 h in the propoxur experiment differed from that in the controls (Figure 5). Eighty-six per-

cent of the remaining cockroaches in the controls were on the filter papers, 4% were on or around the sponge wicks, and 10% were on the floor. In aquaria containing propoxur, only 7% of those remaining aggregated on the papers and 15% were on the floor. Most of the cockroaches (78%) were tightly clustered around the sponge wick. This was particularly true of the early instars. Most were inside the pores or underneath the sponges.

Figures 6 and 7 show the dispersal of females with and females without oothecae from VPI and BP females, respectively. Most dispersal occurred within 2 hours. Consequently, statistical analyses for this experiment were performed on data from 15 min to 2 hours. Very little dispersal occurred in the controls. The low rate of dispersal of gravid females in either the VPI strain ($p>0.42$) or the BP strain ($p>0.87$) did not differ significantly. Exposure to vapors of the propoxur formulation caused immediate dispersal. As with the controls, the rate of dispersal of females with and females without oothecae did not differ significantly in the VPI strain ($p>0.38$) or the BP strain ($p>0.24$).

Since no differences were seen between females, data were pooled with respect to reproductive state (Figure 8) and dispersal of the two strains compared. No difference occurred in the rate of dispersal of BP and VPI females in the

controls ($p > 0.18$). However, the rate of dispersal of the VPI strain ($b = -0.55$) is again significantly faster than that of the BP strain ($b = -0.33$) when exposed to vapors of the propoxur formulation ($F = 6.95$, $p < 0.03$). These results agree with those from the mixed age group where females without oothecae were used.

DISCUSSION

Vapors from the formulation of 1% propoxur in oil have a repellent effect on German cockroaches. Vapors drove cockroaches out of aquaria with optimal resources into aquaria without resources. The repellency of the compound was immediate (within 15 min) and persistent for at least 24 hours. This supplements field observations of increased movement between apartments after treatment with pyrethrins (Owens and Bennett 1982).

The similarity in the rate of movement of the two strains in the control experiments indicates that differences in the propoxur experiments were not due to inherent strain differences (laboratory vs field), but to differences in the response to the insecticide formulation. The results shown here are in accordance with other studies that showed a negative correlation between physiological resistance and avoidance behavior (DeZulueta 1959; Brown 1964; Busvine

1964; Hooper and Brown 1965a, 1965b; Pluthero and Threlkeld 1984).

Insect populations may respond in various ways to selection pressure from insecticides (Georghiou 1972; Gould 1984; Lockwood et al. 1984; Pluthero and Singh 1984). Organisms may 1) evolve an increased avoidance response without developing resistance, 2) develop resistance without a behavioral response, or 3) develop increased physiological resistance along with increased avoidance (Lockwood et al. 1984). None of these adequately explains the results of this study. It is improbable that the first means of selection, evolution by the susceptible strain of a more rapid response to the insecticide, was a factor. No selection pressure from insecticides has occurred on the VPI strain since it has never been exposed to insecticides. The second strategy is an inadequate explanation of the results since a definite behavioral response occurred. Finally, the BP strain developed a greater physiological resistance, but not a greater avoidance response, than the VPI strain. Results herein indicate a fourth possibility, i.e. increased physiological resistance with decreased avoidance. A similar situation has occurred in peach-potato aphids. Two organophosphate resistant strains were less responsive to the alarm pheromone (E)- β -farnesene (Dawson et al. 1983). Current models pro-

vide no explanation for selection for decreased behavioral responses (Gould 1984; Lockwood et al. 1984). Although such a selection might seem deleterious to a population, behavioral strategies do not necessarily need to involve escape or avoidance responses. Resistant house flies minimized contact with DDT by remaining still (Decker and Bruce 1951). This has also been observed in resistant strains of German cockroaches exposed to malathion (D.G. Cochran, personal communication). Grooming is another behavior that does not involve escape. House flies can remove 13% of topically applied fenvalerate in this manner (Golenda 1984).

It is possible that the observed behavioral responses are dependent on physiological resistance. Pluthero and Singh (1984) suggested that a decreased response in resistant strains was due to resistance mechanisms involved. Increased susceptibility and irritability to malathion in a laboratory strain of root maggot was associated with a reduced ability to detoxify malathion (Hooper and Brown 1965b). A positive correlation between toxicity and degree of repellency of pesticides occurred in house fly strains with increased knockdown and decreased cuticular penetration as resistance mechanisms (Virgona et al. 1983). Hydroxylation reactions are common detoxification mechanisms for carbamates (Shrivastava et al. 1970). Rapid detoxification by the resis-

tant strain might limit the effect of the carbamate on the nervous system and hence inhibit an avoidance response. Slower absorption of carbamates, another resistance mechanism (Shrivastava et al. 1970), might slow detection by peripheral sense organs and cause a slower rate of dispersal by the resistant strain. Another form of carbamate resistance is acetylcholinesterase insensitivity (Hama and Iwata 1971). Reduced inhibition of acetylcholinesterase might decrease spontaneous synaptic firings, resulting in decreased movement and activity. DDT has been shown to act first on peripheral sense organs (Hodgson and Smyth 1955). Sensory nerves of DDT-resistant house flies were less sensitive than susceptible flies to both toluol vapors and to topically applied DDT (Weiant 1955). If a carbamate could elicit a similar response, then delayed detection by sensory nerves and reaction by motor nerves could conceivably inhibit dispersal.

It is interesting that adults were responsible for the different responses of the two cockroach strains. It is unclear why the nymphs of the BP resistant strain have not undergone a decreased sensitivity as seen in the adults. The answer may be due to differences in the number of sensory receptors of nymphs and adults. Adult American cockroaches have more antennal chemoreceptors than nymphs (Schafer and

Sanchez 1973). The German cockroach is also known to add antennal annuli at each molt, thus adults have more annuli than nymphs (Campbell and Priestly 1970). With an increase in annuli there is a corresponding increase in olfactory receptors (Ramaswamy and Gupta 1981a, 1981b). A greater number of olfactory receptors might be responsible for the significant differences in response times.

The low dispersal rate of early instars from the first aquarium suggested they were unresponsive to the propoxur formulation. However, within the first aquarium, the vapors caused early instars of the BP strain to move from the filter papers to the sponges. The porous sponges provided ample shelter for the early instars. The pores may have served as a refuge from the propoxur. It is possible that water vapor within the pores and around the sponge surface provided a protective "bubble" that excluded vapor particles of the pesticide formulation. In addition, the water of the sponges may have hydrolyzed propoxur vapors in the immediate vicinity. These possibilities have implications for pest control. The use of pesticides in damp basements, under leaky faucets, in janitors closets, or other wet areas could result in less than effective control efforts.

Differences in behavior of females with and without oothecae have been documented in other studies. Increased

densities of females with oothecae increased aggregation of females, middle instars, and early instars (Bret et al. 1983). Increased densities of females without oothecae decreased aggregation responses. Feeding and drinking patterns also differ. Females without oothecae eat and drink more than when they carry oothecae (Cochran 1983). These strategies have adaptive advantages, but escape from a toxicant would be advantageous regardless of reproductive state. The present results showed no difference in dispersal. Any reproductive differences are apparently overridden by the immediate importance of survival.

This study demonstrates that German cockroaches disperse quickly following exposure to vapors of 1% propoxur in oil. Such a response may exacerbate existing control problems if dispersing individuals infest new areas. On the other hand, control programs can take advantage of the repellent nature of pesticide formulations. Repellent pesticides can be used to keep cockroaches away from specific areas. Repellency can also serve to flush cockroaches from within harborages. As long as pesticide-free refugia are not available, this increases the chances of cockroaches coming into contact with pesticides. The possibility also exists of integrating repellent and non-repellent pesticides in a pest management program. A repellent pesticide can be used to flush or drive

cockroaches towards an artificial refuge, an area where a residual non-repellent pesticide has been applied. However, the effective use of repellents in a cockroach pest management program may be diminished if resistant field strains become less sensitive to these chemicals.

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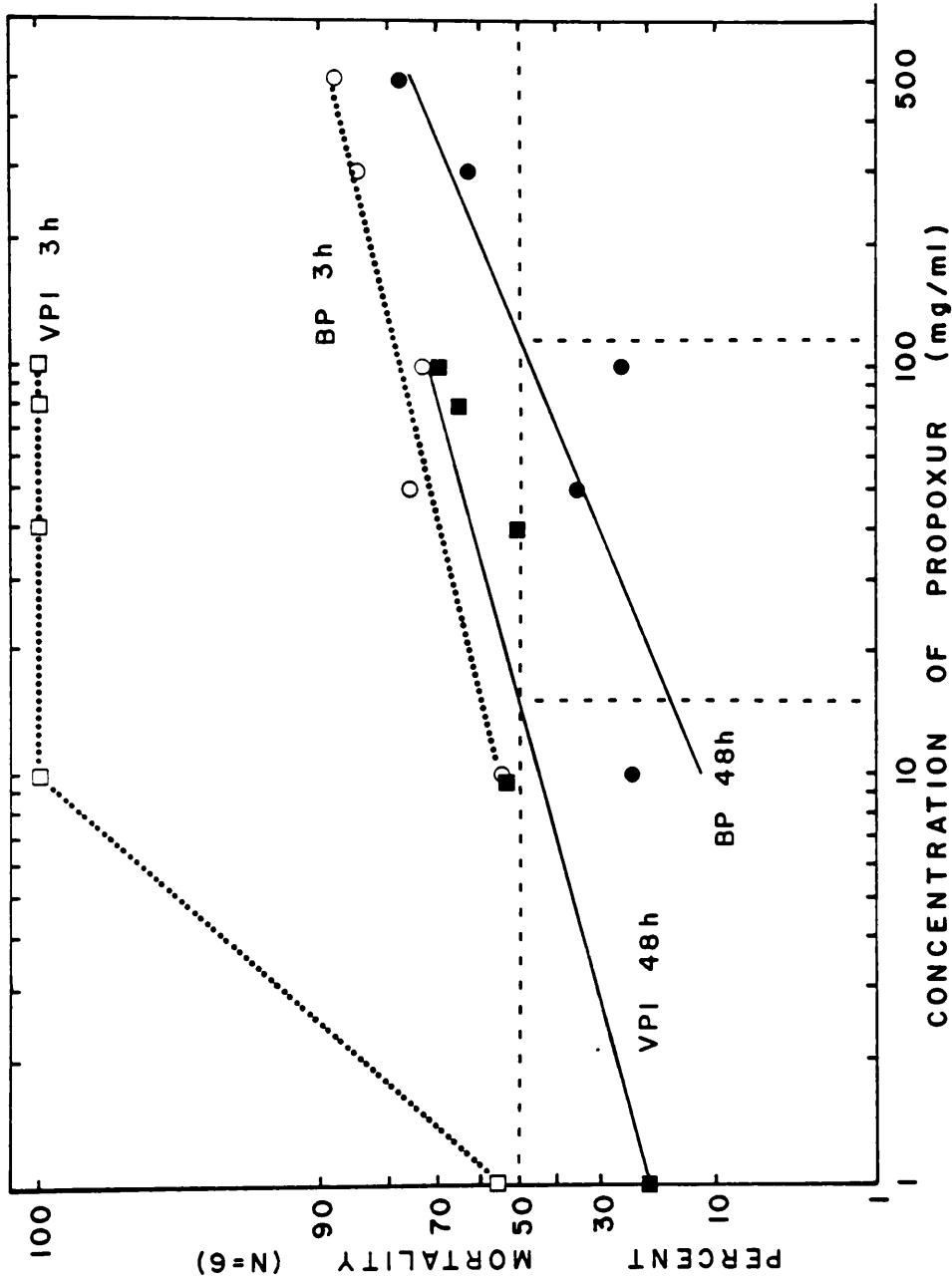


Figure 1 - Probit/log percent mortality (48 h) and knockdown (3 h) of VPI and BP strain males exposed to varying concentrations of technical grade propoxur dissolved in trichloroethylene. (N=6).

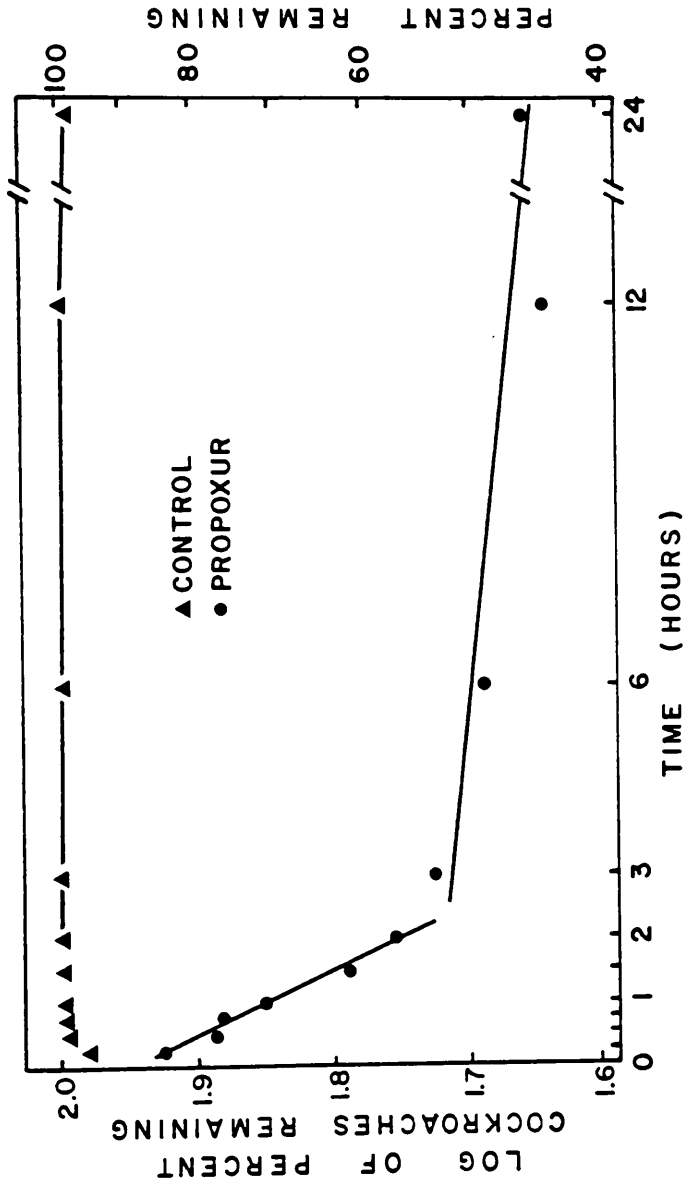


Figure 2 - Percent of German cockroaches remaining in aquaria treated with vapors from a formulation of 1% propoxur in oil or a mineral oil control. (N=96).

