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Absence of a fitness penalty in insecticide-resistant German cockroaches, *Blattella germanica* (L.) (Dictyoptera: Blattellidae)

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We investigated life-history variables of insecticide-resistant and insecticide-susceptible German cockroaches, *Blattella germanica* (L.) with a view to finding evidence of reduced fitness in the resistant strains compared to the susceptible ones. Most resistant strains showed no significant difference in nymphal development period, preoviposition period, incubation period, nymphal and oothecal production, ootheca dimensions, nymphal survivorship, and adult longevity compared to those of the susceptible strain. However, in resistant strains each instar stage was shorter compared to the equivalent instar of the susceptible strain. These results indicate that resistance is not a costly trait in the German cockroach, contrary to expectations.

Keywords: fitness; *Blattella germanica*; insecticide resistance; fecundity; development

1. Introduction

The German cockroach, *Blattella germanica* (L.), is an important pest in the urban environment. In Malaysia and Singapore, it is frequently found in food preparation outlets such as commercial kitchens and restaurants, and occasionally in hotels, theatres, supermarkets, and naval ships (Lee et al. 1996a; Lee and Ng 2009). German cockroaches are mechanical vectors of many pathogens, including bacteria, helminths, protists, and viruses (Brenner 1995; Lee 1997, 2007), and allergies and asthma can be triggered by inhaling or ingesting cockroach allergens such as faeces and saliva (Lee and Ng 2009). The use of insecticides remains the most effective way of managing cockroach populations. However, heavy reliance on insecticides has led to the development of insecticide resistance in domestic cockroaches (Lee et al. 1996a; Chai and Lee 2010).

Previous studies reported that insecticide-resistant German cockroaches showed reduced fitness compared to their susceptible counterparts. For example, Grayson (1953, 1954) reported that insecticide-resistant strains of German cockroach produced fewer nymphs per egg case, fewer nymphs per female, and smaller egg cases (oothecae) than non-resistant strains. The body weight of adult resistant individuals was also significantly lower than that of non-resistant individuals. Differences in life-history variables such as incubation period, nymphal development period, adult longevity (Perkins and Grayson 1961), and preoviposition period (Ross 1991; Lee et al. 1996b) between resistant and non-resistant strains also were documented. Differences in life-history variables between resistant and susceptible strains have also been observed in other arthropods, including green peach aphids (Banks and Needham 1970), houseflies (Pimentel et al. 1951; Afifi and Knutson 1956; Hunter et al. 1958; Underhill and Merrell 1966; Roush and Plapp 1982), spider mites (Lehr and Smith 1957), mosquitoes (Amin and White 1984; Khatib and Georghiou 1985), and boll weevils (Thomas and Brazzel 1961).

Lee et al. (1996b) found that all insecticide-resistant strains of the German cockroach exhibited longer nymphal development, incubation, and preoviposition periods compared to a laboratory susceptible strain. Reduced fecundity and shorter longevity were also detected in resistant strains. In contrast, Perkins and Grayson (1961) found that while DDT-resistant strains had a shorter incubation period and a longer nymphal development period, the longevity of resistant female cockroaches was significantly greater than that of normal females. Ross (1991) showed that one of the pyrethroid-resistant strains of German cockroach was able to reproduce comparably to the susceptible strain, whereas two other resistant strains showed lower reproductive potential than the susceptible strain. Several researchers have reported insecticide resistance-induced increased fitness to exist in green peach aphids (Eggers-Schumacher 1983), diamondback moths (Sayyed and Wright 2001), and green lacewings (Pathan et al. 2010).

A better understanding of how insecticide resistance affects the fitness of the German cockroach will assist in understanding the influence of the life-history

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variables on its population growth, so that a better control strategy can be developed. In this study, we compared the fitness of field-collected resistant German cockroaches and laboratory susceptible German cockroaches, in order to assess whether by evolving insecticide resistance, the cockroaches have incurred a fitness penalty.

2. Materials and methods

2.1. Cockroach strains

The following six resistant strains of German cockroach were used in this study: B1 Tampines Central, Beach Road, Boat Quay, Victoria Street, Cavenagh Road, and Ghimmoh Road. The origin of these strains is detailed in Chai and Lee (2010). Table 1 lists the insecticide resistance profiles for these strains. The cockroaches were maintained in the laboratory without any insecticide selection pressure for 5 years prior to this study. A laboratory susceptible strain obtained from the Environmental Health Institute (EHI), National Environment Agency, Singapore, was used for comparison. All cockroaches were cultured in 38 × 22 × 27-cm polyethylene aquaria under laboratory conditions of 26 ± 1°C, 60 ± 5% RH, and a light:dark regime of 12 h L:12 h D. The insects were provided *ad libitum* with dry dog food and water.

