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Sublethal effects of deltamethrin and propoxur on longevity and reproduction of German cockroaches, *Blattella germanica*

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Abstract

The effects of sublethal doses of deltamethrin and propoxur, applied topically at LD_{10}, LD_{30} and LD_{50} on German cockroaches, were studied by reciprocal crossing. Male and female longevities decreased curvilinearly with increasing sublethal doses of deltamethrin, and decreased linearly with increasing sublethal doses of propoxur. Fecundity of females treated with deltamethrin and propoxur was reduced with increasing sublethal doses of both insecticides. Oothecal production, oothecal hatchability and nymphal production also declined with increasing doses of deltamethrin and propoxur. Preoviposition and incubation periods were not affected by sublethal doses of deltamethrin and propoxur, although some significant differences were observed at certain oothecal numbers. Two-way analysis of variance indicated that only treated females showed an effect on oothecal production while oothecal hatch and nymphal production were governed by both treated females and males. Insecticide susceptibility tests on the progeny of parents treated with sublethal doses demonstrated that these doses did not increase insecticidal tolerance in the F_1 generation.

Introduction

The German cockroach, *Blattella germanica* (Linn.) is the most important indoor urban insect pest in many parts of the world. Current control of this species relies heavily on the use of insecticides. The chance of a cockroach receiving lethal exposure from an insecticide deposit is a result of complicated and dynamic interactions between abiotic and biotic factors. Abiotic factors (e.g., substrate surface, temperature, volatilization of the insecticide, ambient humidity and light) and biotic factors (e.g., poor cuticular penetration and behavioural avoidance) may reduce insecticide performance (Rust, 1995). Often, the result of a cockroach encountering an insecticide deposit is a sublethal exposure, which may induce physiological and behavioural changes.

Gravid female German cockroaches subjected to sublethal amounts of an insecticide exposure have been reported to drop oothecae prematurely (Parker & Campbell, 1940; Harmon & Ross, 1987; 1988; Zhou & Le Patourel, 1990; Appel & Abd-Elghafar, 1990; Abd-Elghafar et al., 1991). In addition, exposure to sublethal amounts of propoxur also induced significant water loss in adult males at 2- and 24-hour post-treatment (Kramer et al., 1989).

Other sublethal effects of insecticides relate to longevity and reproduction. In this area, very few studies, except with the IGRs had been done on the German cockroach. Cochran (1985) reported that avermectin B_1 at doses of $\geq$ 6.5 ppm was able to suppress reproduction of the German cockroach. Exposure to sublethal doses of chlorpyrifos-methyl at LD_{10}, LD_{20} and LD_{60} significantly reduced the longevity and fecundity of adult female German cockroaches compared to untreated females (Hamilton & Schal, 1990). Abd-Elghafar & Appel (1992) have shown that longevity and fecundity of adult male and female German cockroaches were reduced with increasing sublethal doses of cyfluthrin and hydramethylnon. However, fecundity and longevity of adult females increased with increasing sublethal doses of chlorpyrifos.

An earlier study on fecundity involved cross-mating of adult males and females treated with the same sublethal dose (e.g., $LD_{30} \times LD_{30}$, $LD_{50} \times LD_{50}$). Females were then observed for reproduction and longevity (e.g., Abd-Elghafar & Appel, 1992). This however, may not reflect a completely realistic situation. It is assumed that under natural field conditions, cockroaches may very well mate randomly, sometimes even with partners which had survived insecticide poisoning. In addition, most previous studies reported were also unable to determine how and to what extent each sex which had been exposed to sublethal doses of insecticide affect various reproductive parameters. It is also of interest to determine whether sublethal doses of insecticide select for individuals which are more tolerant to insecticide and will then produce F_1 generations that show greater tolerance.

This study reports the sublethal effects of deltamethrin and propoxur on adult German cockroaches. Both adult males and females which survived the LD_{10}, LD_{30} and LD_{50}, and LD_0 (as control) were subjected to reciprocal crossing and several reproductive parameters for each cross were observed. Progeny of males and females dosed differently were reared until adulthood and were tested to determine whether differences occurred in their susceptibility to insecticides at LD_{50}s determined at the parental generation.