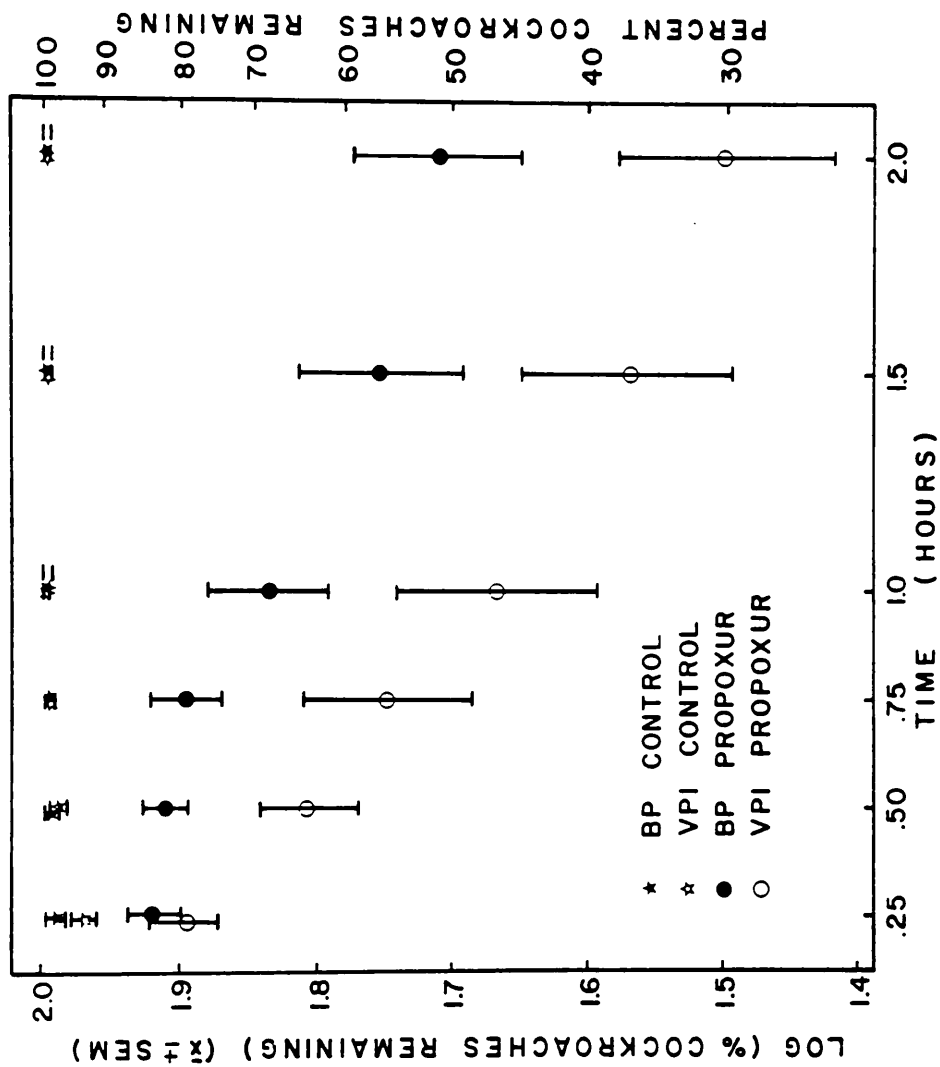


Figure 3 - Percent of German cockroaches of each strain remaining in aquaria treated with a propoxur formulation or a mineral oil control. (N=48). Regression equations as follows: BP control, $Y=1.99 + 0.01X$; VPI control, $Y=1.98 + 0.02X$; BP propoxur formulation, $Y=1.97 - 0.13X$; VPI propoxur formulation, $Y=1.92 - 0.23X$.

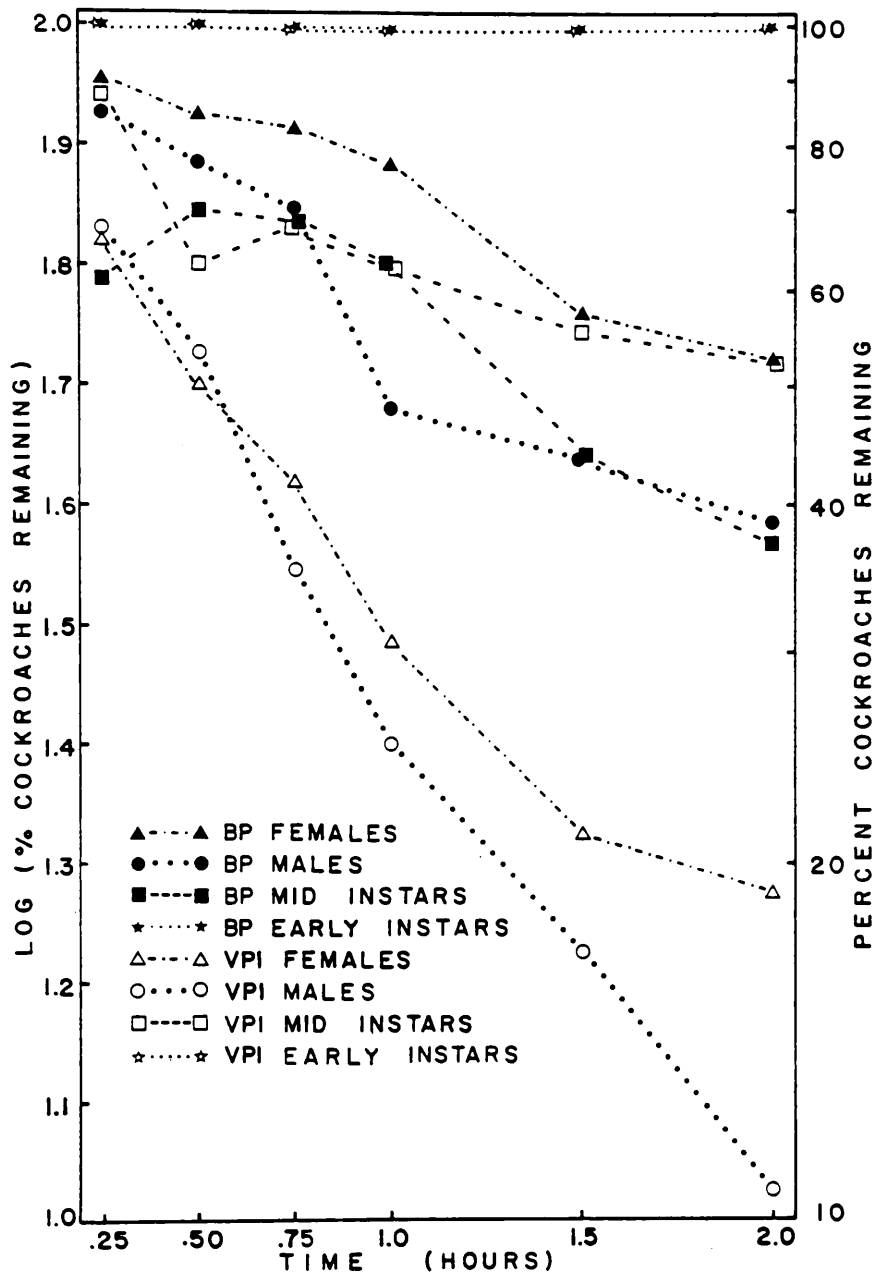


Figure 4 - Percent of German cockroaches of each age/sex class remaining in aquaria treated with a formulation of propoxur in oil. (N=12). Regression equations as follows: BP females, $Y=2.00 - 0.14X$; BP males, $Y=1.97 - 0.21X$; BP middle instars, $Y=1.91 - 0.16X$; BP early instars, $Y=1.99 - 0.01X$; VPI females, $Y=1.86 - 0.32X$; VPI males, $Y=1.92 - 0.46X$; VPI middle instars, $Y=1.91 - 0.10X$; VPI early instars, $Y=2.00 - 0.02X$.

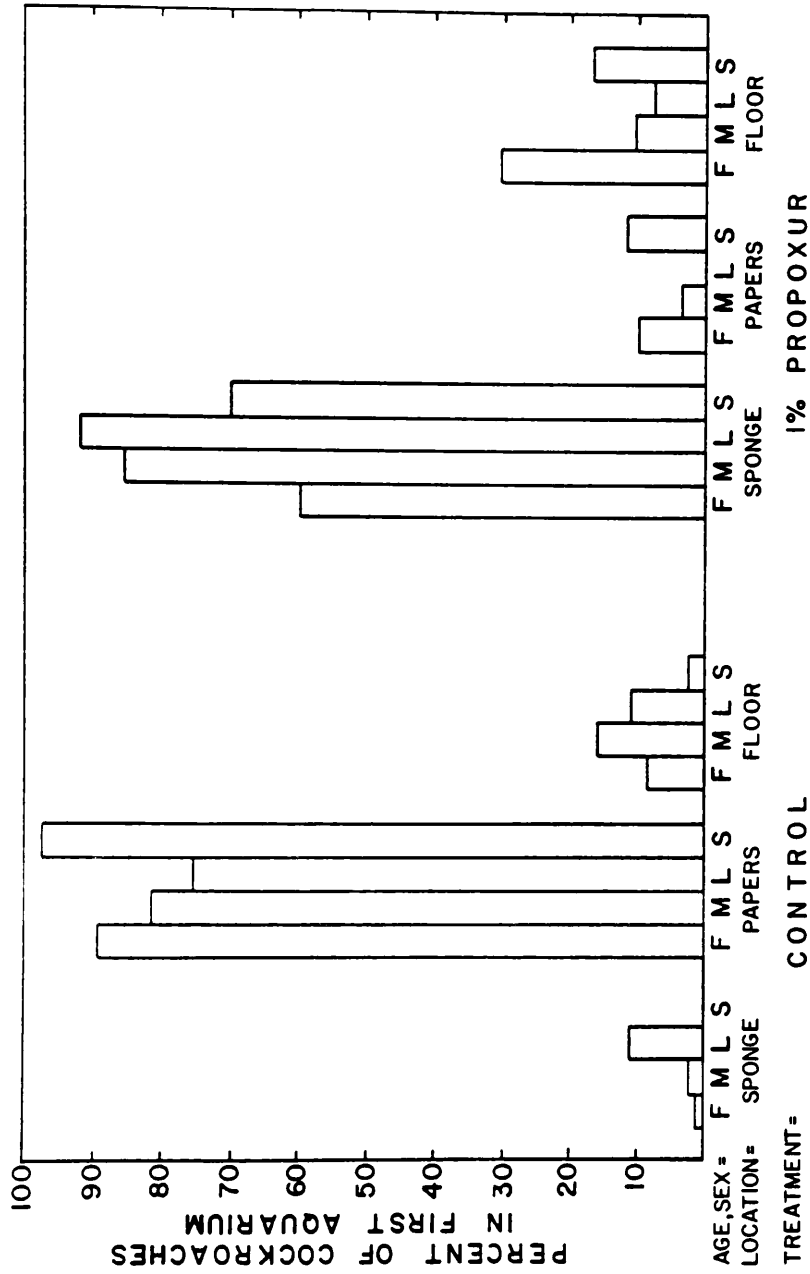


Figure 5 - Distribution of BP resistant strain German cockroaches remaining inside original aquarium 24 h after exposure to vapors of a propoxur formulation or a mineral oil control. (N=9). F=adult females, M=adult males, L=middle instars, S=early instars.