2.2. Nymphal development

Gravid females were separated from culture tanks and reared in plastic containers (1000 ml, 17.5 × 11.5 × 6 cm) with food and water provided. They were observed daily for the emergence of nymphs. Upon emergence, newly hatched nymphs from each strain were collected and kept in small plastic containers (250 ml, 11.5 × 4 cm, diam. × height) with water and food provided. Folded pieces of corrugated cardboard (3 × 4 cm) were used as refuges. The inner surface of the containers was coated with fluon to prevent the nymphs from escaping. Each container (replicate) contained 10 individuals, and the experiment was replicated 12 times for each strain. All nymphs were kept under the laboratory conditions described above. The nymphs were observed daily and each molting event was recorded.

2.3. Fecundity and longevity

Late instar nymphs from each strain were isolated from the rearing tanks into containers (1000 ml, 17.5 × 11.5 × 6 cm). The cockroaches were observed daily, and newly emerged adults were segregated to prevent mating. Males and females were kept separately for 24 h before being paired in plastic containers (250 ml, 11.5 × 4 cm, diam. × height) that were provisioned with dry dog food, water in a cotton-stoppered glass vial, and a folded corrugated cardboard (3 × 4 cm) harbourage. Twenty replicates for each strain were used for this study and they were monitored daily for reproduction events. Nymphs produced from the hatching of each ootheca were counted and transferred into a new container. The hatched oothecae were collected for subsequent measurement. All collected nymphs were reared to adults to determine nymphal survivorship. The emerged adults were sexed to determine the sex ratio. Only adults that originated from the first through to the fifth ootheca were used in sex ratio study.

Data on reproductive traits such as preoviposition period and incubation period were generated from daily observations. The preoviposition period is the interval between the hatching of an ootheca and the emergence of the following one, and the first preoviposition period is the time from pairing until the emergence of the first ootheca. Incubation period refers to the period during which females carry each ootheca. The number of oothecae per female and the total number of hatched oothecae per female were also determined. Observations to determine adult longevity were made until all individuals died. In this study, cockroaches were not replaced after they died.

2.4. Ootheca measurement

The collected oothecae were observed under an Olympus SZ61 stereo microscope (Olympus, Tokyo, Japan) with IC Imaging Standard V2.1 (The Imaging

Table 1. Insecticide resistance profiles of all strains of the German cockroach used in this study.

Strain	Resistance ratio[1], RR_{50}				
	Deltamethrin	Chlopyrifos	Fipronil	Indoxacarb	Imidacloprid
B1 Tampines Central	1.5	0.9	1.5	1.7	2.5
Beach Road	20.9	0.6	1.2	3.0	1.7
Boat Quay	24.7	8.7	1.3	5.3	1.6
Victoria Street	14.4	0.9	1.2	2.6	2.1
Cavenagh Road	55.6	5.8	2.8	9.9	2.0
Ghimmoh Road	5.8	2.6	2.0	2.5	2.3

[1]Ang and Lee, unpublished.

Source Europe, Bremen, Germany). Lengths and widths of the oothecae from each strain were measured using Analysis Image Processing Software (Soft Imaging System, Münster, Germany).

2.5. *Population growth parameters*

The life-history variable data were analyzed according to the theory of age-stage, two-sex life table (Chi and Liu 1985) according to the method described by Chi (1988). Growth parameters such as intrinsic rate of natural increase (r_m), net reproductive rate (R_0) and generation time (T) for all strains of cockroach were calculated using a computer program TWOSEX-MSChart (Chi 2009).

2.6. *Data analysis*

All data were subjected to one-way ANOVA and separated using Tukey's HSD at $P = 0.05$. Data (in percentages) were transformed into arc-sine values prior to ANOVA. The χ^2-test was used to determine whether the adult sex ratio differed from 1:1. The relationship between insecticide resistance levels and population growth parameters was explored using correlation analysis. All statistical analyses were conducted using SPSS version 11.5.0 (SPSS 2002).