Materials and methods

Insects. The VCRU (Vector Control Research Unit) susceptible strain was used in this study. The history of this strain had been reported in Lee et al. (1996a). Late nymphs were separated from the mass culture and reared in 3-liter glass containers (200 cockroaches per container) at 26 ± 2 °C, 65 ± 5% r.h. and 12-h photoperiod. Food and water were provided *ad libitum*. Newly emerged adult cockroaches were segregated by sex every 12 h from the culture to prevent mating. Virgin cockroaches (male and female) aged 3–5 days were used in all studies.

Insecticides. Two technical grade insecticides, deltamethrin (provided by AgrEvo Environmental Health, Singapore) and propoxur (provided by Bayer AG, Germany) were used in this study. They were diluted in analytical grade acetone (purity: >99%).

Method of exposure. Insecticides were applied topically on cockroaches according to procedures described earlier in Lee et al. (1996a, b). The three sublethal doses (LD_{10}, LD_{30} and LD_{50}) used in this study (Table 1) were derived from probit analysis results generated in Lee et al. (1996a). Generally, adult males and females, immobilised with carbon dioxide (20 kpa) for 20 s, were treated on their first abdominal sternites with 1 μl acetone containing a sublethal dose of insecticide. Control individuals were treated with 1 μl of acetone alone. After treatment, groups of twenty cockroaches were placed in polyethylene containers (12 cm diam × 6 cm height), each lined with filter paper (Whatman No. 1, U.K), and provided with food and water. Mortality was assessed at 48 h post treatment. The survivors were isolated and used for subsequent study, provided that the observed mortalities for all doses did not deviate from their expected mortalities, based on χ^2 test at $\alpha = 0.05$.

Table 1. Doses of deltamethrin and propoxur applied topically on adult male and female German cockroaches

LD	Dose of insecticide applied (μg/ insect)[a]			
	Deltamethrin		Propoxur	
	Male	Female	Male	Female
0	0	0	0	0
10	0.007	0.017	0.321	0.711
30	0.009	0.0217	0.555	1.162
50	0.012	0.0257	0.801	1.743

[a]Dose values derived from LD_{50}s in Lee et al. (1996a).

Fecundity and longevity studies. The survivors from the groups exposed to LD_0, LD_{10}, LD_{30} and LD_{50} were subjected to reciprocal crossing with ten replicates per cross. Each pair of cockroaches was kept in a polyethylene cup (Swordman No. 14729 size A-1; 5 cm diam × 10 cm height) with food and water provided *ad libitum*. A folded filter paper (3 × 2 cm) was provided as harborage. All pairs were observed daily for the following parameters (Lee et al., 1996c): preoviposition period (period between hatching of an ootheca and the formation of the next one), incubation period (period between the formation and hatching of an ootheca), number of oothecae per female per lifetime, number of oothecae produced that hatched per lifetime, number of offsprings per hatched ootheca, and longevity of both adult males and females. Total number of offsprings produced per female was calculated from the number of offsprings per hatched ootheca. Individuals which died during the study were

removed from the observation cups and were not replaced.

Offsprings (F_1) insecticide susceptibility. Offsprings produced by the treated parents from the first oothecae of each cross were reared separately in 3-l glass containers until reaching adulthood. Upon maturation, the males were isolated from the rearing container, cultured until 1-week of age and topically tested with a dose of insecticide that equalled the LD_{50} for their parents. For each cross, 2–5 replicates of 15–20 males were used. The number of replicates and the number of cockroaches tested depended on the availability of adult males in each cross. Mortality of cockroaches was scored at 48 h post treatment and the percentage mortality was calculated at each replicate for each cross.

Preliminary study on mating behaviour. In order to ascertain whether decreases in fecundity might be due to changes in mating behaviour, a preliminary study was conducted on 5 replicate pairs of cockroaches treated with deltamethrin in the following crosses: LD_0 [male] × LD_0 [female], LD_0 [male] × LD_{50} [female], LD_{50} [male] × LD_0 [female] and LD_{50} [male] × LD_{50} [female]. Each pair was observed for mating activity every 30 min for 24 h post-pairing. During scotophase, observation was made under red light (light intensity and wavelength not determined).