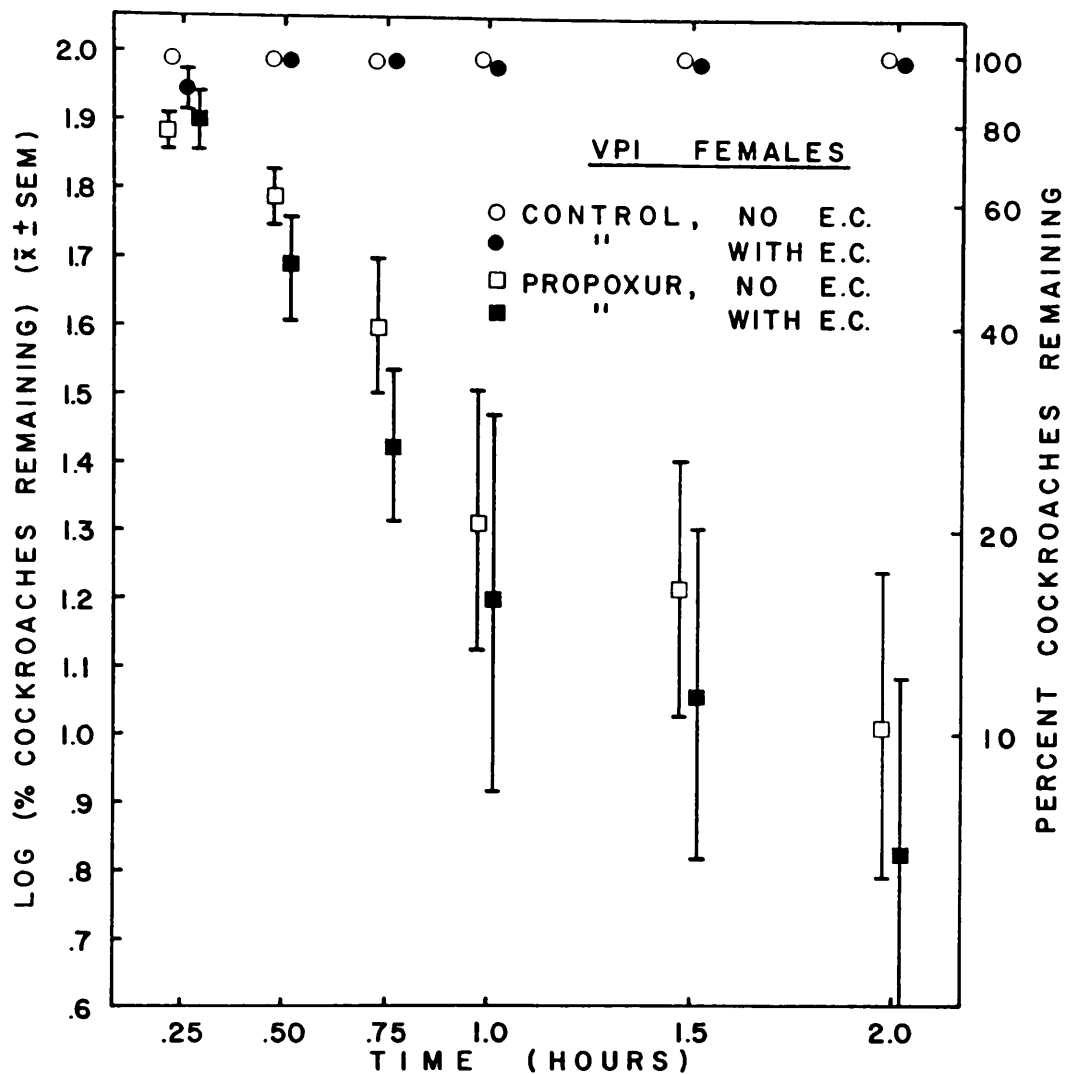


Figure 6 - Percent of VPI strain females with and without oothecae remaining in aquaria exposed to vapors from a propoxur formulation or a mineral oil control. e.c.=egg case (ootheca). (N=8). Regression equations as follows: control females with oothecae, $Y=1.97 + 0.12X$; control females without oothecae, $Y=1.99 + 0.01X$; propoxur exposed females with oothecae, $Y=1.94 - 0.06X$; propoxur exposed females without oothecae, $Y=1.98 - 0.51X$. Standard error of data points without error bars is less than 0.02.

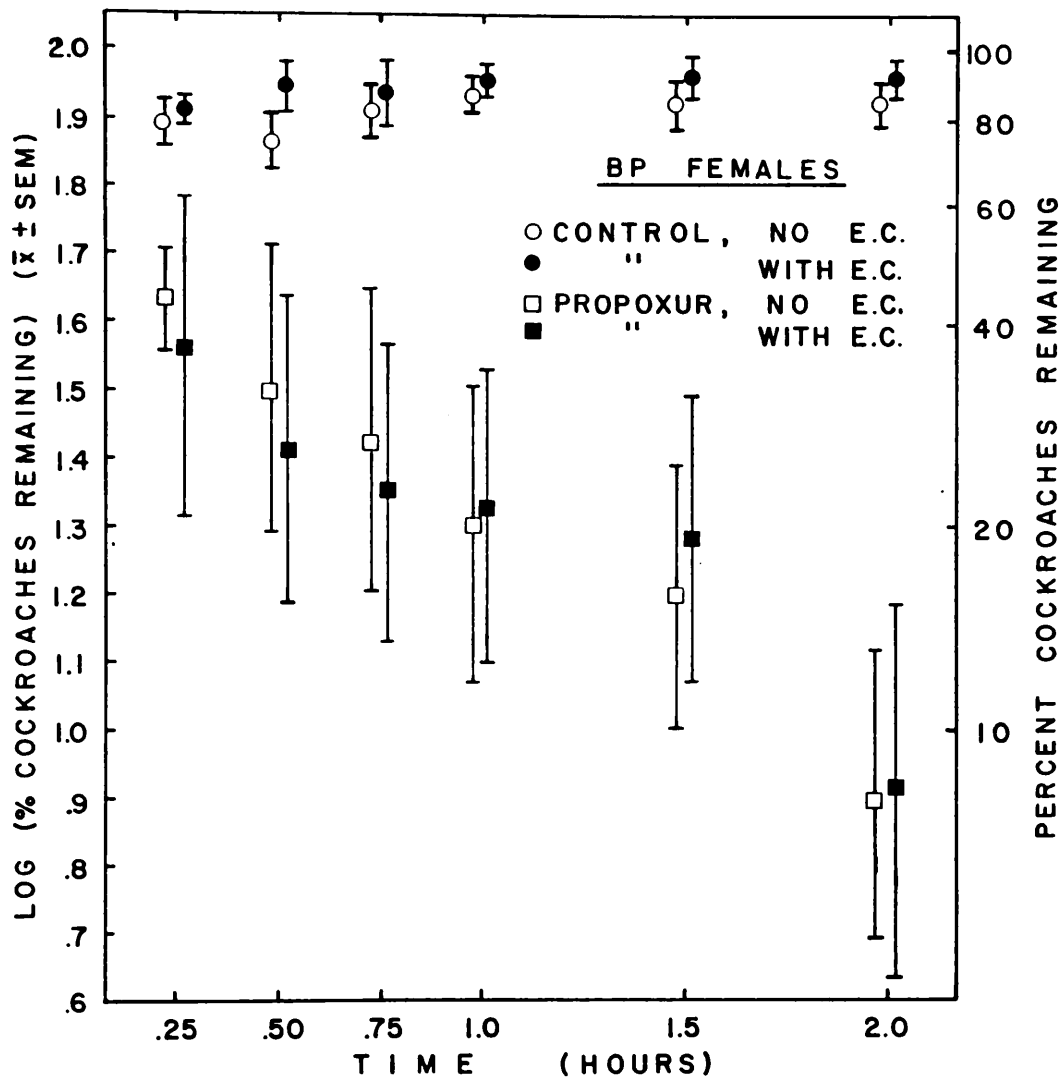


Figure 7 - Percent of BP strain females with and without oothecae remaining in aquaria exposed to vapors from a propoxur formulation or a mineral oil control. e.c.=egg case (ootheca). (N=8). Regression equations as follows: control females with oothecae, $Y=1.92 + 0.02X$; control females without oothecae, $Y=1.88 + 0.03X$; propoxur exposed females with oothecae, $Y=1.61 - 0.31X$; propoxur exposed females without oothecae, $Y=1.72 - 0.39X$.

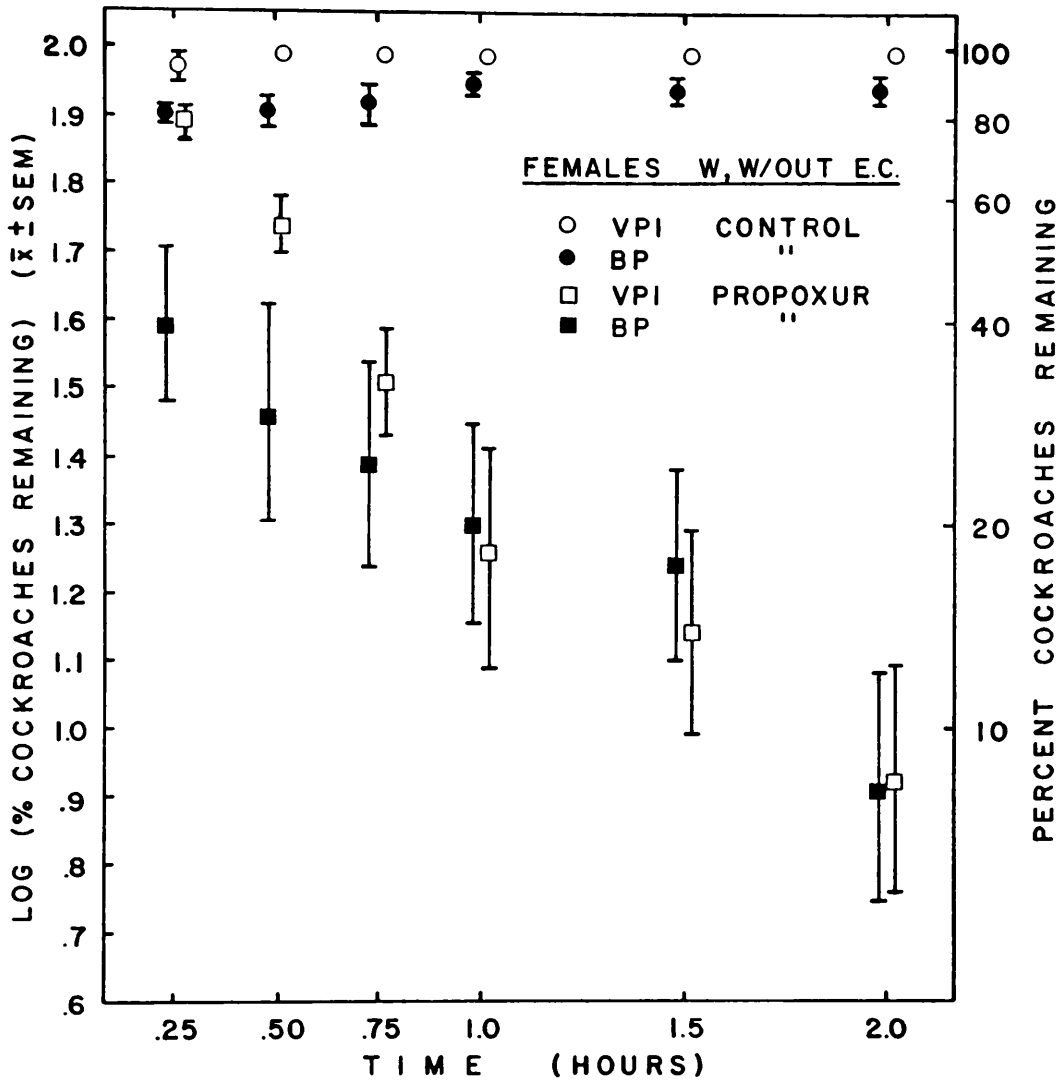


Figure 8 - Percent of German cockroaches with and without oothecae remaining in aquaria exposed to vapors from a propoxur formulation or a mineral oil control. Reproductive states pooled. (N=16). Regression equations as follows: VPI controls, $Y=1.98 + 0.01X$; BP controls, $Y=1.90 + 0.03X$; VPI propoxur, $Y=1.96 - 0.55X$; BP propoxur, $Y=1.67 - 0.35X$. Standard error of data points without error bars is less than 0.02.

PART II. BEHAVIORAL RESPONSES TO VAPORS

INTRODUCTION

Exposure to pesticides can stimulate a variety of behavioral responses in arthropods. Some are attributable to the repellency of the compounds or their formulations. Many compounds are known to be repellent to the German cockroach, Blattella germanica (Ebeling et al. 1966, 1967, 1968; Rust and Reiersen 1977). One of the best known responses to pesticides is avoidance. Spider mites are capable of two distinct avoidance behaviors when subjected to treated surfaces. They may "walk off" the surface or produce fine threads and "spin down" from the surface (Moon et al. 1972; Gemrich et al. 1976; Iftner and Hall 1983). Adult and middle instar German cockroaches dispersed from aquaria immediately following exposure to propoxur vapors (Part I).

Repellency can often hamper control efforts. For example, DDT elicits an excitatory response and increased positive phototaxis in mosquitoes (Kennedy 1947). What was initially interpreted as improved control efforts inside buildings was really aversion to treated surfaces (Muirhead-Thomson, R.C. 1968; Muirhead-Thomson, E.C. 1982). The most toxic compounds used for cockroach control are often less effective in the field than are less toxic, but less repellent, com-

pounds (Ebeling et al. 1968). Repellent pesticides can increase the movement of cockroaches between apartments, making control efforts more difficult (Owens and Bennett 1982).

Avoidance is not the only type of behavioral response that has been reported. One strain of house flies survived DDT treatments by remaining still, thereby limiting contact with the pesticide (Decker and Bruce 1951). This type of response was also noted in malathion resistant cockroaches exposed to malathion (D.G. Cochran, personal communication).

Repellency is seldom active over long distances, but is usually detected upon close or direct contact (Pluthero and Singh 1984). Chemoreceptors on the antennae, tarsi, and to some extent the rest of the body, detect irritant compounds (Dethier 1972), which often leads to immediate grooming behavior (Reingold and Camhi 1977, 1978). Advanced orders of insects use the spines and/or spurs of their tibia to clean the antennae and other legs of particulate matter (Hlavac 1975). House flies removed up to 13% of dorsally applied fenvalerate by scraping it off with their hind legs, scraping the hind legs with the front legs, then scraping the front legs together and depositing the insecticide on the substrate (Golenda 1984). Primitive orders use their mouthparts to clean their antennae and legs (Jander 1966).

In Blattella germanica, dispersal of a propoxur-resistant strain following exposure to vapors of a propoxur formulation was less than that of a susceptible strain (Part I). Differences were limited to the adults; no interstrain differences occurred among the nymphs. The present study is a continuation of an investigation on insecticide-induced behavioral responses of the German cockroach. Excitatory behavior was studied in terms of stimulated movement within an arena. In addition, grooming behavior was measured as a response to the irritant characteristics of a pesticide formulation. Responses of a susceptible strain and a resistant strain were compared. A better understanding of the effects of repellent insecticides on individuals can aid in understanding population responses, and in interpreting control results.