3. Results and discussion

3.1. *Nymphal development*

The mean nymphal developmental period for the EHI susceptible strain was 55.1 ± 0.8 d (Table 2). This result agrees with that reported by Ross (1991), who found that two susceptible strains had nymphal developmental periods of 53.9 and 58.6 d, respectively. In contrast, a shorter nymphal developmental period was reported by Lee et al. (1996b) and Nurmastini (2004) for another susceptible strain (ICI) (45.6 ± 0.3 d and 42.4 ± 0.4 d, respectively). Perkins and Grayson (1961) reported that the nymphs of a susceptible strain took only about 33 d to develop from the immature stage into adults. These variations in nymphal developmental period may be due to differences in strain origin (Roush and McKenzie 1987), experimental conditions such as temperature and relative humidity, nutrition (Noland et al. 1949; Khuhro et al. 2007), and aggregation effects (Izutsu et al. 1970). The nymphal developmental periods in this study ranged from 41 to 105 d among resistant strains. The Beach Road strain had the longest developmental period for both males and females (54.9 ± 1.0 d and 55.7 ± 1.1 d, respectively), whereas the Boat Quay strains required only 50.1 ± 0.5 d to reach adulthood (Table 2). The nymphal developmental period for both males and females of resistant strains B1 Tampines Central, Beach Road, and Cavenagh Road was not significantly different compared with the EHI strain. There were no significant differences between Victoria Street and EHI strains, except for the female individuals in both strains. However, the developmental period for both males and females of the Boat Quay and Ghimmoh Road strains was significantly shorter than that of the EHI strain. Pathan et al. (2010) reported that insecticide-resistant populations of the lacewing *Chrysoperla carnae* (Stephens) required a significantly shorter period to reach adulthood compared to a susceptible laboratory population. Egger-Schumacher (1983) also found a shorter nymphal developmental period in insecticide-resistant individuals of the aphid *Myzus persicae* (Sulzer) compared to susceptible individuals. That author proposed that the differences between resistant and susceptible individuals were adaptive. The females of the B1 Tampines Central, Beach Road, Boat Quay, and Cavenagh Road strains matured earlier than the males. In contrast, the males of EHI, Victoria Street and Ghimmoh Road strains reached adulthood faster than the females.

In this study, the number of moults required to reach adulthood for both resistant and susceptible cockroaches was five to six for males and six for females. This result is consistent with that reported by Tanaka and Hasegawa (1979). Several authors (Willis et al. 1958; Roth and Stay 1962) previously reported that the number of instars in German cockroaches varies from five to seven for males and six to seven for females. This variation in the number of moults may be due to differences in environmental conditions (Tanaka

Table 2. Nymphal development period of all strains of the German cockroach.

Strain	Mean ± SEM[1] (d)						
	n	Male	Range	*n*	Female	Range	Overall
EHI (susceptible)	44	55.5 ± 1.3 c	43–73	55	54.9 ± 1.1 cd	44–94	55.1 ± 0.8
B1 Tampines Central	55	53.8 ± 0.7 bc	42–68	45	54.7 ± 1.4 bcd	46–105	54.2 ± 0.7
Beach Road	56	54.9 ± 1.0 bc	42–79	48	55.7 ± 1.1 d	44–74	55.3 ± 0.7
Boat Quay	50	49.4 ± 0.8 a	41–67	59	50.8 ± 0.6 ab	43–65	50.1 ± 0.5
Victoria Street	63	53.2 ± 0.9 abc	42–90	49	51.2 ± 1.0 abc	45–80	52.3 ± 0.7
Cavenagh Road	44	52.2 ± 1.1 abc	42–76	62	53.3 ± 0.9 abcd	44–73	52.8 ± 0.7
Ghimmoh Road	52	50.9 ± 0.9 ab	41–70	57	50.4 ± 0.8 a	45–76	50.7 ± 0.6

[1]Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD).

1981). Generally, the EHI strain took longer to complete each instar compared with the resistant strains (Figure 1). The Ghimmoh Road strain took the least amount of time. The durations of each instar of all strains ranged from 6 to 10 d. The durations of the first and second instars of the B1 Tampines Central, Beach Road, Boat Quay, Cavenagh Road, and Ghimmoh Road strains were significantly shorter than those of the EHI and Victoria Street strains (Figure 1). However, the durations of the third and fourth instars of all resistant strains were significantly shorter than that of the EHI strain, with the exception of the fourth instar of the Beach Road strain. The duration of the fifth instar did not differ significantly among the B1 Tampines Central, Beach Road, Cavenagh Road, and EHI strains, whereas the Boat Quay, Victoria Street, and Ghimmoh Road strains had a significantly shorter instar period than the EHI strain (Figure 1). The nymphs of the EHI strain also required a shorter time to develop from the fifth to the sixth instar compared with the resistant strains (Figure 1).

3.2. *Preoviposition periods*

The mean preoviposition period for the EHI strain was 7.0 ± 0.2 d (Table 3). This result is accords with those obtained by Archbold et al. (1987) on the UCR (fungus-uninfected) strain (7.1 ± 0.4 d). Durbin and Cochran (1985) recorded a shorter preoviposition period in a normal wild-type stock strain (6.4 ± 0.9 d). However, Roth and Stay (1962), Abd-Elghafar and Appel (1992), and Lee et al. (1998) recorded a longer preoviposition period in normal (~10 d), susceptible (8.1 ± 1.1 d), and ICI strains (10.0 ± 0.5 d) under similar rearing conditions. Generally, the mean preoviposition periods did not differ significantly between EHI and all resistant strains analyzed in this study

