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Comparison of selected biological parameters of laboratory susceptible and field collected strains of the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae)

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ABSTRACT Selected biological parameters of five field collected strains (GoldenSand, Melia I, Kuantan, Lumut and Subang) of the German cockroach, *Blattella germanica* (L.) in Peninsular Malaysia, were compared with that of the laboratory susceptible strain (ICI). All field strains demonstrated longer nymphal development, preoviposition and incubation period, lower fecundity and shorter longevity than the ICI strain. The GoldenSand strain had a lower intrinsic rate of increase (r_n) than the ICI strain, but Melia I showed a comparable r_n value to that of the susceptible strain.

ABSTRAK Parameter-parameter biologi yang terpilih pada lima strain (GoldenSand, Melia I, Kuantan, Lumut dan Subang) lipas Jerman, *Blattella germanica* (L.) dari lapangan, dibanding dengan ciri berkenaan pada strain rentan makmal (ICI). Semua strain lapangan menunjukkan perkembangan nimfa, tempoh pra-peneluran dan pengeraman yang lebih panjang, fekunditi yang lebih rendah dan tempoh hayat yang lebih pendek dari strain ICI. Strain GoldenSand mempunyai kadar peningkatan dalaman (r_n) yang lebih rendah daripada strain ICI, tetapi Melia I menunjukkan nilai r_n yang serupa dengan strain rentan berkenaan.

(German cockroach, biological parameters, field collected strains)

INTRODUCTION

Information on biological parameter differences (e.g. immature development, longevity and fecundity) in susceptible and resistant insects is often conflicting. Crow [1] stated that field populations selected with insecticides often resulted in them being less fit than their susceptible counterparts. Reduced fitness in the resistant German cockroach in the forms of nymphal development [2,3], fecundity [3,4] and longevity [3] had been reported. These reduced fitness were also observed in other insects such as mosquitoes [5-7], house flies [8,9] and boll weevils [10].

Conversely, an increase in or a similarity in fitness in biological parameters in resistant insects when compared to those of the susceptible strains had also been reported. In the German cockroach, Perkins and Grayson [2] reported that organochlorine-resistant strains had longer female longevity than their susceptible counterpart, but no differences were found with male longevity. Wright [11] found that some field collected chlordane-resistant strains had higher fecundity and longer longevity than the susceptible strain. Ross [3] also obtained a pyrethroid-resistant strain collected from a naval ship which had similar reproductive potential to those of two other field collected susceptible strains.

During the course of rearing field-collected German cockroaches for insecticide resistance studies, it was observed that variation occurred in the development of the nymphs of different strains. It was suspected that differences in other biological parameters such as longevity and reproduction were also present. As biological parameter information is essential to a resistance management programme [12,13], the present study was initiated to investigate the above observation.

MATERIALS AND METHODS

German cockroach strains

The five field collected strains used in this study were: GoldenSand, Kuantan, Lumut, Melia I and Subang. The GoldenSand, Melia I and Subang strains were collected from hotels in Penang and Kuala Lumpur, Malaysia, while the Kuantan and Lumut strains originated from naval ships. The susceptibility of these strains to some commonly used insecticides and treatment histories of the premises where the cockroaches were collected have been reported [14]. A brief resistance profiles for these strains are shown in Table 1. For nymphal developmental and longevity studies, the F_1 generation of all strains (except for the Kuantan and Lumut strains for which the F_2 generations were used) were used. On the other hand, the F_2 generations were used for experiments on intrinsic rate of increase (r_n),. The ICI sus-

Table 1. Resistance profile of field collected strains used in this study[1].

Insecticide	Resistance ratio at LD_{50} (RR_{50})				
	GoldenSand	Kuantan	Lumut	Melia I	Subang
propoxur	17.6	4.7	2.8	66.4	91.7
bendiocarb	30.7	5.2	3.7	>60.4	>53.7
chlorpyrifos	5.9	3.0	3.0	6.7	7.6
cypermethrin	1.3	1.3	1.1	14.4	9.5
permethrin	1.2	1.1	1.0	9.6	11.6
phenothrin	-	-	-	13.2	-
deltamethrin	-	-	-	6.2	-
DDT	-	-	-	>6.1	-

[1]data obtained from Lee *et al.* [14].

ceptible strain obtained from Zeneca Agrochemicals, Jealotts Hill, Bracknell, U.K. was used as a comparison. All cockroach strains were reared under laboratory conditions of 26 ± 2°C, 60 ± 5% R.H. and 12 h photoperiod.