MATERIALS AND METHODS

Adult males were obtained from two strains: VPI and Bowling Park (BP). The VPI strain has been in the laboratory for over forty years and has never been exposed to pesticides. It is widely used in toxicological studies because of its susceptibility. A field strain, BP, was collected from Bowling Park Redevelopment and Housing Authority in Roanoke, VA. LC-50 studies showed the BP strain to be 7-8 times as resistant to propoxur as the VPI strain.

Experiments on movement and grooming were conducted on groups of five adult male German cockroaches of either the VPI or BP strain. New cockroaches were used for each replicate. Cockroaches were confined on a piece of No. 1 Whatman filter paper by a glass arena (15 cm diam X 18 cm high). Experiments were initiated after a minimum of 30 min, or after the cockroaches became quiescent. Cockroaches were then exposed to vapors of either an inert mineral oil (Risella Oil, Shell Chemical Co.) used as a control or a formulation of 1% propoxur in a mineral oil (Octagon Roach Spray, Octagon Process Inc.). The formulation of Octagon Roach Spray is proprietary but probably includes a solvent system. References to the insecticide are meant to include the technical grade propoxur as well as any solvents involved. Five ml of either the formulated propoxur or the oil control were placed in a 57 mm aluminum weight pan and covered with a 5 X 5 cm wire screen. This prevented direct physical contact with the liquid but allowed exposure to the vapors. A glass pane was placed over the glass chimney to contain vapors.

Movement. Two of the cockroaches were marked on the dorsum of the thorax with one or two dots of white Liquid Paper Correction Fluid (Liquid Paper Corp.). Movement of the marked individuals was recorded for 5 min after exposure via a video camera and a video cassette recorder. Tapes of the

experiments were replayed onto a television monitor. Each minute of movement was traced on a piece of acetate laid over the television screen. Lengths of each minute's movement were measured using a cartographer's wheel (map measurer). Experiments were replicated four times providing a total of eight repetitions (2 individuals per each of 4 replicates). This was done for BP control, BP exposed to insecticide, VPI controls, and VPI exposed to insecticide for a total of 48 experiments.

Grooming. The number of antennal and tarsal cleaning motions within 1 min were recorded visually for 30 min. The behavior of each of the 5 cockroaches was observed and recorded together. Results are the total number of grooming responses per 5 individuals. Ten replicates were done for each strain exposed to each chemical.

For both movement and grooming experiments, an analysis of variance with Tukey's studentized range test was used to test for significance between factors (strains or chemicals) (SAS 1982). Rates of grooming were tested using the interaction between numbers of cleaning motions and time in an analysis of variance (SAS 1982).

RESULTS

Exposure to vapors from the propoxur formulation caused an increase in antennal and tarsal cleanings and movement. Increased movement was the most rapid response. Movement peaked within 3 min of the beginning of the test. Antennal grooming was less immediate, with peak activity at 8-10 min. Tarsal grooming did not peak until 24-30 min after exposure to propoxur.

Movement. Figures 1a and 1b show examples of movement by a cockroach during five minutes of exposure to the insecticide or the oil control. Cockroaches in the controls moved around the perimeter and throughout the center of the arena. The average distance moved by an individual in 5 min was 264 cm for pooled data from both strains. Of this, 21% (55 cm) occurred on the wire screen above the Risella Oil. Greater movement occurred by cockroaches exposed to insecticide vapors. The average distance per cockroach per 5 min was 619 cm. Only 4% (27 cm) of this was on the wire screen in the center of the arena.

Figure 2 shows the variability in the distance moved by individuals of the two strains. Only 2 of 16 males in the controls traveled over 500 cm in 5 min. When exposed to propoxur vapors, 13 of 16 males moved over 500 cm. One BP male moved 1006 cm in 5 minutes. Most movement by VPI males

in the control experiment was less than 300 cm whereas most movement by BP males was over 300 cm. Similarly, in the propoxur experiments, most movement by VPI males was less than 600 cm while most movement by BP males was greater than 600 cm.

Figure 3 shows the average distance traveled during the 5 min of the study. Movement of VPI males in the control experiments increased slightly through time. BP control males exhibited increasing activity during the first 3 min, followed by a decrease of similar proportions. Movement by VPI males exposed to propoxur increased during the first 3 min, then gradually decreased. This is in sharp contrast to the response of the BP males. A large amount of activity during the first minute was followed by decreased movement in the remaining 4 min.

The total movement by BP males was significantly greater than VPI males in both the control ($F=14.02$, $p<0.0004$) and propoxur experiments ($F=6.58$, $p<0.0125$). However, the change in response between control and propoxur experiments was greater for the VPI males. VPI males showed a 3.2-fold increase in total movement between control and propoxur while BP males showed only a 2-fold increase.

Grooming. Antennal grooming was initiated by a flagellum being drawn downward ventrally. A prothoracic leg was then

elevated and the front tarsus extended above the antenna, often at the base of the scape or pedicel. As the leg flexed towards the body, the flagellum was pulled towards the mouthparts. Grooming often began at the base of the antenna and continued in a systematic manner towards the tip. Labial and maxillary palps aided the tarsi in maneuvering the antenna between the mandibles. Mandibles moved in a chewing motion over the entire length of the antenna.

Tarsal grooming also involved the mouthparts in a similar pattern to that seen in antennal grooming. No effort was made to quantify grooming to the pro-, meso-, or metathoracic legs. Grooming of all legs was observed, although it was predominant on the prothoracic pair. Cleaning the tarsal segments was most common, but grooming of all leg segments was observed. In such instances, grooming began at the coxae or femur and continued towards the tarsus.

Figure 4 shows the number of antennal cleanings of VPI and BP strain males through time (30 min). In the controls, the number remained low and stable. In contrast, exposure to the propoxur formulation resulted in a sharp increase in antennal cleanings with a peak around 10 min, followed by a slow decline. No differences ($p > 0.99$) occurred in the rate of cleanings (number/minute) between BP and VPI strain cockroaches in the control experiments. However, the total num-

ber of cleaning motions by BP was significantly greater than by VPI strain males ($F=10.58$, $p<0.002$). This response was reversed when cockroaches were exposed to propoxur. The number of antennal cleanings was significantly greater among VPI males ($F=13.16$, $p<0.0003$). This was reflected in a significantly faster rate of cleaning by VPI males ($F=2.26$, $p<0.007$). VPI strain cockroaches exposed to the propoxur formulation had a 9.5-fold increase in the total number of antennal cleanings over that in the controls. In contrast, the BP strain showed a 5.4-fold increase.

The number of tarsal cleanings in controls was low and stable throughout the 30 min exposure periods (Figure 5a). Exposure to propoxur formulation caused a slow but steady increase in the number of tarsal cleanings with a peak at the end of the 30 min (Figure 5b). No significant difference occurred in the rate of tarsal cleanings between the two strains in the controls ($p>0.25$) or following exposure to vapors of the propoxur formulation ($p>0.90$), even though the total number of tarsal cleanings was significantly greater by the BP males ($F=15.441$, $p<0.0001$ and $F=9.79$, $p<0.001$ for control and insecticide experiments respectively). As in the movement study and the antennal grooming study, the VPI males had a greater response to insecticide relative to the control experiments. The number of tarsal

cleanings by VPI strain males was 2.5 times greater in the propoxur experiments than in the controls. A 1.9-fold increase occurred in the BP strain males.

DISCUSSION

Vapors of a formulation of 1% propoxur in oil had a definite effect on the behavior of adult male German cockroaches. Movement was clearly stimulated by the irritancy of the mixture. The increased movement around the perimeter can be seen as an avoidance response, an attempt to move away from the source of irritation in the center of the arena. The decline in movement at the end of the 5 min exposure periods indicates that the cockroach nervous system may have become adapted to the vapors. Adaptation apparently occurred sooner in the BP than VPI males.

The grooming study supported Jander's (1966) observation that mouthparts are used by more primitive orders for grooming. Antennae are the primary receptor sites for volatile odors (Reddy 1970a, 1970b). The increased grooming activity observed in both strains almost certainly served to clean receptor sites on the antennae. The decline after 10 min has three possible explanations. First, the arena quickly became permeated with vapors. Continued grooming in a permeated environment might cease to effectively clean receptor sites.

Secondly, cockroaches may have become adapted to the vapors. Finally, signs of intoxication began to appear in some individuals due to the vapors. Loss of motor coordination was frequently observed towards the end of the 30 min time period. This led to unsuccessful attempts to clean the antennae. In unsuccessful attempts, antennae could not be lowered towards the mouthparts, nor could the front legs reach out and grasp the antennae.

Tarsal grooming was a delayed response. The importance of tarsal grooming was minimal in this study, as much of it seemed to be due to secondary causes. Unsuccessful attempts to groom antennae frequently resulted in tarsal grooming. As antennal grooming decreased, tarsal grooming increased. Increased movement by the cockroaches increased attempts to escape from the arena. Escape was prevented by a thin film of petroleum jelly spread on the inside surface of the glass. Increased tarsal grooming may have been an attempt to clean petroleum jelly off the legs and thus was a secondary response to the increased movement.

Differences in insecticide-induced responses are difficult to interpret where there were differences in the control experiments. Males of the resistant field strain were more active than the susceptible laboratory males. In contrast, no strain difference occurred in dispersal studies of

the strains using two aquaria (Part I). Likewise, no difference in dispersal rates was seen between the VPI strain and a phenotypic mutant crossed to a recently collected field strain (Bret and Ross 1985). In both of these experiments, cockroaches were allowed to acclimate to their surroundings overnight, and were provided with food, water, and vertical resting sites. These resources were not provided in the current experiments and the period of acclimatization was very short. The greater activity with respect to movement and grooming of the resistant strain relative to the susceptible may have been related to the unusual, and perhaps stressful, environment of the glass arena. Nocturnal movement within a large, empty observation chamber was also greater by a field strain than the VPI strain and another laboratory strain (Akers and Robinson 1983). It appears as if absence of resources and shelter may stimulate a faster behavioral response by some field strains than laboratory strains.

In interpreting these data, it is important to note that there was no change in the repertoire of behavioral responses between the VPI and BP strains. Both responded to stimulation in a similar manner. The type of responses, and the sequence of responses were identical: first movement, then antennal grooming, and finally tarsal grooming. To compensate for differences in controls, it is necessary to compare

the degree of changes in response between control and propoxur experiments. When this is done, the VPI males are seen to have a greater relative response to insecticide vapors. This corresponds to the results and interpretation of the previous study (Part I). The results are probably related to differences in physiological resistance. It is unlikely that this is an example of behavioristic resistance since the VPI strain has never been exposed to pesticides. More likely, the resistant adults have either evolved a less intense response or the mechanism of resistance dampened the expression of behavioral traits.

The behavioral responses seen in this study are of definite survival value to the individuals, and hence, to the population as a whole. Increased movement enables dispersal away from the repellent source, increasing chances for survival. Antennal and tarsal cleaning may serve two functions. First, removing toxic compounds from the body surface decreases cuticular exposure to the compound. However, the use of mouthparts may entail a risk of ingestion. This risk may be offset by a second function. Cleaning the surface of the receptors would allow continued detection of the pesticide. This would be particularly important in recognizing vapor gradients so that dispersal would be away from the source, not towards it.

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Figure 1 - Example of movement of male German cockroaches exposed to vapors of a) a mineral oil control and b) a propoxur formulation. (N=16).

Figure 2 - Frequency distribution of distances moved by adult males of a laboratory susceptible strain (VPI) and a field-collected resistant strain (BP) upon exposure to vapors of a 1% propoxur formulation or a mineral oil control.

Figure 3. Average distance traveled for each minute by VPI and BP strain males exposed to vapors of a propoxur formulation or a mineral oil control for 5 minutes. (N=8).

Figure 4. Number of antennal cleaning motions, at two minute intervals, by VPI and BP strain males exposed to propoxur vapors (top) or a control (bottom) for 30 minutes. (N=8).

Figure 5. Number of tarsal cleaning motions, at two minute intervals, by VPI and BP strain males exposed to control vapors for 30 minutes. (N=10).

Figure 6. Number of tarsal cleaning motions, at two minute intervals, by VPI and BP strain males exposed to vapors of a propoxur formulation for 30 minutes. (N=10).