Data analyses. All data were analyzed with analysis of variance (ANOVA) and means were separated using least significant difference (LSD) test, or Scheffe's *S* procedure. The relationship for each sex between insecticide dose applied and longevity was determined by regression analysis. The effects of males and females treated with different lethal doses of insecticide on reproduction parameters (total no. oothecae produced per female, total no. oothecae hatched per female and total no. offsprings per female) were determined with two-way analysis of variance. By using the mean value calculated for each cross, the relationship between insecticide dose applied on male and female insects, and each reproduction parameter was predicted by multiple regression. Predicted relationships were later used to establish response surface plots. The observed mortality of the F_1 generation for each cross was tested with a χ^2 test at $\alpha = 0.05$ to determine whether it deviated from its expected 50% mortality. All analyses were performed with a statistical software program, StatGraphics® Ver 5.0 (StatGraphics Inc, New York, U.S.A).

Results

Adult longevity. Mean longevity of combined control (acetone-treated) males was 107.6 ± 5.6 days ($n = 80$) with a mean ranging from 93.8 ± 7.8 days to 122.9 ± 5.9 days (Table 2). However, the means for control in deltamethrin and propoxur did not differ significantly ($P > 0.05$). Male longevity decreased curvilinearly with increasing sublethal doses of deltamethrin [$y = (92.9 \pm 1.0) - (1.8 \pm 0.1)x + (0.020 \pm 0.002)x^2$; $R^2 = 0.995$] and decreased linearly with increasing dose of propoxur [$y = (121.4 \pm 1.7) - (0.8 \pm 0.2)x$; $R^2 = 0.993$], where y = longevity of males (days) and x = level of sublethal dose of insecticide ($0 \leq x \leq 50$).

Mean longevity of untreated female German cockroaches was 142.3 ± 7.8 days ($n = 80$), with a mean ranging from 135.7 ± 9.8 days to 153.7 ± 6.4 days (Table 2). When treated with deltamethrin, female longevity decreased curvilinearly with increasing sublethal doses [$y = 133.6 \pm 2.4) - (2.3 \pm 0.3)x + (0.015 \pm 0.005)x^2$; $R^2 = 0.992$], where y = longevity of females (in days) and x = level of sublethal doses ($0 \leq x \leq 50$). The longevity of those treated with LD_{30} and LD_{50} was significantly lower ($P < 0.05$) than that of the untreated females (Table 2). Females treated with LD_{50} of deltamethrin had their longevity reduced by 58% compared to untreated females. Longevity of females decreased linearly with increasing sublethal doses of propoxur [$y = (153.4 \pm 0.5) - (1.0 \pm 0.1)x$; $R^2 = 0.999$].

Oothecal production per female. Mean total number of oothecae produced per female in the control was 3.5 ± 0.3 oothecae ($n = 20$), with a mean ranging from 3.2 ± 0.8 to 3.7 ± 0.8 oothecae. The total oothecae produced by those females receiving LD_{50} of deltamethrin (crossed with LD_0 to LD_{50} treated males) ranged from only 14% (LD_{50}[F] × LD_{50}[M]) to 30% (LD_{50}[F] × LD_0[M]) of those produced by the untreated females (mean = 3.7 oothecae) in the deltamethrin category (Table 3)

When treated with propoxur, only crosses of LD_{50}[F] × LD_{30}[M] and LD_{50}[F] × LD_{50}[M] showed significantly lower ($P < 0.05$) oothecal production than the control (Table 3). This indicated that propoxur exhibits a less profound sublethal effect relative to the doses that cause lethal effects, when compared

Table 2. Effect of sublethal doses of deltamethrin and propoxur on the longevity of the adult German cockroach

LD	Mean longevity ± S.E.M. (days)[a]			
	Deltamethrin		Propoxur	
	Male	Female	Male	Female
0	93.8 ± 7.8a	135.7 ± 9.8a	122.9 ± 5.9a	153.7 ± 6.4a
10	75.5 ± 8.2ab	108.5 ± 10.4ab	111.0 ± 5.3a	143.3 ± 6.3a
30	58.5 ± 6.2b	81.7 ± 9.4bc	99.7 ± 4.8bc	125.2 ± 6.9ab
50	53.4 ± 4.2b	57.0 ± 7.2c	80.7 ± 7.5c	103.6 ± 11.7b