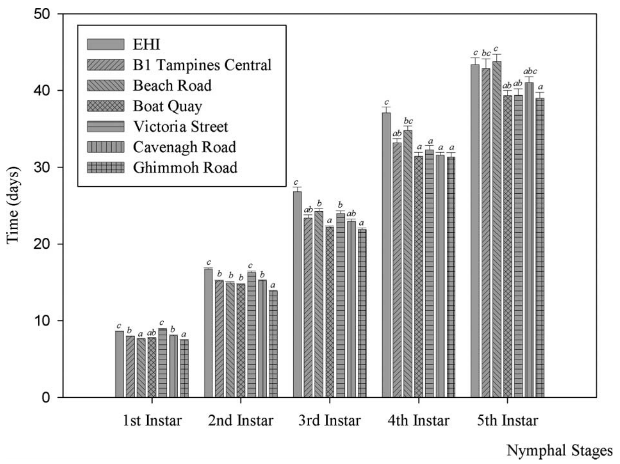

Figure 1. Cumulative duration of the first five instar stages for all strains of the German cockroach. Means followed by different letters within different strains are significantly different ($P < 0.05$; Tukey's HSD).

(Table 3). Our results also show that the first preoviposition period was longer than the subsequent preoviposition periods in all strains. A similar observation was reported by Willis et al. (1958) for most cockroach species. Female German cockroaches of the EHI strain required an average of 8.5 d after pairing to produce the first ootheca. This period was shorter than that reported by Roth and Stay (1962) and Durbin and Cochran (1985). However, our result accords with that reported by Lee et al. (1996b) for the ICI strain (8.4 ± 0.2 d).

3.3. *Incubation periods*

Table 3 shows the oothecal incubation periods for all strains. The mean incubation period for the EHI strain was 19.7 ± 0.2 d, which accords with that reported by Lee and Heng (2000) for the ICI strain (~18–20 d). However, the period was longer than that reported for the UCR strain (15.6 ± 0.2 d) (Archbold et al. 1987) and a normal strain (14–17 d) (Khuhro et al. 2007) and shorter than that of the ICI strain (25.0 ± 0.2 d) (Lee et al. 1996b). Tanaka (1976) also reported that the whole developmental process of the cockroach embryo took 24 d to reach the last stage prior to hatching. Previous studies showed that the incubation period could be reduced by improving diet (Khuhro et al. 2007), food, and water availability (Durbin and Cochran 1985; Lee and Heng 2000) and increasing the temperature (~30°C) (Archbold et al. 1987; Khuhro et al. 2007). Overall, the mean incubation periods for all oothecae were not significantly different between the EHI and resistant strains, except for Boat Quay for the first (21.7 ± 0.2 d) and second ootheca (20.6 ± 0.2 d) (Table 3).

3.4. *Fecundity*

Table 3 shows the number of nymphs produced per oothecae for all strains. There was no significant difference between the EHI and resistant strains, except Boat Quay (24.7 ± 4.9 nymphs) and Victoria Street (25.8 ± 3.9 nymphs) at the first ootheca. Both resistant strains showed significantly lower nymphal production compared to the EHI strain. Overall, females in all strains produced consistent numbers of nymphs after the first oothecal production. Mean number of nymphs produced per ootheca in the EHI strain was 36.4 ± 1.1. This result is similar to that reported by Lee and Heng (2007) for the ICI strain (34.9 ± 0.8 nymphs). The mean number of nymphs produced per ootheca (overall) in all resistant strains showed no significant difference from that of the EHI strain, except for the Victoria Street strain which produced a significantly lower number of nymphs per ootheca (29.7 ± 2.5 nymphs).

There was no significant difference between the EHI and resistant strains in term of the number of

Table 3. Mean preoviposition, incubation period and number of nymphs produced per oothecae for the first and subsequent oothecae in all strains of the German cockroach.