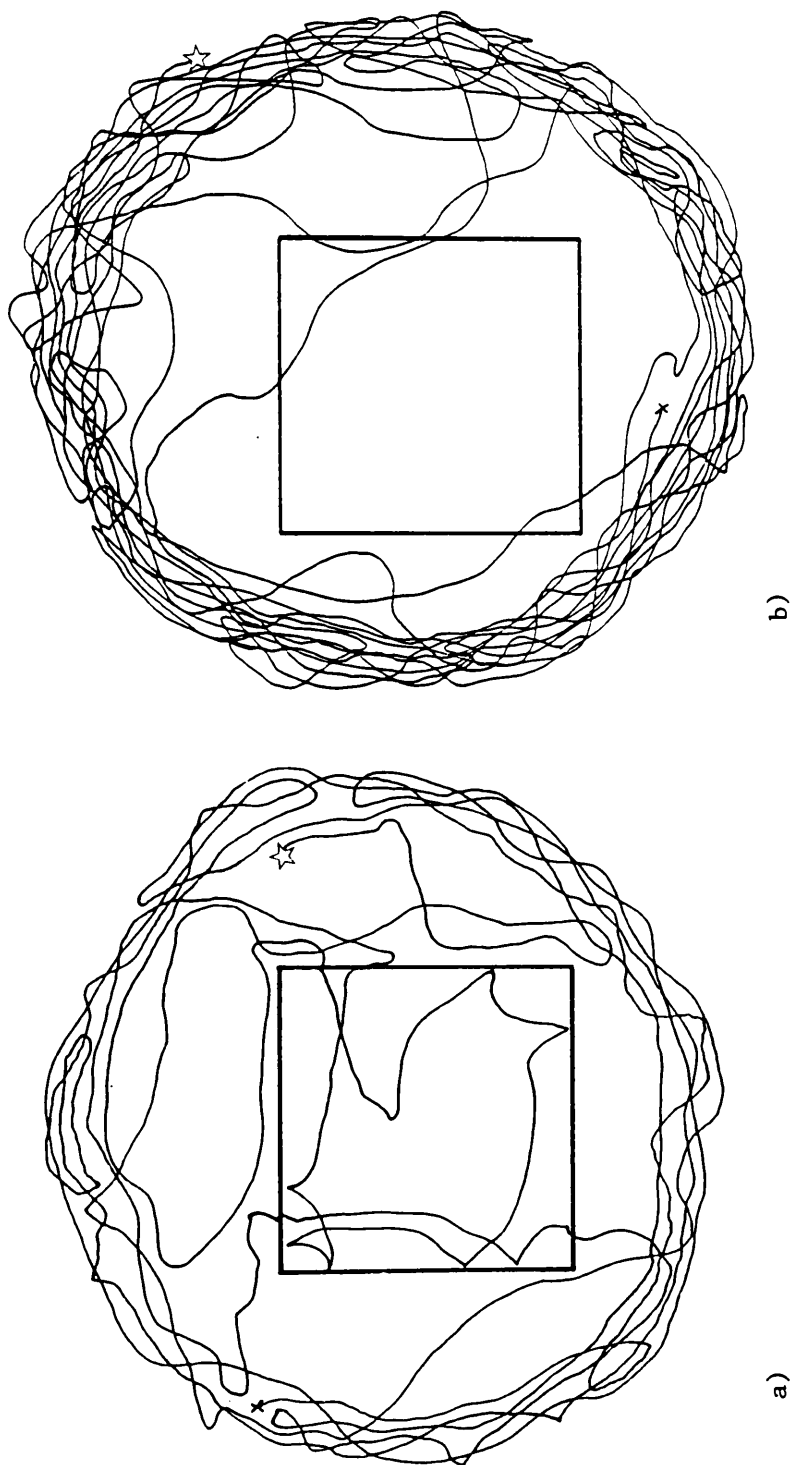


Figure 1 - Example of movement of male German cockroaches exposed to vapors of a) a mineral oil control and b) a formulation of 1% propoxur in oil. a) Avg distance moved throughout arena in 5 min = 264 cm; avg distance moved in center = 55 cm. (N=16). b) Avg distance throughout arena = 619 cm; avg distance in center = 22 cm. (N=16).

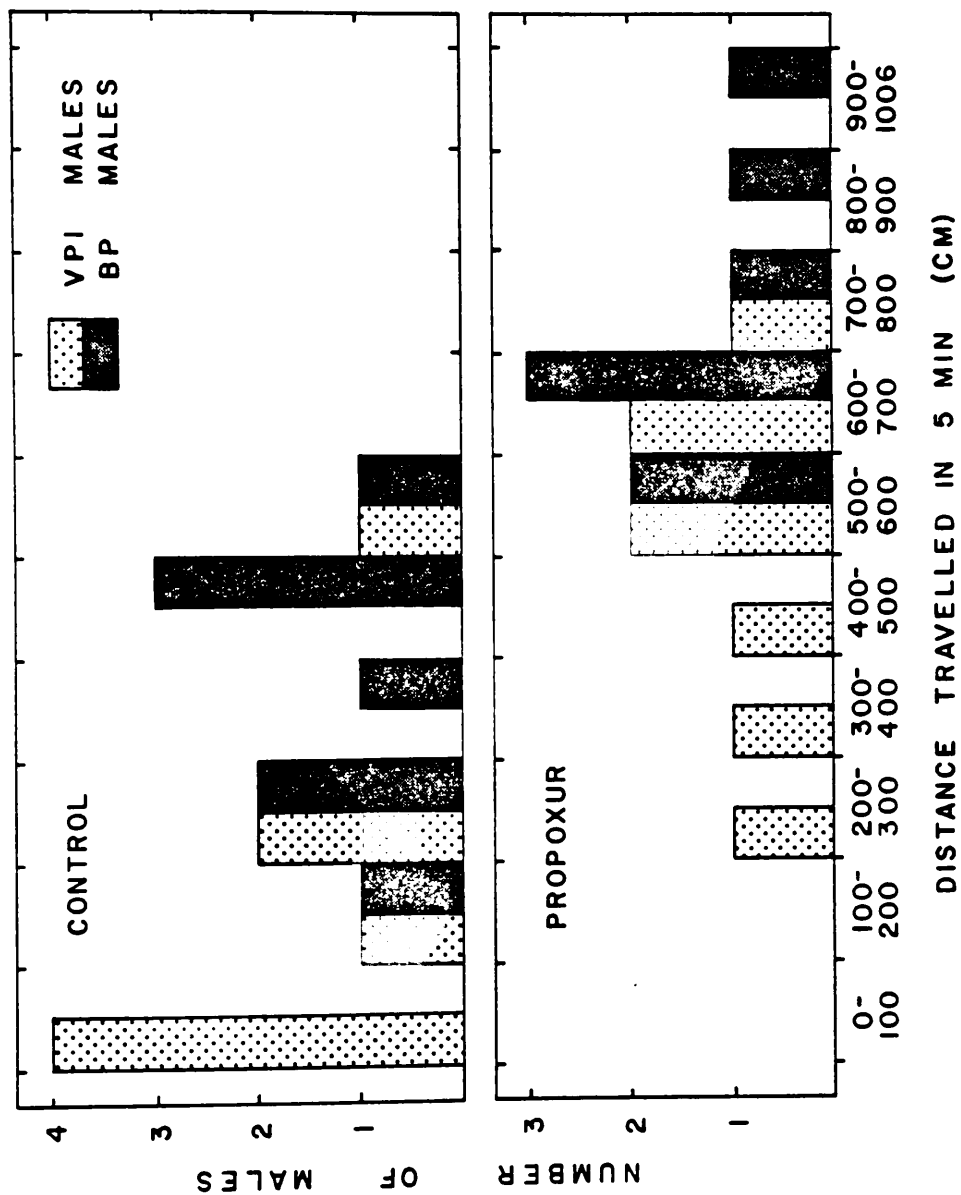


Figure 2 - Frequency distribution of distances moved by adult males of a laboratory susceptible strain (VPI) and a field-collected resistant strain (BP) upon exposure to insecticide vapors of a 1% propoxur formulation or a mineral oil control.

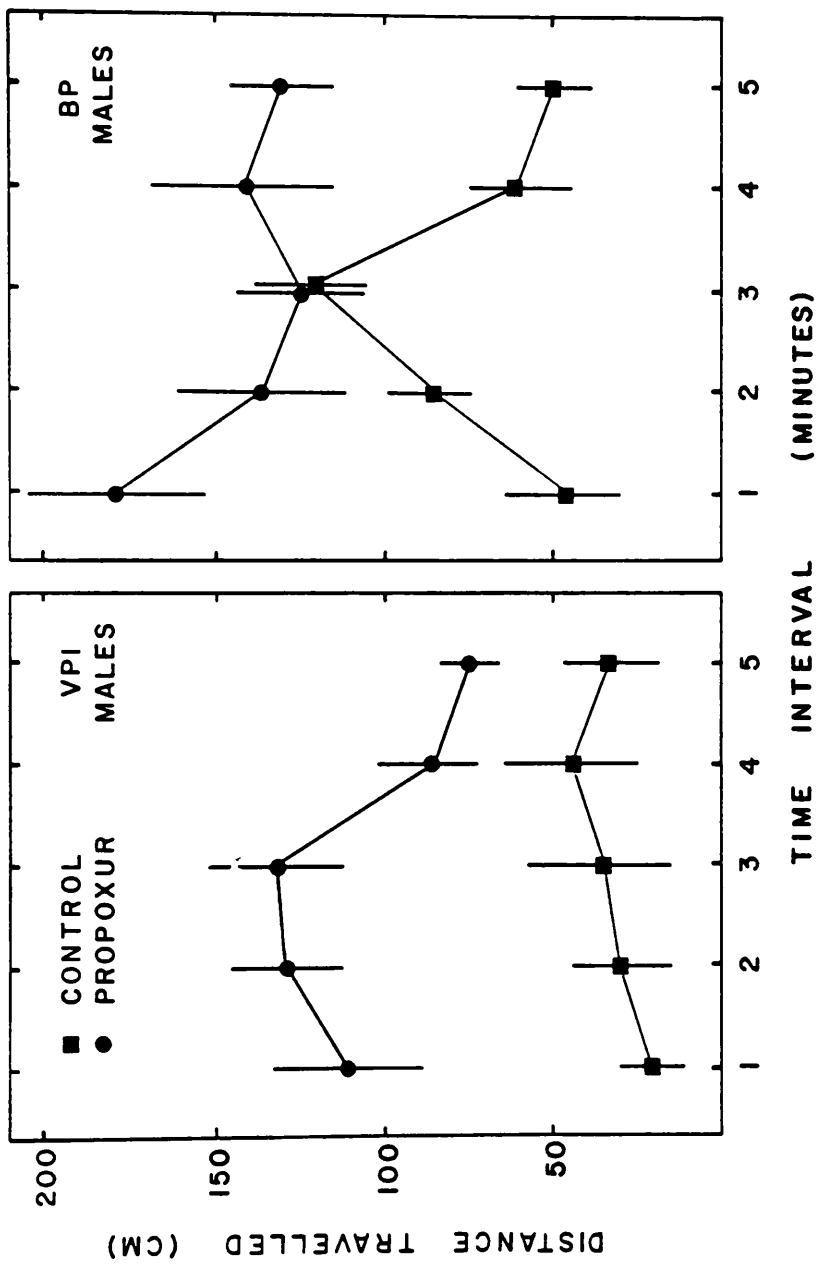


Figure 3 - Average distance travelled for each minute by VPI and BP strain males exposed to vapors of a propoxur formulation or a mineral oil control for 5 minutes. (N=8).

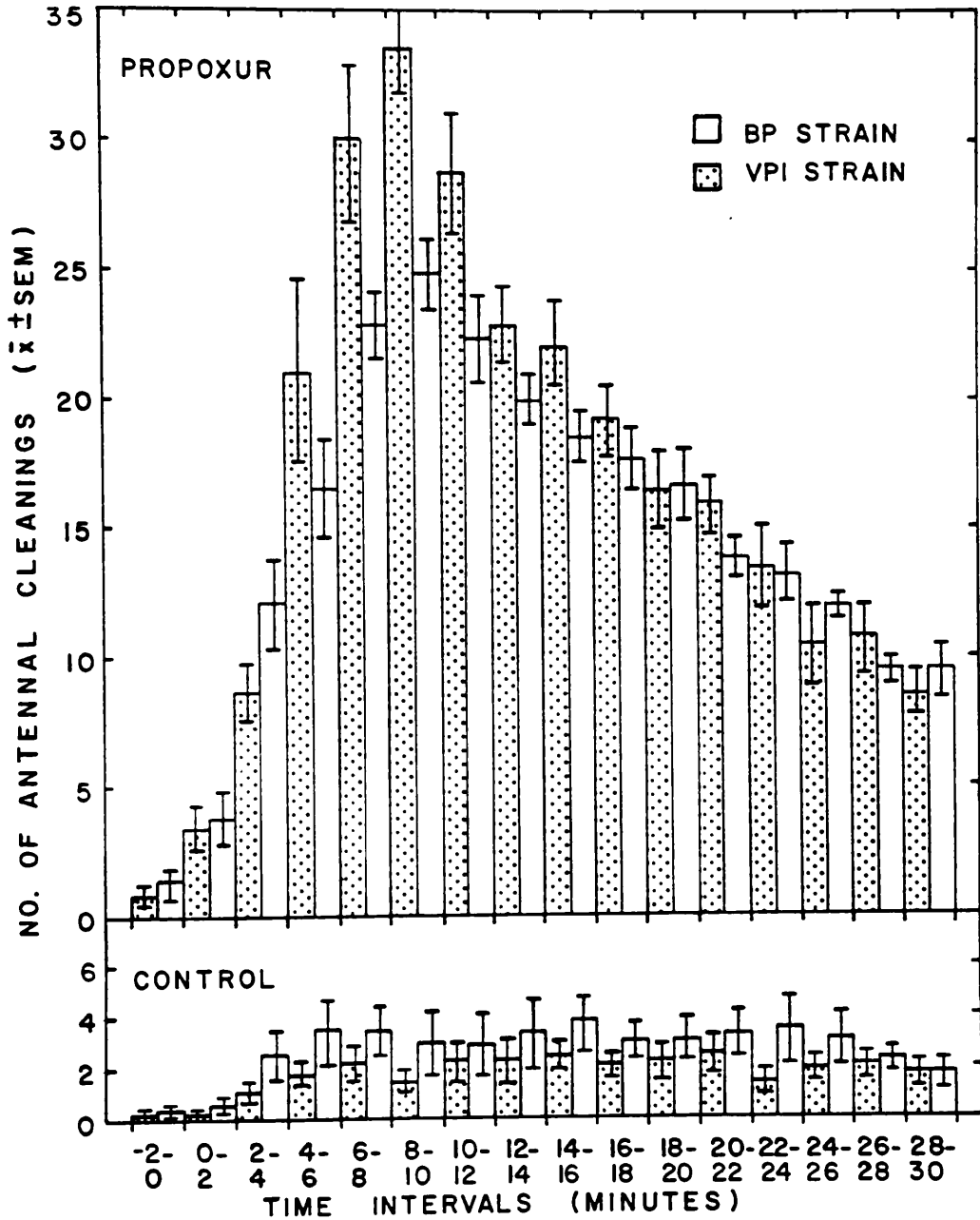


Figure 4 - Number of antennal cleaning motions, at two minute intervals, by VPI and BP strain males exposed to vapors of a propoxur formulation or a mineral oil control for 30 min. (N=10)