Nymphal development

Gravid females of each strain were collected with a glass vial from the cockroach culture and reared separately in 3-liter glass containers with food and water (*ad libitum*). Folded cardboard (10 x 12 cm) was provided as harbourage. Newly emerged nymphs from each strain were then placed into polyethylene cups (Swordman No. 14729 size A-1; 5 cm diam x 10 cm height) with four individuals per cup and provided with food, water and a folded cardboard (3 x 2 cm) as harbourage. The upper inside surface of the cup was smeared with talcum powder to prevent the nymphs from escaping. Talcum powder was used instead of petroleum jelly here because the early instars were capable of crawling across the grease band. Ten to 21 replicates (depending on the availability of nymphs) were used for each strain. All cockroaches were held under environmental conditions previously mentioned. Nymphs were observed daily for events in moulting.

Longevity and fecundity

Approximately 40 late instar male and female cockroaches, respectively, of each strain were separated from the culture and kept in 3-liter glass jars. Each day, the matured cockroaches were removed from the jar to prevent mating. They were then paired (1 male and 1 female) in polyethylene cups (as mentioned earlier) provided with a harbourage (a 2 x 3 folded cardboard), food and water. For each strain, 20 pairs were held and observed daily for events in reproduction including the number of offsprings from each ootheca, preoviposition period (period between the hatching of an ootheca to the emergence of the following one) and incubation period (period between emergence and hatching of an ootheca). For nymphal sex-ratio studies, 100 nymphs were selected randomly from each strain from the first, second and third oothecae, respectively and sexed using morphological keys proposed by Ross and Cochran [15]. Identification of nymphs was made each time under a dissecting microscope after the nymphs were anesthetised with 10 seconds of CO_2 (20 kPa) in batches of five. The CO_2 dose chosen had been found not to cause any growth retardation effect on the nymphs (CY Lee, unpublished data). All nymphs were reared separately according to each replicate and strain until reaching adulthood. The proportion of nymphs which successfully matured into adults was then calculated.

All raw data were then used to calculate the following: mean no. oothecae per female, mean no. oothecae hatched, mean total no. offsprings per ootheca, mean preoviposition period, mean incubation period and nymphal sex ratio. Observation was made until all individuals died and mean longevity for both adult males and females for each strain were generated. No replacement was made on any of the individuals which died in the observation cups during the study.

Intrinsic rate of increase (r_n)

Five pairs (male and female) of newly emerged adults of the ICI susceptible, GoldenSand and Melia I were established in a plastic aquarium (40 x 32 x 23 cm), provided with 50 pieces of folded corrugated cardboard (15 x 12 cm), food and water *ad libitum*. Six replicates were done for each strain. The cockroaches were allowed to breed freely under conditions mentioned above.

After 70 days (10 weeks), the number of cockroaches in three aquaria of each strain was counted by removing them from the culturing tank using a glass vial. A similar count was made at 140 days (20 weeks) post treatment using the other three aquaria for each strain.

The calculation for r_n follows exactly that of Lim [16]: $r_n = [\log_e (n_{t+1}) - \log_e (n_t)]/$ time, where r_n = daily rate of population increase, n_t = population at time t, n_{t+1} = population at time t+1, and time = difference between t+1 and t.

Data analysis

Comparisons of biological parameters in different strains were conducted with analysis of variance; their means were separated using least significant difference test (LSD) at $\alpha = 0.05$. Data on proportion nymphs achieving adulthood (%) were subjected to arc-sine transformation before analysis of variance. Relationships between oothecal number and number of offsprings produced per female were determined with regression analysis. Nymphal sex-ratio of each strain was tested with χ^2 ($\alpha = 0.05$) to determine whether they deviated from 1:1. All analyses were conducted with a statistical analysis software program, StatGraphics® version 5.0 (StatGraphics Inc, New York).

RESULTS

Nymphal development

The development periods of the immature stages ranged from 42-50 days in the susceptible strain (ICI) and 45-73 days in the resistant strains (Table 2). All field collected strains showed longer nymphal development periods than the susceptible strain. Females usually eclosed at a later period when compared with males in all strains.

The mean development period recorded for the ICI strain (45.6 ± 0.30 days) was comparable to that reported earlier by Lim [16] on a different laboratory susceptible strain (49.3 ± 0.3 days). This period however was longer than that of the VPI normal strain (~33 days) [2] and the UCR susceptible strain (~38 days) [17], but shorter than other susceptible strains (53.9-58.6 days) [3]. Variation in strain and experimental conditions might have contributed these differences.