		Preoviposition period (d)		Incubation period (d)		Number of nymphs/ ootheca	
Oothecal no.	Strain	*n*	Mean ± SEM[1]	*n*	Mean ± SEM[1]	*n*	Mean ± SEM[1]
1	EHI (susceptible)	20	8.5 ± 0.3 ab	20	20.4 ± 0.1 a	20	38.7 ± 0.8 b
	B1 Tampines Central	20	9.3 ± 0.6 ab	19	21.0 ± 0.3 ab	20	38.9 ± 1.2 b
	Beach Road	20	8.1 ± 0.3 ab	20	20.5 ± 0.2 a	20	40.8 ± 1.7 b
	Boat Quay	20	10.1 ± 0.8 b	20	21.7 ± 0.2 b	20	24.7 ± 4.9 a
	Victoria Street	20	9.6 ± 0.7 ab	19	20.8 ± 0.1 a	20	25.8 ± 3.9 a
	Cavenagh Road	20	9.3 ± 0.5 ab	20	20.3 ± 0.1 a	20	35.1 ± 1.0 b
	Ghimmoh Road	20	8.1 ± 0.2 a	20	21.0 ± 0.2 ab	20	40.8 ± 1.0 b
2	EHI (susceptible)	17	6.5 ± 0.4 ab	15	19.5 ± 0.2 a	17	35.7 ± 2.1 ab
	B1 Tampines Central	14	6.1 ± 0.3 ab	13	20.3 ± 0.2 ab	14	38.3 ± 1.2 ab
	Beach Road	19	5.8 ± 0.2 ab	18	19.3 ± 0.2 a	19	42.3 ± 1.5 b
	Boat Quay	15	5.2 ± 0.4 a	13	20.6 ± 0.2 b	15	35.4 ± 1.7 ab
	Victoria Street	17	7.3 ± 0.6 b	14	20.0 ± 0.0 ab	17	29.7 ± 8.4 a
	Cavenagh Road	18	6.3 ± 0.5 ab	17	19.5 ± 0.2 a	18	32.7 ± 3.2 ab
	Ghimmoh Road	13	5.7 ± 0.3 ab	13	20.3 ± 0.3 ab	13	38.2 ± 1.4 ab
3	EHI (susceptible)	13	6.4 ± 0.6 a	13	19.5 ± 0.2 a	13	36.0 ± 1.9 a
	B1 Tampines Central	13	6.2 ± 0.4 a	13	19.6 ± 0.2 a	13	35.6 ± 1.0 a
	Beach Road	18	6.0 ± 0.3 a	16	19.3 ± 0.2 a	18	41.0 ± 1.5 a
	Boat Quay	12	5.2 ± 0.2 a	11	19.8 ± 0.2 a	12	33.6 ± 2.8 a
	Victoria Street	14	6.0 ± 0.0 a	12	19.5 ± 0.5 a	14	39.0 ± 2.0 a
	Cavenagh Road	16	6.3 ± 0.4 a	15	19.5 ± 0.2 a	16	36.7 ± 1.1 a
	Ghimmoh Road	12	5.4 ± 0.2 a	12	19.9 ± 0.1 a	12	40.9 ± 0.7 a
4	EHI (susceptible)	13	5.9 ± 0.5 a	13	19.5 ± 0.3 a	13	33.8 ± 4.9 a
	B1 Tampines Central	10	6.4 ± 0.5 a	10	19.0 ± 0.0 a	10	33.6 ± 3.6 a
	Beach Road	16	6.0 ± 0.4 a	16	19.1 ± 0.3 a	16	40.8 ± 1.4 a
	Boat Quay	10	5.5 ± 0.5 a	9	19.8 ± 0.4 a	10	36.4 ± 1.9 a
	Victoria Street	6	6.0 ± 1.0 a	5	19.0 ± 1.0 a	5	34.5 ± 3.5 a
	Cavenagh Road	13	6.0 ± 0.6 a	13	19.5 ± 0.5 a	13	38.0 ± 1.0 a
	Ghimmoh Road	9	5.5 ± 0.2 a	9	19.5 ± 0.2 a	9	39.5 ± 2.2 a
5	EHI (susceptible)	10	5.5 ± 0.5 a	10	17.3 ± 0.3 a	9	38.0 ± 4.0 a
	B1 Tampines Central	8	5.5 ± 0.3 a	8	17.3 ± 0.3 a	8	37.3 ± 2.3 a
	Beach Road	13	5.7 ± 0.5 a	13	17.0 ± 0.2 a	14	37.8 ± 2.9 a
	Boat Quay	8	5.4 ± 0.5 a	8	16.7 ± 0.3 a	8	34.0 ± 3.1 a
	Victoria Street	3	6.0 ± 0.0 a	1	17.0[2]	2	38.0 ± 0.0[2]
	Cavenagh Road	11	5.0 ± 1.0 a	11	16.0 ± 0.0 a	9	34.5 ± 0.5 a
	Ghimmoh Road	9	4.7 ± 0.2 a	12	17.0 ± 0.3 a	8	37.8 ± 3.2 a
6[3]	EHI (susceptible)	8	6.0 ± 0.6 a	1	18.0	2	27.0 ± 15.0
	B1 Tampines Central	6	5.5 ± 0.3 a	1	20.0	1	39.0
	Beach Road	13	6.3 ± 0.7 a	13	19.4 ± 0.2	9	35.2 ± 5.0
	Boat Quay	7	7.3 ± 1.2 a	1	19.0	1	38.0
	Victoria Street	1	5.0[2]	1	20.0	1	27.0
	Cavenagh Road	4	6.5 ± 0.5 a	1	19.0	1	39.0
	Ghimmoh Road	6	5.0 ± 0.0 a	6	19.0 ± 0.0	2	39.5 ± 1.5
7[3]	B1 Tampines Central	1	6.0	1	20.0	1	35.0
	Beach Road	5	7.4 ± 1.0	2	17.0 ± 5.7	2	25.5 ± 0.5
	Boat Quay	1	7.0	1	20.0	1	9.0
	Cavenagh Road	1	4.0	1	21.0	1	31.0
	Ghimmoh Road	2	5.0 ± 0.0	2	21.0 ± 0.0	2	27.0 ± 9.0
8[3]	B1 Tampines Central	1	6.0	1	20.0	1	35.0
	Beach Road	1	6.0	1	20.0	1	9.0
	Cavenagh Road	1	8.0	1	18.0	1	19.0
	Ghimmoh Road	2	5.0 ± 0.0	1	21.0	1	36.0
9[3]	Cavenagh Road	1	6.0	1	19.0	1	20.0
Overall	EHI (susceptible).	20	7.0 ± 0.2 ab	20	19.7 ± 0.2 a	20	36.4 ± 1.1 bc
	B1 Tampines Central	20	7.1 ± 0.3 ab	20	19.8 ± 0.2 a	20	37.1 ± 0.8 c

(*continued*)

Table 3. (*Continued*).