[a] Mean values followed by the same letters within the same column are not significantly different ($P > 0.05$; Scheffe's *S* procedure).

with deltamethrin. At these crosses, the treated females produced only 50% (LD_{50}[F] × LD_{30}[M]) and 47% (LD_{50}[F] × LD_{50}[M]) of the mean total oothecae produced by the control (3.2 oothecae).

The predicted relationships between the total no. oothecae per female, and insecticide dose on males and females were as follows: (1) deltamethrin: $z = (3.510 \pm 0.215) - (0.024 \pm 0.016)x - (0.085 \pm 0.016)y - (0.0004 \pm 0.003)x^2 + (0.0012 \pm 0.003)y^2$, where z = total no. oothecae produced per female ($z \geq 0$), x = deltamethrin dose level applied on females ($0 \leq x \leq 50$) and y = deltamethrin dose level applied on males ($0 \leq y \leq 50$), $R^2 = 0.8854$; (2) propoxur: $z = (3.215 \pm 0.218) - (0.039 \pm 0.017)x - (0.0012 \pm 0.0003)x^2$, where z = total no. oothecae produced per female ($z \geq 0$), x = propoxur dose level applied on females ($0 \leq x \leq 50$) and y = propoxur dose applied on males ($0 \leq y \leq 50$), $R^2 = 0.7660$.

Oothecal viability and hatchability per female. Not all oothecae that were produced were viable. Some of them were non-viable and were aborted. From this study, two distinct periods were observed during which non-viable oothecae were dropped. The first period ranged from day 1 to 7, while the second one ranged from day 20 to 50. The percentage of non-viable oothecae was highest at the first oothecal production in most crosses.

Increasing sublethal doses of deltamethrin and propoxur caused a decline in oothecal viability (Table 3). The mean hatched oothecae produced by females treated with LD_{30} and LD_{50} doses of deltamethrin were only 0 to 30% of the total hatched oothecae produced by the untreated pairs (Table 3). When treated with propoxur, significant reduction in total no. hatched oothecae was only observed in the LD_{50}[F] × LD_{50}[M] cross (Table 3). Only 27% of the oothecae produced by this group hatched. When compared with that of deltamethrin, the effect of propoxur is seen to be less adverse.

For both deltamethrin and propoxur, the number of hatched oothecae decreased with increasing levels of sublethal doses applied on both female and male cockroaches. Predicted relationships between total no. hatched oothecae per female, insecticide dose level on females and males were as follows: (1) deltamethrin: $z = (2.466 \pm 0.163) - (0.077 \pm 0.012)x - (0.047 \pm 0.012)y + (0.0008 \pm 0.0002)x^2$, where z = total no. hatched oothecae per female ($z \leq 0$), x = deltamethrin dose level applied on females ($0 \leq x \leq 50$) and y = deltamethrin dose level applied on males ($0 \leq y \leq 50$), $R^2 = 0.9069$; (2) propoxur: $z = (2.729 \pm 0.184) - (0.028 \pm 0.014)x - (0.018 \pm 0.014)y - (0.0007 \pm 0.0003)x^2$, where z = total no. hatched oothecae per female ($z \geq 0$), x = propoxur dose level applied on females ($0 \leq x \leq 50$) and y = propoxur dose level applied on males ($0 \leq y \leq 50$), $R^2 = 0.8232$.

Total nymphal production per female. Mean total number of offsprings produced per female in the control was 105.3 ± 7.7 ($n = 20$), with mean no. offsprings ranging from 97.6 ± 20.8 (deltamethrin) to 111.9 ± 15.2 (propoxur). Treatment with deltamethrin caused nymphal production to be reduced significantly ($P < 0.05$), compared to the control (Table 3). When one of the parents received a dose of LD_{30} or above, the number of offsprings produced per female was reduced significantly. The nymphal production of female cockroaches upon treatment with LD_{30} or LD_{50} was reduced at least 73%, irrespective of whatever dose their partner received.