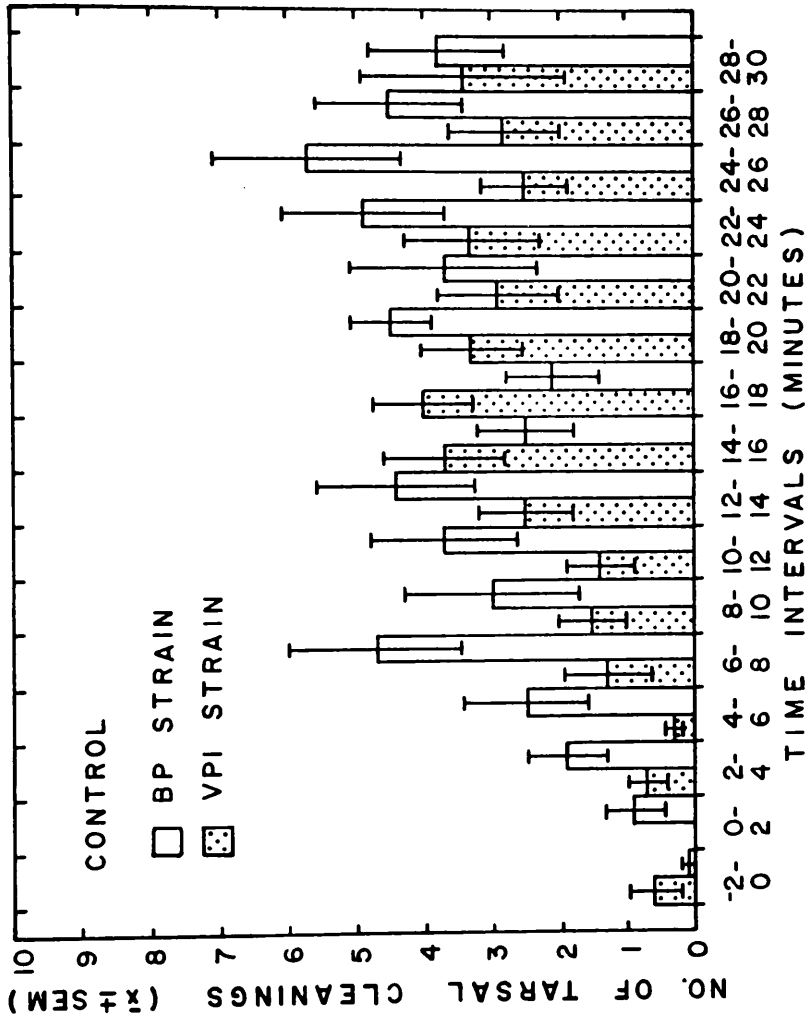


Figure 5 - Number of tarsal cleaning motions, at two minute intervals, by VPI and BP strain males exposed to control vapors for 30 minutes. (N=10).

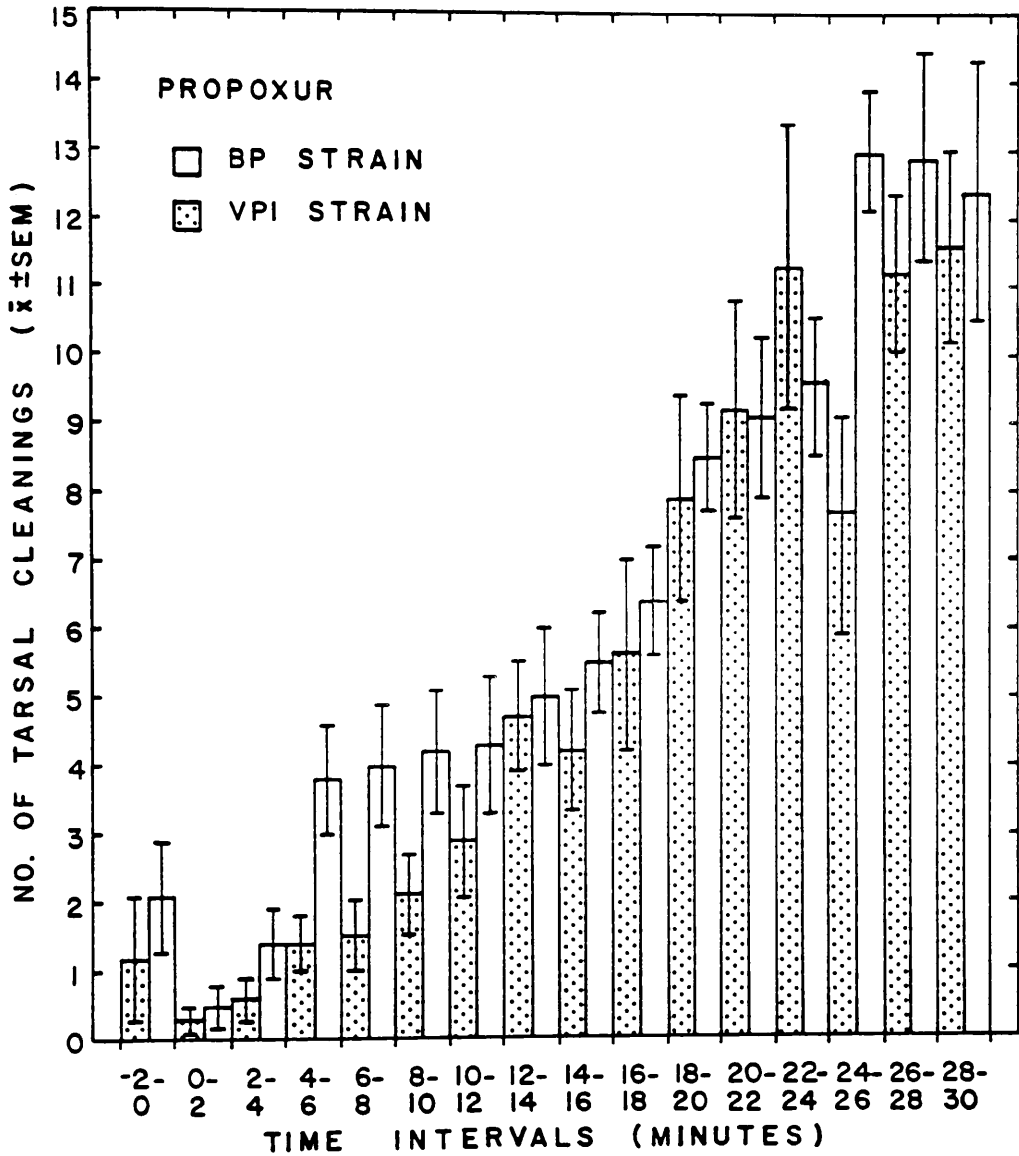


Figure 6 - Number of tarsal cleaning motions, at two minute intervals, by VPI and BP strain males exposed to vapors of a propoxur formulation for 30 minutes. (N=10).

PART III. ELECTROPHYSIOLOGICAL STUDIES

INTRODUCTION

Antennal receptors of many cockroach species have been well studied (Schafer 1971, 1973; Slifer 1968; Roth and Barth 1967). This is particularly true of the American cockroach, Periplaneta americana. The most numerous sensory receptors on the antennae are olfactory and contact chemoreceptors (Schafer and Sanchez 1973; Norris and Chu 1974). These chemoreceptors are more numerous on adult males than females (Schafer and Sanchez 1973; 1976a; Schaller 1978). This sexual dimorphism is regulated by juvenile hormone (Schafer and Sanchez 1976b). Not surprisingly, many of the receptors added at the last ecdysis are sex attractant receptors (Schafer 1977a, 1977b).

Four types of chemoreceptors have been identified on the antennae of the American cockroach in studies using scanning and transmission electron microscopy (Toh 1977, 1981). Chaetotic sensilla B are characterized by a terminal pore and a flexible socket. Consequently they may function as both mechanoreceptors and contact chemoreceptors. G-basiconic sensilla also have a terminal pore but lack a flexible socket, and have a longitudinally grooved surface. They are identified as contact chemoreceptors. P-basiconic sensilla are

thin-walled hairs with numerous wall pores. Trichoid sensilla are slender, pointed hairs with wall pores along their length. Wall pores are characteristic of olfactory chemoreceptors (Altner et al. 1983).

The specific function of sensilla can not be determined by external morphology alone. The function of a sensillum is dependent upon the number and selectivity of its sense cells. For instance, different sense cells of the same sensilla respond to different food odors. The encoding of food odors is the result of patterns of excitation by different sense cells rather than the detection of key odors by a single type of sensilla (Sass 1973, 1976, 1978).

The sensillae of German cockroach antennae have been well described. Chaetica sensilla B (bristle hairs), basiconic sensilla (peg hairs), and trichoid sensilla (thin wall sensilla) are the olfactory and contact chemoreceptors of German cockroaches (Roth and Willis 1952; Ishii 1970, 1971; Ramaswamy and Gupta 1981a). Sexual dimorphism occurs in the adults with males having more chemoreceptors than females (Roth and Willis 1952; Ishii 1972; Ramaswamy and Gupta 1981a, 1981b). As with the American cockroach, this is controlled by juvenile hormone (Ramaswamy and Gupta 1981b). In Blattella germanica, sex discrimination, and in turn courtship behavior, is achieved by means of a contact sex

pheromone produced by the female (Nishida et al. 1975, 1976; Burgstahler 1975, 1977). It differs from the sex pheromone of the American cockroach since the latter pheromone is volatile and can be detected by antennal receptors from a distance (Bell et al. 1984). German cockroach antennae are also essential in detecting the aggregation pheromone. Like the sex pheromone, the aggregation pheromone is a contact pheromone and can not be detected over long distances (Izutsu et al. 1970; Ishii and Kuwahara 1967).

The ability of the species to detect pheromones over distances is apparently quite low. There is confusion among reports concerning the ability of German cockroaches to detect food odors from a distance. Food detection has been reported to depend on maxillary palpation and gustatory (contact) chemoreceptors more than olfactory receptors (Miesch and Howell 1967). The addition of a commercial bait to sticky traps did not increase their effectiveness (Sastry 1984). Ballard and Gold (1982) also found the commercial bait to be ineffective, but showed that white bread was an effective attractant. White bread was also shown to be an attractant by Ebeling and Reiersen (1974). Of 30 compounds tested, 10 were attractants, 6 were repellents, but almost half had no visible effect (Wileyto and Boush 1983). It seems that German cockroaches are capable of responding to some chemical odors, but usually from short distances.

One exception to the poor ability to respond to odors may be an ability to detect, and respond to, noxious compounds. Many pesticides and their spray components elicit an avoidance response by German cockroaches (Ebeling et al. 1966, 1967, 1968; Bennett and Wright 1971; Sterling and Howell 1972). The vapour phase of repellents is detected primarily by the antennae, secondarily by the legs, and barely by the palps (Reddy 1970a, 1970b). Liquid phases can also be detected by antennae and tarsi.

The purpose of this study was to study the role of the antennae in detecting a pesticide formulation. The electrophysiological response of antennae to a common insecticide and a control compound was compared and described. In addition, differences in the location of the recording electrode and the area of stimulation were investigated. A modified stimulus delivery system was designed to facilitate changes of the test compound with minimum disturbance of the recording system. The delivery system is described herein.

MATERIALS AND METHODS

Specimen Preparation. Adult males of the VPI strain were decapitated and whole head mounts were used. Heads were trimmed of labial and maxillary palps and one antennae to prevent muscular and/or neural interference. The head was

lightly imbedded in molding clay on a glass slide that in turn was imbedded in clay at ca. a 45 degree angle in a glass petri dish (Figure 1). The petri dish was filled with saline solution until the head was covered. The antenna was stretched up the incline of the slide and out of the saline.

Recording System. Electroantennograms (EAG) were recorded in a manner similar to that of Grant (1970). Glass microelectrodes were filled with insect Ringer's solution. Composition of the solution was 9.0 g NaCl, 0.2 g KCl, 0.2 g CaCl₂, 4.0 g glucose, and 10 ml PO₄ buffer at 7.4 pH to make 1 l in distilled water. The reference (negative) electrode was placed in the cockroach head. Two locations were used for the recording (positive) electrode. The first location was the 30th antennal segment (annulus). The second location was in the 40th antennal segment. A silver-chloride electrode was placed in the saline solution near the head and grounded. The electrode was prepared by placing a silver electrode (connected to a positive pole) in a 10% solution of hydrochloric acid (with a negative pole immersed in it) and running a 5-10 V DC current through it. All recordings were made in a faraday cage.

Reference and recording electrodes were connected to a Grass P16 MicroElectrode DC Amplifier (Grass Instrument Co.) which amplified the electrical output by 1000 (Figure 2).

The amplifier fed into the first channel of a Tektronix RM 564 Oscilloscope (Tektronix, Inc.) with a Type 2B67 Timebase and a two-channel Type 3A6 Dual-trace Amplifier. The second channel of the oscilloscope was connected to a Grass S48 Stimulator to record the onset and termination of the stimulus pulse. EAG's were recorded with a PC-2A Oscilloscope Continuous Recording Camera (Nihon Kohden Kogyo Co., Ltd.) on Kodak Linagraph 1930 photographic paper (Eastman Kodak Co.).