Oothecal no.	Strain	Preoviposition period (d)		Incubation period (d)		Number of nymphs/ootheca	
		n	Mean ± SEM[1]	n	Mean ± SEM[1]	n	Mean ± SEM[1]
	Beach Road	20	6.4 ± 0.2 a	20	19.2 ± 0.2 a	20	40.1 ± 0.9 c
	Boat Quay	20	6.8 ± 0.5 ab	20	20.1 ± 0.3 a	20	31.4 ± 1.9 ab
	Victoria Street	20	8.0 ± 0.5 b	20	20.1 ± 0.3 a	20	29.7 ± 2.5 a
	Cavenagh Road	20	7.3 ± 0.3 ab	20	19.4 ± 0.2 a	20	35.7 ± 0.7 bc
	Ghimmoh Road	20	6.1 ± 0.2 a	20	19.8 ± 0.2 a	20	39.0 ± 0.8 c

[1]Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD).
[2]Not included in the statistical analysis because only one ootheca was produced.
[3]Oothecae 6, 7, 8, and 9 were not included in the statistical analysis because fewer than three strains produced more than three oothecae.

produced and hatched oothecae per female. Beach Road strain produced the highest number of oothecae (5.5 ± 0.6 oothecae) among all strains and 4.7 ± 0.5 oothecae were viable. In contrast, the Victoria Street strain produced the lowest number of oothecae (2.6 ± 0.6 oothecae) compared with the other strains. The mean total nymphs produced per female in the EHI strain was 97.2 ± 17.3 nymphs. This result differed from that reported by Lee et al. (1996b) for the ICI strain (139.4 ± 8.0 nymphs). The discrepancy of nymphal production in our study might be explained by a difference in the number of hatched oothecae. The ICI strain (4.2 ± 0.3 oothecae) showed greater fecundity (Lee et al. 1996b) than the current EHI strain (2.7 ± 0.5 oothecae). The Victoria Street strain produced the lowest number of viable oothecae, which subsequently affected the total nymphal production (59.4 ± 24.0 nymphs). The Beach Road strain had the highest nymphal production per female (193.9 ± 17.9 nymphs) because it produced the highest number of nymphs per ootheca (40.1 ± 0.9 nymphs) (Table 3). We also observed a higher oothecal abortion rate in older females of all strains. This was presumably due to the poor physiological condition of the older female cockroach (Atkinson et al. 1991). The incubation periods for non-viable oothecae and viable oothecae were similar. This scenario was reported previously by Willis et al. (1958). They found that in *Blattella vaga* (Hebard), the older females produced and carried normal-sized oothecae and carried them for the same length of incubation period as viable oothecae but the eggs were unable to hatch. Willis et al. (1958) suggested that after a single mating, the number of sperm present in the female was insufficient to completely fertilize the oothecae, which subsequently resulted in the production of some non-viable oothecae.

3.5. *Nymphal survivorship*

Table 4 shows the mean nymphal survivorship as a percentage. Nymphal survivorship was highest for the Victoria Street strain (97.0 ± 0.8%), and this was the only resistant strain with significantly higher survivorship than the EHI strain (90.0 ± 1.9%). This result accords with the findings of Lee et al. (1996b). They reported that the ICI strain showed higher nymphal survivorship (90.9 ± 0.3%) than the resistant strains (~85–90%).

Table 4. Total number of nymphs produced per female and nymphal survivorship (%) for all strains of the German cockroach.

Strain	n	Total of nymphs produced per female[1]	Mean nymphal survivorship[1] (%)
EHI (susceptible)	20	97.2 ± 17.3 a	90.0 ± 1.9 ab
B1 Tampines Central	20	148.3 ± 25.3 ab	85.9 ± 1.9 a
Beach Road	20	193.9 ± 17.9 b	91.7 ± 1.2 ab
Boat Quay	20	121.3 ± 32.9 ab	86.3 ± 2.6 a
Victoria Street	20	59.4 ± 24.0 a	97.0 ± 0.8 c
Cavenagh Road	20	107.0 ± 18.3 ab	92.8 ± 1.9 bc
Ghimmoh Road	20	152.5 ± 24.2 ab	94.5 ± 0.9 bc

[1]Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD).