In the propoxur category, a significant decline ($P < 0.05$) in nymphal production, compared to the control, was observed in crosses of LD_{50}[F] × LD_{30}[M] and LD_{50}[F] × LD_{50}[M] when compared to that of

Table 3. Effect of sublethal doses of deltamethrin and propoxur on the total number of oothecal production, hatchability and total number of offsprings produced per female

Cross LD (female) × LD (male)		Mean total no. oothecae/female ±S.E.[a]		Mean total no. hatched oothecae/ female ±S.E.[a]		Mean total no. offspring produced/female ± S.E.[a]	
		Deltamethrin	Propoxur	Deltamethrin	Propoxur	Deltamethrin	Propoxur
0	0	3.7 ± 0.8 a	3.2 ± 0.4 ab	2.4 ± 0.6 a	2.7 ± 0.6 ab	97.6 ± 20.8 a	111.9 ± 15.2 a
	10	2.5 ± 0.7 abc	3.5 ± 0.3 a	1.7 ± 0.6 abc	2.5 ± 0.6 ab	61.3 ± 23.3 a–d	95.5 ± 22.8 ab
	30	2.2 ± 0.4 a–d	3.0 ± 0.3 ab	1.4 ± 0.3 a–d	2.3 ± 0.4 ab	52.4 ± 13.2 b–e	87.1 ± 16.4 ab
	50	2.2 ± 0.4 a–d	2.6 ± 0.5 a–d	1.3 ± 0.4 b–e	2.3 ± 0.5 ab	47.3 ± 16.1 b–f	80.6 ± 18.1 ab
10	0	3.4 ± 0.7 a	3.2 ± 0.5 ab	2.0 ± 0.7 ab	3.3 ± 0.5 a	68.2 ± 23.3 ab	111.9 ± 18.5 a
	10	2.4 ± 0.6 abc	3.0 ± 0.5 ab	1.7 ± 0.5 abc	2.5 ± 0.5 ab	64.0 ± 19.3 abc	92.1 ± 16.8 ab
	30	1.5 ± 0.4 b–e	3.4 ± 0.5 a	1.0 ± 0.3 b–f	2.5 ± 0.6 ab	36.9 ± 12.6 b–g	83.6 ± 21.1 ab
	50	2.2 ± 0.5 a–d	2.9 ± 0.4 abc	0.3 ± 0.2 ef	1.9 ± 0.4 ab	10.2 ± 7.4 fg	63.6 ± 14.3 abc
30	0	2.7 ± 0.6 ab	3.3 ± 0.4 ab	0.7 ± 0.4 c–f	2.9 ± 0.4 ab	26.4 ± 13.9 c–g	106.0 ± 16.3 a
	10	1.4 ± 0.5 b–e	3.5 ± 0.5 a	0.5 ± 0.3 def	2.4 ± 0.7 ab	18.4 ± 12.4 efg	87.4 ± 24.2 ab
	30	1.4 ± 0.3 b–e	2.5 ± 0.5 a–d	0 f	2.0 ± 0.5 ab	0 g	69.0 ± 16.7 ab
	50	1.7 ± 1.1 b–e	3.2 ± 0.5 ab	0.1 ± 0.1 f	2.1 ± 0.7 ab	3.6 ± 3.6 g	71.0 ± 23.2 ab
50	0	1.1 ± 0.5 cde	2.2 ± 0.6 a–d	0.7 ± 0.4 c–f	2.2 ± 0.6 ab	23.3 ± 13.1 d–g	79.6 ± 21.9 ab
	10	0.8 ± 0.3 de	2.0 ± 0.4 bcd	0.1 ± 0.1 f	2.0 ± 0.4 ab	2.5 ± 2.5 g	63.4 ± 13.0 abc
	30	0.8 ± 0.3 de	1.6 ± 0.7 cd	0.2 ± 0.2 f	1.6 ± 0.7 bc	7.0 ± 7.0 g	48.7 ± 20.8 bc
	50	0.5 ± 0.2 e	1.5 ± 0.6 d	0.1 ± 0.1 f	0.4 ± 0.3 c	2.9 ± 2.9 g	13.2 ± 10.2 c

[a] Mean values followed by the same letters within the same column are not significantly different ($P > 0.05$; LSD test).

the control (Table 3). Females, when treated with LD_{50} and crossed with males which received the same propoxur dose, produced only 12% of the mean total number of nymphs produced by the untreated pairs. Overall, the effect of propoxur on nymphal production was less marked than that of deltamethrin.