Stimulus Delivery System. The stimulator triggered a 5.0 V microswitch powered by an Epsco D-612T DC Power Supply (Epsco, Inc.) (Figure 2). The switch controlled air flow through a three-way solenoid valve. Breathing air from a gas cylinder entered the inlet port and flowed through one exit port. Tygon tubing (0.64 cm OD X 0.16 cm wall) carried the airstream over an empty reservoir. Upon triggering the stimulator, the switch shunted the air supply from the first exit port through the second exit port. Tygon tubing carried the airstream from the second port over a reservoir of the test compound. The compound was either 1% propoxur in oil (Octagon Process, Inc.) or a control of Risella Oil (Shell Chemical Co.). Reservoirs were constructed of 6 ml disposable pipettes (14.5 cm long X 1.0 cm OD base, 0.2 cm OD tip). A 2.5 X 2.5 cm piece of No. 1 Whatman filter paper was

placed inside each pipette and impregnated with 1.0 ml of the test compound.

The key feature of the system was the use of interchangeable syringes and hypodermic needles that facilitated exchange of pipettes without disturbing the system (Figure 3). Pipette tips were inserted into shortened 1 cc disposable syringes. The black rubber tip from the syringe plungers could be removed, bored, and placed over the pipette tips to provide stability inside the syringes. The 1 cc syringes fit into No. 18 hypodermic needles. The needles were fitted into the arms of a Y-shaped glass connector. A sleeve of 2 mm minibore Teflon tubing over the needles provided a secure fit inside the arms of the Y-connector. The stem of the Y-connector was fastened to a No. 13 hypodermic needle, the point of which was positioned 1 cm from the antenna being studied.

Air flow from the tank of breathing air was regulated by gas regulator valve. The flow rate from the tip of the No. 13 terminal needle was calibrated before each antennal preparation. The average flow rate was 30-32 ml/min. The duration of each test impulse was 5 sec. This was long enough to ensure complete evacuation of the test compound from the 6 ml pipette, as tested using a smoke plume.

RESULTS

Very little response was seen in the controls when recorded from the 30th antennal segment. Figures 4a-c show very slight EAG's that can be attributed to stimulus artifacts. Figures 4d-f show a negative EAG response when the same antenna was exposed to the vapors of the propoxur formulation. The amplitude ranged from -0.13 mV to -0.19 mV, stronger than that seen in the controls. The response does not remain throughout the 5 second exposure period. Recovery begins to occur within 0.5 sec and full recovery is achieved by 1.0 second. The resting potential is maintained for the remaining 4 seconds of exposure.

A different type of response was seen when the recording was made from the 40th antennal segment. Figures 5a-c showed hyperpolarizations of -0.050 to -0.075 mV at the beginning of the control stimulus. This may be due to a large stimulus artifact, to changes in the rate of air flow, or due to a small response to the Risella Oil. In any case, the response was small and short-lived. Recovery began within 1 sec with full recovery of the resting potential occurring by 2 seconds. In contrast, long persistent wave forms were obtained when the antennae were exposed to propoxur vapors (Figures 5d-f). The amplitude was only slightly greater than that of the controls, with a range from -0.075 to -0.15 mV. The pri-

mary difference was the duration of the wave form. It lasted beyond the duration of the propoxur stimulation. The negative EAG lasted for 6 sec, 1 sec beyond the stimulus period. By 6 sec, recovery began to occur with full recovery of the resting potential reached at about 8 seconds.

The type of EAG's seen are in accordance with what one would expect from this type of experiment. Monophasic signals were recorded since only one recording electrode was used. A decrease in the resting potential occurred when responses were recorded. This is indicative of extracellular recordings. No attempt at intra-cellular recordings, which would have created a positive wave form, was made. Very little drift occurred using the method described. Preliminary studies using severed antennae resulted in considerable electrical drift and a short recording life. Use of head mounts extended the recording life of the antennae and decreased drift.

DISCUSSION

Differences between the control and propoxur experiments clearly indicate the detection of insecticide vapors by olfactory chemoreceptors on the antennae. EAG's show that the propoxur affects the antennae, but they can not be used to predict behavioral responses. Stimulation of sensory neu-

rons can result in an increase, decrease, or no change in behavior. Results must be considered in light of behavioral studies (Birch 1971). When this is done, there is a direct relationship in the detection of propoxur vapors by the antennae and the dispersal, movement, and grooming responses observed in the previous studies. In fact, detection of the vapors by the antennae support the hypothesis in Part II that grooming was an attempt to clean receptors on the antennae.

Two antennal preparations were successfully recorded before equipment malfunction necessitated an early end to the study. More replicates would be needed to support the results obtained. If the results obtained are indicative of antennal responses to the vapors, differences between the two locations of the recording electrodes must be explained. Experiments were done at different times on different days. The experiment recording from the 30th segment was done in the afternoon while the recordings from the 40th segment were in the late morning. Susceptibility to insecticides is dependent on the time of day, increasing at the onset of dark (Beck 1963) and just before dawn (Shipp and Otton 1976). A circadian rhythm should not have affected the experiments since they were conducted in the middle of the cockroaches' inactive period (Cloudsley-Thompson 1953; Dreisig and Nielson 1971).

Temperature and humidity can be a factor in the strength of the EAG's. Propoxur is more toxic at 10 or 35 degrees C than at 23 degrees C and more toxic at low than high humidities (Reichenbach and Collins 1984). It is very unlikely that such temperature extremes were reached in the course of the experiment.

A more likely explanation is that more receptors were being recorded when the recording electrode was placed at the 40th than the 30th segment. EAG's record the summed activity of many receptors (Schneider 1962). More receptors elicit stronger responses. Electrophysiological responses are linearly proportional to the number of sensilla stimulated (Mayer et al. 1984). Adult German cockroaches have an average of 90 antennal segments (Campbell and Priestly 1970; Ishii 1971; Ramaswamy and Gupta 1981a). An electrode in segment 30 records the basal 1/3 of the antenna while one in segment 40 records from the basal 1/2. Not only are the number of segments greater, but the number of chemoreceptors are especially greater. The number of chemoreceptors per segment increases from the base of the German cockroach flagellum to the middle of the antenna and then decreases to the tip (Ramaswamy and Gupta 1981b). Thus, segments closer to number 40 will have more chemoreceptors than those close to number 30. In male American cockroaches, EAG's were

strongest when recorded from the middle 1/3 of antennae exposed to three sex pheromones and a general odor, nerol (Nishino and Takayanagi 1979).

The antenna in the first experiment was partially imbedded in the molding clay. In the second experiment, only the segments distal to, and including, number 40 were imbedded. More surface area was available for olfactory stimulation. This may also explain the larger impulses in the controls of the second experiment than in the first. Switching the route of air flow would more likely trigger mechanoreceptor of free-standing, flexible segments than imbedded segments.

Propoxur is a carbamate insecticide that acts as an acetylcholinesterase inhibitor at the neural synapse. It generally penetrates the exoskeleton of insects to affect the central nervous system. This experiment showed an effect on the sensory nervous system. The propoxur vapors most likely penetrated the pores of the chemoreceptors and were able to bind to, or stimulate, the olfactory receptor sites. Propoxur exerted a non-synaptic effect on the cockroaches.

The methods described in this study provide a means of studying the effects of different volatile compounds on insect antennae. The system of interlocking and interchangeable syringes and needles is an easy means of studying different compounds without disturbing the antennal preparation.

LIST OF FIGURES

Figure 1 - Diagram of antennal preparation. H=insect head; A=insect antenna; C=molding clay; S=microscope slide; P=petri dish; NaCl=saline solution; AgCl=silver chloride electrode (ground); (-)=negative reference electrode; (+)=positive recording electrode.

Figure 2 - Diagram of stimulus delivery system and recording apparatus.

Figure 3 - System of interchangeable syringes and needles used to deliver air-borne odors to the antennae. P=pipette reservoir; S=lcc syringe; PT=plunger tip from syringe; 18N=No. 18 hypodermic needle; Y=glass Y-connector; 13N=No. 13 hypodermic needle.

Figure 4 - EAG's from antennal segment 30 when exposed to a-c) the control compound and d-f) propoxur vapors. Horizontal divisions = 1 sec. Vertical divisions = 0.05 mV.

Figure 5 - EAG's from antennal segment 40 when exposed to a-c) the control compound and d-f) propoxur vapors. Horizontal divisions = 1 sec. Vertical divisions = 0.05 mV.

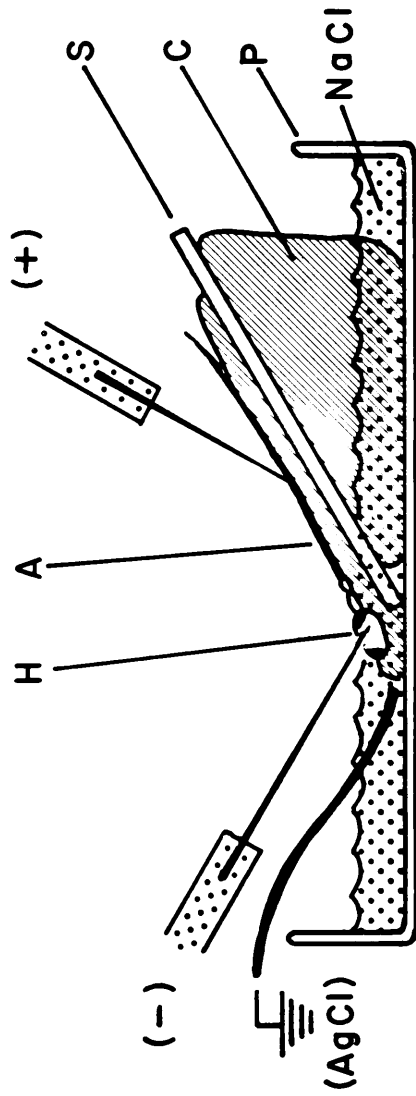


Figure 1 - Diagram of antennal preparation. H=insect head; A=insect antenna; C=molding clay; S=microscope slide; P=petri dish; NaCl=saline solution; AgCl=silver chloride electrode (ground); (-)=negative reference electrode; (+)=positive recording electrode.

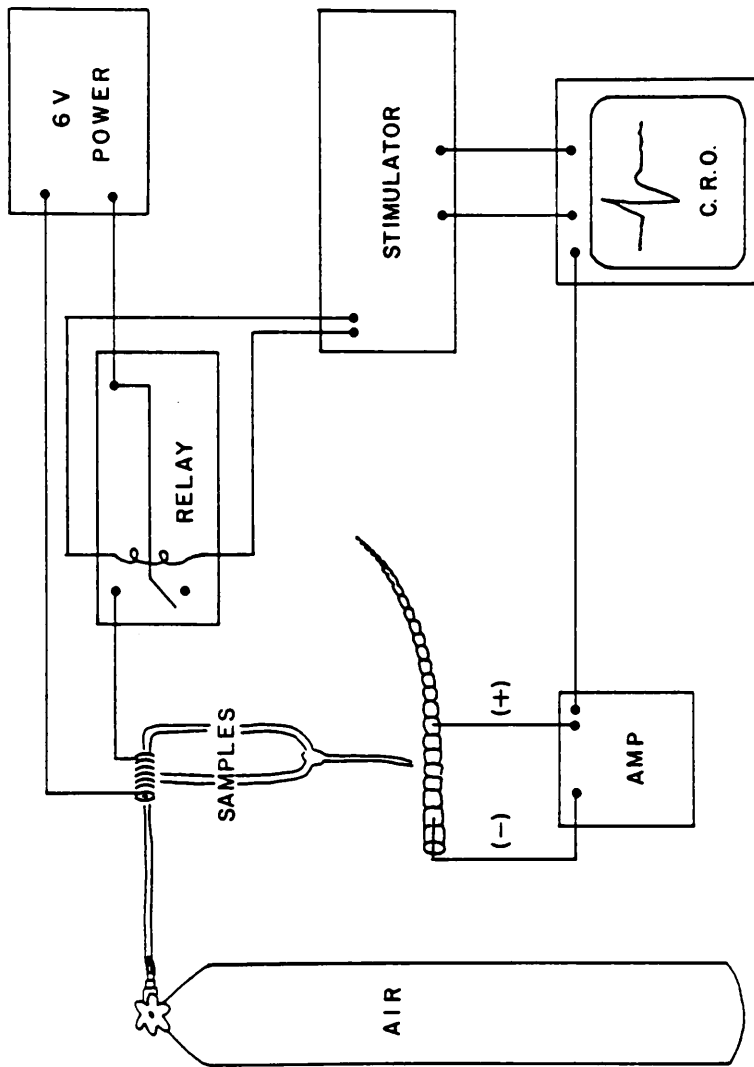


Figure 2 - Diagram of stimulus delivery system and recording apparatus as described in text.