The GoldenSand strain possessed the longest development period (54.5 ± 0.8 days) for both male and female nymphs; however, this period did not differ significantly from other strains (Kuantan, Melia I and Lumut) for male nymphs. Conversely, the mean total development period for Subang was the shortest among the resistant strains (50.0 ± 0.8). In addition, there was no significant difference between Kuantan, Lumut and Melia I strains for both male and female nymphal development periods.

The nymphal maturation pattern of each strain was studied by comparing the percentage of adult emergence

Table 2. Nymphal development period in susceptible and field-collected strains of the German cockroach.

Strain	Mean ± S.E. (days)[1]						
	n	Male	range	n	Female	range	Combined
ICI	21	44.7 ± 0.5 *a*	42 -50	20	46.5 ± 0.3 *a*	45 - 60	45.6 ± 0.3
GoldenSand	33	51.7 ± 0.5 *b*	47 - 58	36	57.0 ± 1.2 *b*	46 - 73	54.5 ± 0.8
Kuantan	41	51.7 ± 0.5 *b*	47 - 60	42	52.6 ± 0.6 *c*	46 - 62	52.2 ± 0.4
Melia	23	50.7 ± 0.7 *b*	46 - 60	22	51.6 ± 0.5 *c*	45 - 57	51.1 ± 0.4
Lumut	31	51.6 ± 0.6 *b*	47 - 61	40	51.9 ± 0.7 *c*	46 - 70	51.8 ± 0.5
Subang	20	48.7 ± 0.9 *c*	45 - 58	18	51.4 ± 1.4 *c*	44 - 63	50.0 ± 0.8

[1] Means followed by the different letters within the same column are significantly different ($P < 0.05$; LSD test).