The relationship between total number of offspring produced per female and insecticide dose on females and males was determined with regression analysis. It showed that nymphal production decreased with increasing sublethal doses of deltamethrin and propoxur on both male and female cockroaches. The predicted relationships were as follows: (1) deltamethrin: $z = (93.445 \pm 6.094) - (2.980 \pm 0.464)x - (1.790 \pm 0.464)y + (0.030 \pm 0.009)x^2 + (0.015 \pm 0.009)y^2$, where z = total no. offsprings produced per female ($z \geq 0$), x = deltamethrin dose level applied on female ($0 \geq x \geq 50$) and y = deltamethrin dose level applied on male ($0 \pm y \leq 50$), $R^2 = 0.9105$; (2) propoxur: $z = (107.353 \pm 5.361) + (0.509 \pm 0.408)x - (1.045 \pm 0.408)y - (0.021 \pm 0.007)x^2 + (0.009 \pm 0.007)y^2$, where z = total no. offsprings produced per female ($z \geq 0$), x = propoxur dose level applied on female ($0 \pm x \pm 50$) and y = propoxur dose level applied on male ($0 \leq y \leq 50$), $R^2 = 0.9033$.

Maternal and paternal effects on reproductive parameters. When both parents were treated with insecticides, only the females showed an effect on oothecal production, based on two-way analysis of variance (Table 4). However, oothecal hatchability and nymphal production were governed by both maternal and paternal factors. Interaction between both sexes did not demonstrate an effect on any of the parameters measured.

Preoviposition period. The mean first preoviposition period (period between mating and the emergence of the first ootheca) for the three controls combined ($n = 19$) was 8.8 ± 0.3 days (ranging from 8.4 ± 0.3 to 9.3 ± 0.4 days). Subsequent preoviposition periods were slightly longer than the first one (mean ± S.E. = 10.0 ± 0.5 days in the controls). Generally, there was no significant difference in preoviposition period between different crosses involving deltamethrin when compared with that of the control.

Table 4. Main effect and interaction of ANOVA values (F value, degree of freedom [df], probability [P]) for total oothecal production, total oothecal hatchability and total nymphal production per female

Parameter Independent variable	Dependent variable[a] (F value, df, P)	
	deltamethrin	propoxur
Oothecal production		
Female	8.76, 3, <0.0001*	7.23, 3, 0.0001*
Male	2.62, 3, 0.0529	0.95, 3, 0.4168
Female × male	0.83, 3, 0.5874	0.40, 3, 0.9344
Oothecal hatchability		
Female	12.82, 3, <0.0001*	3.00, 3, 0.0326*
Male	3.07, 3, 0.0297*	3.04, 3, 0.0309*
Female × male	1.17, 3, 0.3197	0.40, 3, 0.9351
Nymphal production		
Female	14.87, 3, <0.0001*	4.19, 3, 0.0071*
Male	3.57, 3, 0.0158*	4.19, 3, 0.0071*
Female × male	1.38, 3, 0.2007	0.20, 3, 0.9934

[a] An independent variable with an * has a significant effect on the parameter studied.

Incubation period. Mean incubation period for the two controls combined was 28.1 ± 1.3 days, with a mean ranging from 26.8 ± 0.3 to 29.3 ± 0.3. In most crosses, the incubation period increased with oothecal number and did not differ significantly ($P>0.05$) between different crosses.

Susceptibility of the F_1 generation to insecticide. The F_1 progenies of all crosses for both deltamethrin and propoxur were shown to have a susceptibility comparable to their parents as their mortalities values did not deviate from the expected 50% ($P > 0.05$) when treated with LD_{50} generated from the parental generation (Table 5). However, for deltamethrin, the progenies from five crosses (LD_{30}[F] × $LD_{30,50}$[M] and LD_{50}[F] × LD_{10--50}[M] were not tested due to insufficient number of cockroaches produced.