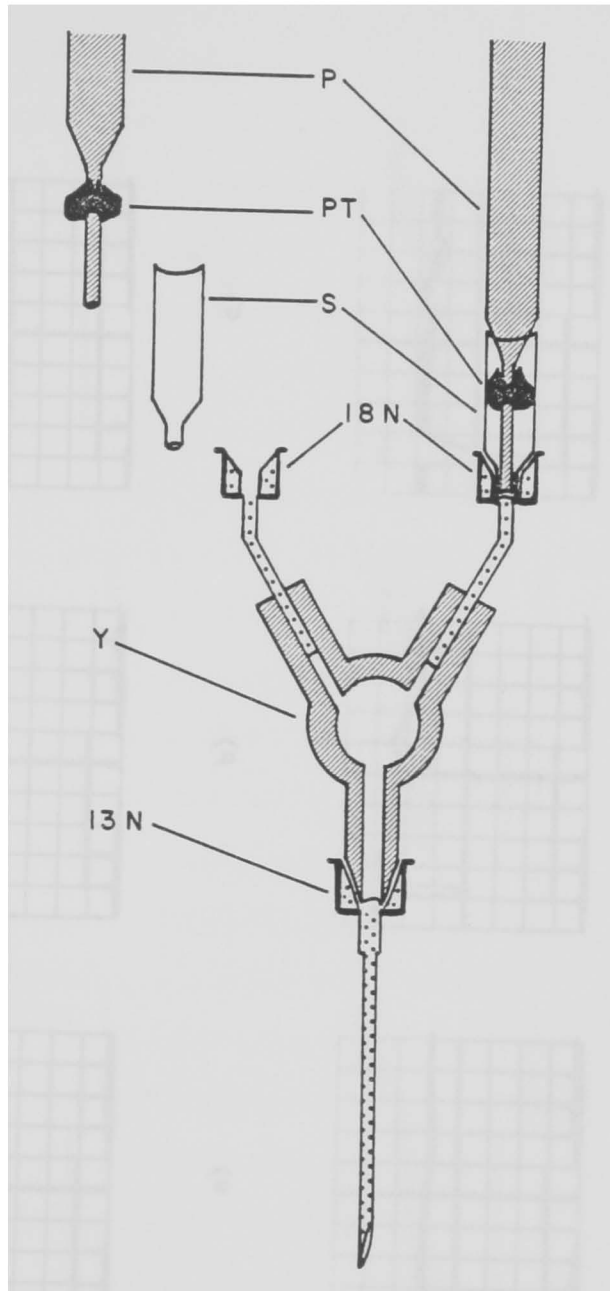


Figure 3 - System of interchangeable syringes and needles used to deliver air-borne odors to the antenna. P= pipette reservoir; S=1cc syringe; PT=plunger tip from syringe; #18=No. 18 hypodermic needle; #13=No. 13 hypodermic needle; Y=glass Y-connector.

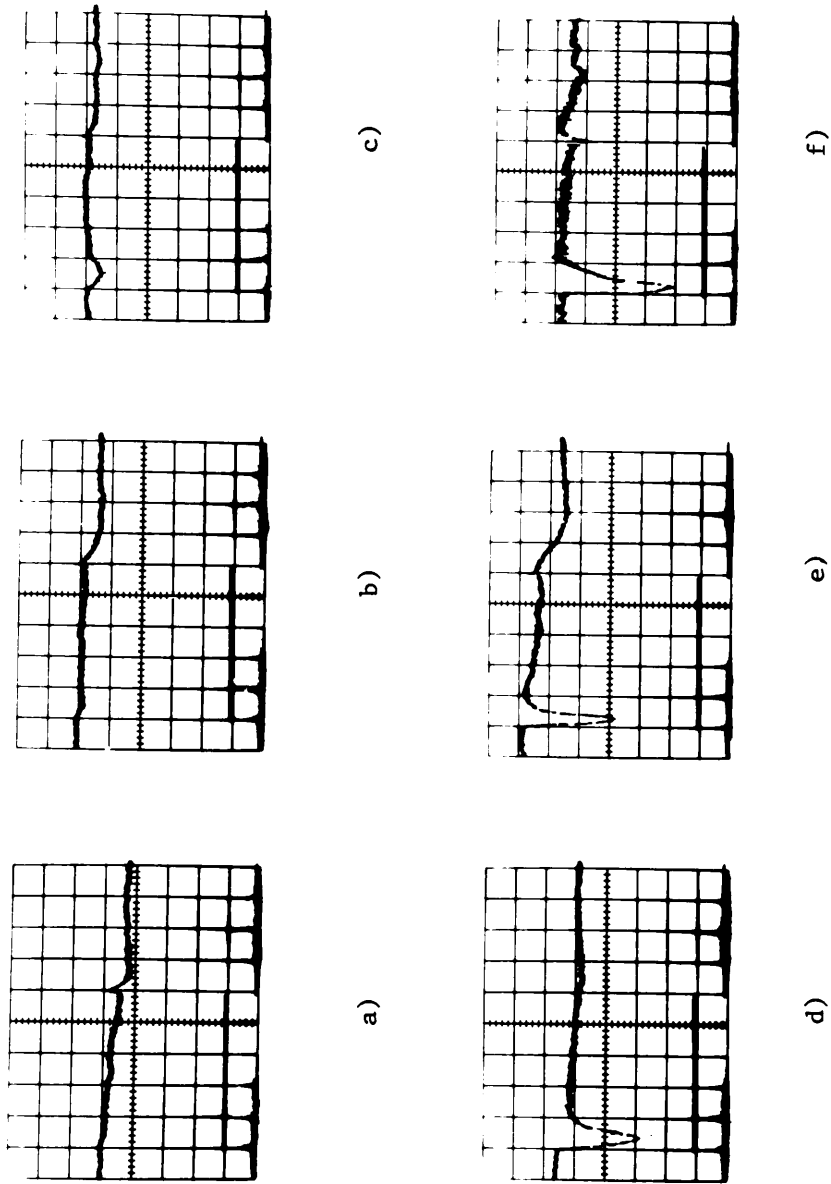


Figure 4 - EAG's from antennal segment 30 when exposed to a-c) the control vapors and d-f) vapors from a propoxur formulation. Horizontal divisions = 1 sec. Vertical divisions = 0.05 mV.

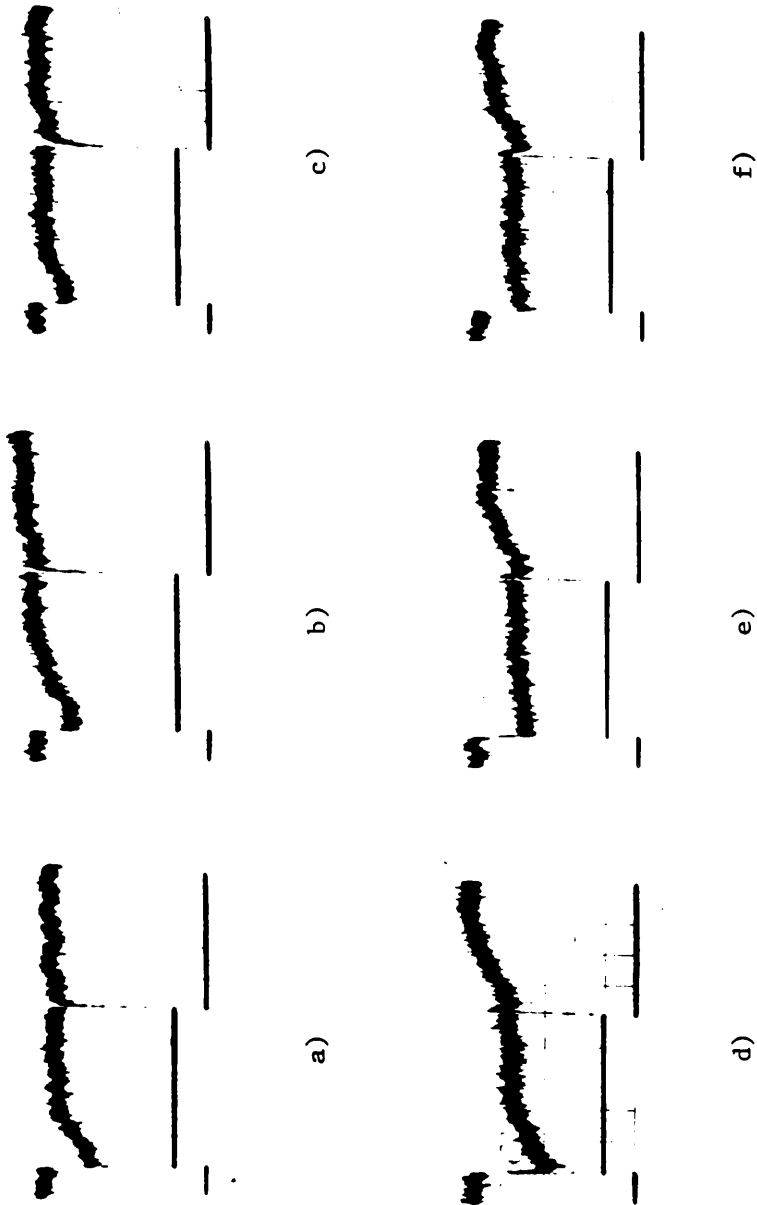


Figure 5 - EAG's from antennal segment 40 when exposed to a-c) the control vapors and d-f) vapors from a propoxur formulation. Horizontal divisions = 1 sec. Vertical divisions = 0.05 mV.

SUMMARY

Vapors from a formulation of 1% propoxur in oil caused an avoidance response by the German cockroach, Blattella germanica (L.), regardless of age, sex, or female reproductive state. Irritation of adult males was indicated by increased movement, antennal grooming, and tarsal grooming. Adult males, adult females, and middle instars dispersed from aquaria containing the pesticide formulation. Early instars did not leave the aquaria, but responded by seeking shelter within the pores of water-filled sponges.

Vapors from the propoxur itself undoubtedly played a role in the avoidance behaviors observed. However, the effect of a solvent system can not be ignored. Many spray components commonly used in commercial formulations are known to be repellent to insects (Bennett and Wright 1971; Sterling and Howell 1972). Volatilization of a solvent system may have compounded the repellent effects of the propoxur. It is improbable that the oil base of the propoxur formulation was responsible for the repellent and irritant effects since the mineral oil of the controls did not affect cockroach behavior.

German cockroaches of both a susceptible laboratory strain (VPI) and a resistant field strain (BP) responded to

the vapors of the propoxur formulation. No difference between the two strains occurred in the controls in Part I. Adult males of the BP strain showed more activity in the controls in Part II, particularly total movement, and total amount of antennal and tarsal grooming. This may indicate a greater responsiveness to disturbance or environmental novelty by the field strain than the laboratory strain. In all experiments, the adults of the VPI strain displayed a greater response to the insecticide, relative to the controls, than BP strain adults. This difference was apparently related to the difference in physiological resistance. Physiological resistance was to technical grade propoxur. It follows that the behavioral difference was due to selection pressure from the propoxur itself rather than other components of the commercial formulation. Solvents may have contributed to the repellency of the formulation, but differences between strains was most likely due to the propoxur alone.

Although physiological resistance is well established in the BP strain, there is no evidence of behavioral resistance in either strain. Behavioral resistance could not have developed in the VPI strain since it has never been exposed to selection pressure. The BP strain could not have developed it since it was least responsive to the insecticide. The negative correlation between physiological resistance and

behavioral responses is best explained by considering the two factors as dependent upon each other. A behavior is an organism's expression of physiological/neurological events. Consequently, a change in the physiology of an organism could be expected to alter its behavioral expressions. The development of physiological resistance to propoxur resulted in decreased behavioral responses to a propoxur formulation, as has happened in other insects exposed to pesticides (Hooper and Brown 1965b; Virgona et al. 1983).

This does not imply that other relationships are not possible. Positive correlations between physiological resistance and behavioral responses have also been made (Silverman and Mer 1952; Drobozina et al. 1977; Gaaboub and Dawood 1974; Fay et al. 1958; Kilpatrick and Schoof 1958; and Schmidt and LaBrecque 1959). The relationship between resistance and behavior may ultimately depend on the genetic predisposition of the population, the parameters of the selection pressure, the exclusivity and resistive ability of the resistance mechanism (Lockwood et al. 1984) and the frequency and dominance of alleles responsible for behavioral avoidance, frequency and dominance of alleles responsible for physiological resistance, pest mobility, and patterns of pesticide usage (Gould 1984).

Several qualitative and quantitative methods were used to study the repellency of an insecticide. All methods employed only the vapor phase. This eliminated mortality as a factor in the evaluation. The insecticide-induced dispersal from the aquaria (Part I) was the best technique used. It provided information on the immediate and long-term (24 h) effects of the insecticide formulation. Different age/sex classes could be studied at the same time under identical conditions. Variation was not great. The movement study within the glass arenas (Part II) was very time consuming and labor-intensive. This technique could be considerably facilitated if video recordings could be fed into an electronic digitizer via computer software packages as is possible with moving image analyzers. Considerable individual variation occurred, but nevertheless, comparisons between the strains showed strain differences. Numbers of antennal cleanings provided a means of measuring the reaction of the males to vapors. Variation was minimal and comparisons between strains could be made. Obviously, this method is only suitable for the evaluation of volatile compounds. Quantification of tarsal grooming provided less information. Tarsal grooming may be best suited for studies involving contact irritancy to liquid and solid phases of chemicals.

An advantageous feature of the above methods is that they show response through time. The rate of response through time is an important aspect of insecticide repellency that is not measured by other methods (Flynn and Schoof 1966; Ebeling, et al. 1966). Insects with a slow avoidance response to a toxic compound may obtain a lethal dose before dispersal. A rapid avoidance response would increase the chances of survival before toxicity occurred.

The electroantennogram study (Part III) was a means of quantifying the response of antennae to chemical vapors. Results showed that vapors of the propoxur formulation were detected by the antennae. Future EAG studies could be used to determine the concentration thresholds for neurological detection of compounds. As with antennal grooming, use of EAG's is restricted to olfactory reception of volatile chemicals. Any electrophysiological study must be supplemented with behavioral studies. Reception by sensory receptors does not always indicate the type, or even presence, of behavioral response.

This research has implications for cockroach control techniques. That early instars sought shelter in the pores of the wet sponges indicates the importance of even short range dispersal. Cockroaches could find refuge in wet mops and sponges in janitors closets, around leaky plumbing, or

near pipes wet with condensation. Such areas could provide cockroaches with safe harborage. Also, some repellent residuals have been used to establish barrier zones. If physiological resistance can diminish behavioral responses, such repellent barriers may become less effective. Control procedures may need to be modified according to both the resistant characteristics and the behavioral characteristics of target populations.

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