3.6. *Ootheca measurement*

Table 5 shows the ootheca measurements of susceptible and resistant strains of the German cockroach. All resistant strains showed no significant difference from the EHI strain in terms of the length of measured oothecae, except for the Victoria Street strain (5.73 ± 0.42 mm), which was significantly shorter than the EHI strain (6.89 ± 0.13 mm). The lengths and widths of oothecae produced by the EHI strain were smaller than the susceptible laboratory-reared strain (length, 8.21 ± 0.69 mm; width, 3.58 ± 0.19 mm) reported by Wright (1968) and those of the non-resistant strain (length, ~8.1 mm; width, ~3.7 mm) reported by Grayson (1954). The only significant difference in width between the EHI and resistant strains was for the Boat Quay strain; the oothecae produced by the Boat Quay strain (3.24 ± 0.05 mm) were significantly wider than those of the EHI strain (3.04 ± 0.03 mm).

3.7. Adult sex ratio

The adult sex ratios in all strains did not deviate from the 1:1 ratio. The male:female ratios ranged from 0.89–1.18:1.00 with χ^2 values of 0.07 – 2.67. This result was similar to that reported in previous studies (Wright 1968; Archbold et al. 1987; Ross 1991; Lee et al. 1996b).

3.8. Adult longevity

The mean adult longevity of all strains is shown in Table 6. Generally, adult females lived longer than adult males (Perkins and Grayson 1961; Archbold et al. 1987; Ross and Mullins 1995; Lee et al. 1996b). Comparison of the longevity of males and females in all strains indicated no significant difference among the strains, except for the Beach Road strain. Both adult males and females in the Beach Road strain had the highest mean longevity (123.8 ± 10.8 d and 161.0 ± 19.1 d, respectively) of the strains studied. Longevities of adult males (72.1 ± 9.7 d) and adult females (136.4 ± 19.4 d) of the EHI strain were shorter than the values reported for the ICI strain (male, 115.1 ± 7.4 d; female, 165.8 ± 10.3 d) (Lee et al. 1996b) and the UCR strain (male, 122.8 ± 3.0 d; female, 181.5 ± 2.4 d) (Archbold et al. 1987). However, the female longevity of the EHI strain was higher than that of the females in the laboratory-susceptible strain (57.28 ± 29.97 d) and the normal strain (43.37 ± 2.2 d) studied by Wright (1968) and Perkins and Grayson (1961), respectively.

3.9. Population growth parameters

The population growth parameters of all strains of the German cockroach are shown in Table 7. The mean intrinsic rate of natural increase for EHI susceptible strain was 0.0368 and this value was lower than reported for that of the other susceptible strains such as the ICI strain ($r_m = 0.0468$), and that of the UCR strain ($r_m = 0.052$) (Lee et al. 1996b; Archbold et al. 1987), respectively. Variation in r_m was likely due to differences in strain and experimental conditions (Lee et al. 1996b). All resistant strains showed no significant difference from the EHI strain for all growth parameters. In addition, no significant correlations were found between resistance levels and the various growth parameters (Pearson's correlation, $P > 0.05$).

Our study has revealed many similarities in the life-histories of insecticide-susceptible and resistant strains of the German cockroach. One possible reason for the

Table 5. Ootheca measurements for all strains of the German cockroach.

Strain	n^2	Mean ± SEM[1] Length (mm)	Mean ± SEM[1] Width (mm)
EHI (susceptible)	25	6.89 ± 0.13 b	3.04 ± 0.03 a
B1 Tampines Central	13	6.94 ± 0.23 b	3.15 ± 0.04 ab
Beach Road	26	7.09 ± 0.13 b	3.24 ± 0.03 ab
Boat Quay	12	6.76 ± 0.22 b	3.24 ± 0.05 b
Victoria Street	9	5.73 ± 0.42 a	3.19 ± 0.09 ab
Cavenagh Road	13	6.41 ± 0.17 ab	3.12 ± 0.08 ab
Ghimmoh Road	15	7.10 ± 0.16 b	3.24 ± 0.03 ab

[1]Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD).
[2]Total number of oothecae measured from first, second, and third oothecae.

Table 6. Mean longevity of adult males and females for all strains of the German cockroach.

Strain	n	Mean ± SEM[1] (d) Male	Mean ± SEM[1] (d) Female
EHI (susceptible)	20	72.1 ± 9.7 a	136.4 ± 19.4 ab
B1 Tampines Central	20	111.6 ± 13.3 ab	105.2 ± 17.5 ab
Beach Road	20	123.8 ± 10.8 b	161.0 ± 19.1 b
Boat Quay	20	93.9 ± 11.8 ab	100.9 ± 19.0 ab
Victoria Street	20	74.3 ± 9.3 a	77.7 ± 10.2 a
Cavenagh Road	20	69.3 ± 9.7 a	106.6 ± 12.9 ab
Ghimmoh Road	20	81.4 ± 14.4 ab	111.2 ± 21.4 ab

[1]Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD).