Preliminary study on mating behaviour. It was found that all replicate pairs of cockroaches in the control mated during 24 h post-pairing. No incidence of mating was observed for deltamethrin crosses of LD_{50}[F] × LD_0[M] and LD_{50}[F] × LD_{50}[M]; only 3 replicate pairs mated in LD_0[F] × LD_{50}[M] during the observation period. Many times, the untreated male was observed to court the treated female through antenna sparring and wing-raising, but the female was unreceptive.

Discussion

Reduction in adult longevity of the German cockroach upon treatment with sublethal doses of deltamethrin and propoxur was observed in this study. Earlier, Abd-Elghafar & Appel (1992) reported similar findings with cyfluthrin; they suggested that increased respiration due to sustained muscle contraction and the release of a paralysis inducing stress factor were the reasons for the decrease in longevity.

The fecundity of female cockroaches in this study also declined upon exposure to sublethal doses of deltamethrin and propoxur. This could be due to the following possibilities: A direct toxic effect of the insecticide which had been left unmetabolized in the body of the parents may be transmitted into the eggs (Abd-Elghafar et al., 1991). This will decrease the oothecal viability. In this study, non-viable oothecae were dropped at 2 different periods. Those dropped between day 1–7 may be infertile oothecae (Hamilton & Schal, 1990), while those aborted after 20 days might be due to reduction in number of viable embryos caused by insecticidal toxic effects transmitted from the parent (Keil & Ross, 1977; Hamilton & Schal, 1990).

On the other hand, parental reproductive physiology may be disrupted due to disturbances of the neurosecretory system. Insect neurosecretory neurons are sensitive to low concentrations of pyrethroids

Table 5. Percentage mortality of F_1 adult males when treated with LD_{50} of deltamethrin and propoxur

LD (F) × LD (M)		Deltamethrin					Propoxur				
		n	No. repl.	% mortality ± S.E.M.	χ^2	P	*n*	No. repl.	% mortality ± S.E.M.	χ^2	P
0	0	100	5	57 ± 3.4	1.9	0.7541	100	5	57 ± 3.7	2.1	0.7174
	10	100	5	57 ± 5.4	3.3	0.5089	100	5	61 ± 1.9	2.7	0.6092
	30	100	5	59 ± 7.0	5.5	0.2397	100	5	53 ± 4.6	1.9	0.7541
	50	100	5	54 ± 4.3	1.8	0.7725	100	5	57 ± 5.2	3.1	0.5412
10	0	100	5	52 ± 4.6	1.8	0.7725	100	5	50 ± 6.1	3.0	0.5578
	10	100	5	60 ± 5.2	4.2	0.3796	100	5	45 ± 5.9	3.3	0.5089
	30	60	3	48 ± 6.0	0.9	0.6376	100	5	56 ± 3.7	1.8	0.7725
	50	30	2[a]	57 ± 3.4	0.5	0.4795	100	5	52 ± 7.8	5.0	0.2873
30	0	60	3	52 ± 1.7	0.1	0.9512	100	5	53 ± 2.0	0.5	0.9735
	10	40	2	55 ± 10.0	1.0	0.3173	100	5	56 ± 2.9	1.4	0.8442
	30	–	–[b]	–	–	–	100	5	49 ± 6.2	3.1	0.5412
	50	–	–[b]	–	–	–	100	5	45 ± 5.0	2.5	0.6446
50	0	40	2	55 ± 5.0	0.4	0.5271	100	5	52 ± 6.6	3.6	0.4628
	10	–	–[b]	–	–	–	100	5	54 ± 3.7	1.4	0.8442
	30	–	–[b]	–	–	–	100	5	39 ± 4.0	3.0	0.5578
	50	–	–[b]	–	–	–	60	3	40 ± 3.9	1.8	0.4066

[a]Only 15 adult males were tested in each replicate.
[b]Not tested due to insufficient adult males.

and the neuroendocrine function can be disrupted (Soderlund & Bloomquist, 1989). As reproduction is neurohormone-regulated, neurohormone inbalances upon insecticide poisoning may affect the normal function (Maddrell & Reynolds, 1972).

Also, disruption of mating behaviour is likely to have an effect on the fecundity of the treated insects. In this study, mating activity was not recorded in LD_{50}[F] × LD_0[M] and LD_{50}[F] × LD_{50}[M] deltamethrin-treated crosses within 24 hours post-pairing in the preliminary study; however, in the LD_0[F] × LD_{50}[M] combination, this activity was present. Treated females were observed to be unreceptive to male courtship. This suggests that the mating behaviour of female cockroaches treated with LD_{50} might have been affected.

Mating behaviour in insects consists of a complex series of behavioural events which are coordinated by the nervous and hormonal systems in a very precise manner. Each behavioural event may be affected by sublethal doses of insecticides, leading to reproductive failure. Effects on mate-locating, courtship and copulation time may also result in a decrease in offspring production (Haynes, 1988). Disruption of mating behaviour by sublethal doses of insecticides has been documented in many insects. Floyd & Crowder (1981) reported that permethrin-treated male pink bollworm moth (*Pectinophora gossypiella*) failed to respond by wing-fanning at low concentrations of pheromone. The male flight and courtship frequencies of the cabbage looper moth (*Trichoplusia ni*) also decreased upon contacting sublethal doses of cypermethrin and chlordimeform (Clark & Haynes, 1992a, b). The effect of sublethal doses of insecticides on mating behaviour of the German cockroach has never been fully documented and should be studied in future.

Doses of insecticides applied on adult females showed effects on oothecal production while this parameter was not dependent on the doses of insecticides applied on the adult males. This finding supported earlier reports that virgin female German cockroaches were capable of producing oothecae, although the oothecae will not hatch (Roth & Stay, 1962; Adiyodi & Adiyodi, 1974). For the hatching of oothecae and production of offsprings, the eggs must be fertilized and this is where paternal contribution will come in. This explains why insecticides applied on adult males have an effect on these two parameters. No interaction between insecticide dose levels applied on males and females were seen; this suggested that the effect

of insecticides on both sexes was additive, rather than interactive.

All crosses (including LD_{50}[F] × LD_{50}[M]) did not cause an increase in insecticidal tolerance in the F_1 generation. In an earlier review, Crow (1957) had listed some studies which also showed similar findings. This may be due to the low resistance gene frequency of the susceptible cockroach strain used in this study. If a similar study is conducted on a field strain, the results may be different. With a field collected strain of *Culex quinquefasciatus* mosquito, a 3-fold increase in malathion tolerance was obtained when mass-crossing between male and female survivors of LC_{50} was done (C.Y. Lee, unpublished).

One problem often faced in studies on sublethal effects of insecticides is the difficulty of differentiating whether the effect is due to insecticidal action or to the inherent characteristics of the insecticide-selected individuals (Croft, 1990). This is because resistant insects often have reduced reproductive potential and longevity when compared with their susceptible counterpart (Lee et al., 1996c). With the result obtained in this study (where it has been found that sublethal doses of insecticides did not increase tolerance in the F_1 generation), the possibility of having reduced longevity and fecundity due to selection of resistant individuals is ruled out.

Although fecundity and longevity of adult cockroaches were reduced with sublethal deltamethrin and propoxur exposures, applications of lower rates of these insecticides should not be practised. Many studies have shown that sublethal amounts of insecticides induced dispersal of German cockroaches from treated surfaces (Bret & Ross, 1985, 1986a, b) and from its vapour (Wooster & Ross, 1989), thus resulting in control failures.

Abd-Elghafar & Appel (1992) predicted that if an insecticide reduced the longevity and fecundity of the adult German cockroach with increasing sublethal doses, a population exposed to sublethal amounts of this insecticide would decrease rapidly due to shorter longevity and will result in a distribution of predominantly small nymphs. If the prediction is accurate, similar findings will also be obtained with deltamethrin and propoxur. It would be interesting to study the effect of sublethal doses of insecticide on the age-class distribution of the German cockroach population under field conditions; the information generated will ultimately help in better planning of insecticide application.

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