Table 7. Population growth parameters for all strains of the German cockroach.

Strain	Growth parameter (Mean ± SEM)[1]: Net reproductive rate, R_0	Intrinsic rate of natural increase, r_m (d^{-1})	Generation time, T (d)
EHI (susceptible)	36.48 ± 6.58 a	0.0368 ± 0.003 a	97.58 ± 5.18 a
B1 Tampines Central	30.53 ± 15.90 a	0.0294 ± 0.005 a	104.35 ± 3.16 a
Beach Road	61.13 ± 13.13 a	0.0364 ± 0.003 a	110.58 ± 3.17 a
Boat Quay	21.23 ± 8.63 a	0.0240 ± 0.006 a	105.45 ± 6.08 a
Victoria Street	13.13 ± 7.77 a	0.0261 ± 0.005 a	90.55 ± 6.00 a
Cavenagh Road	33.13 ± 10.65 a	0.0326 ± 0.004 a	98.33 ± 5.05 a
Ghimmoh Road	44.03 ± 23.75 a	0.0342 ± 0.004 a	100.42 ± 4.37 a

[1]Means followed by different letters within the same column are significantly different ($P < 0.05$; Tukey's HSD).

similarities could be the absence of a co-adaptation effect (i.e. when resistant strains are at a serious fitness disadvantage compared with normal strain) (Roush and Mckenzie 1987). Whitehead et al. (1985) reported that six generations of backcrossing between resistant and susceptible individuals might not be sufficient to isolate the fitness modifiers in *Musca domestica* (L.) However, in our study, the resistant strains we used were reared under laboratory conditions for about 5 years. If there were any fitness modifiers, the performance of the resistance allele would already have been improved via the demonstration of a disadvantageous phenotype. Thus, we suggest that the mechanism of resistance was not deleterious and that fitness modifiers were absent in the resistant strains used in our study. All the cockroach populations have been maintained in laboratory conditions without any insecticide pressure. Resistance level became stable after long period of maintenance in the laboratory (Fragoso et al. 2005). This condition may have minimized the fitness cost among the resistant strains and resulted in fitness reversion to those closely resembles to laboratory-susceptible population.

Another possible explanation for the observed findings is that most resistant individuals are heterozygous, and heterozygotes are resistant but less compromised in fitness. Ferrari and Georghiou (1981) reported that homozygous resistant individuals of the mosquito *Culex quinquefasciatus* (Say) exhibited reproductive disadvantages (lower fecundity, longer developmental period, and poorer egg viability) compared with susceptible individuals, but heterozygous resistant individuals showed limited or no reproductive disadvantage. Curtis et al. (1978) suggested that heterozygous resistant mosquitoes may have higher reproductive rates and are less sensitive to insecticide treatment after being exposed to a sublethal insecticide dose. Roush and Plapp (1982) reported that in the housefly *Musca domestica*, the biotic potential of heterozygous individuals is minimally different than that of susceptible individuals, and they suggested that the resistant gene is dominant in terms of resistance expression but recessive in terms of adverse effects on biotic potential. Although the resistant genotypes of the cockroaches used in our study are unknown, it is possible that the resistant gene in our strains may be recessive in the expression of biotic potential.

Perkins and Grayson (1961) noted that the nymphal developmental period in a field-resistant strain was similar to that in the normal strain, whereas two resistant strains evolved under laboratory selection were significantly different from the normal strain with respect to that trait. Roush and Mckenzie (1987) reported that resistant strains selected under laboratory condition usually developed polygenic resistance, whereas the field-selected resistant strains were only able to generate monogenic resistance. All resistant strains used in this study were field-collected strains, and they demonstrated moderate resistance to pyrethroids, and low resistance to other insecticide classes. Besides, previous studies (Roush and Mckenzie 1987; Wang et al. 2004) suggested there is a direct relationship between a specific resistance mechanism and fitness disadvantages. Fitness disadvantages are mostly associated with resistance due to the esterase enzyme (Roush and Mckenzie 1987), while other authors reported a few disadvantages in the case of target site insensitivity (Oliveira et al. 2007) and oxidative detoxification. Rodcharoen and Mulla (1997) hypothesized that the lower fecundity and fertility in resistant individuals of *C. quinquefasciatus* likely were related to metabolic resistance that developed during the selection process. In our study, the Beach Road, Boat Quay, Victoria Street, and Cavenagh Road strains were possibly exhibiting target site insensitivity (*kdr* type) for pyrethroid resistance (Chai and Lee 2010). Chai and Lee (2010) also suggested that fipronil resistance, which was detected in all resistant strains used in this study, is likely to be due to target site insensitivity (*Rdl* mutation).

Resistance mechanisms and resistance alleles play a role in the determining its fitness of insect pests. However, how these factors interact with one another to affect fitness remains unknown. Further studies are needed to provide a better understanding of this issue. Such an understanding ultimately will assist in insecticide resistance management of the German cockroach.

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