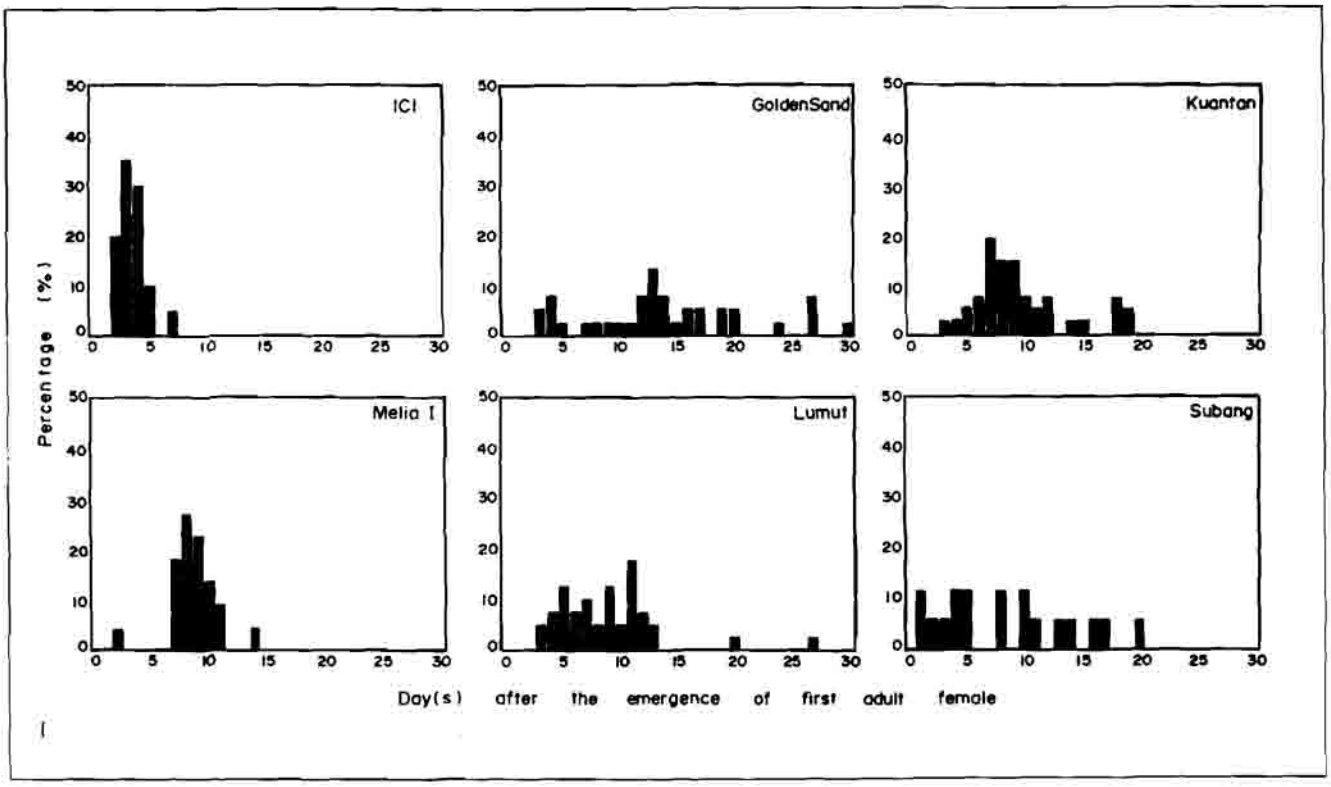

Figure 1. Emergence patterns of adult males from the final instar in laboratory susceptible and field-collected strains of the German cockroach.

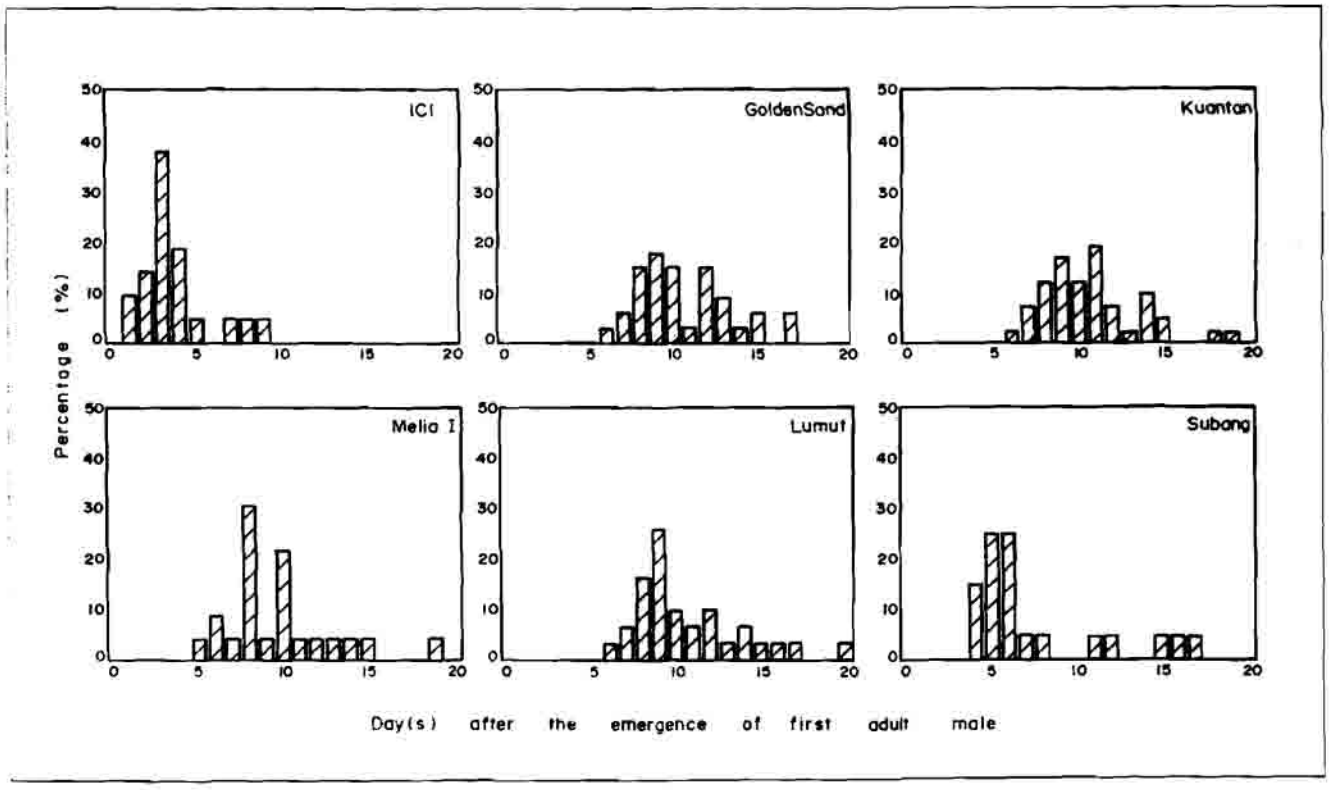

Figure 2. Emergence patterns of adult females from final instar in laboratory susceptible and field-collected strains of the German cockroach.

at each succeeding day following the emergence of the first adult of each sex (all strains combined). The time in which the first adult male/female emerged in the experiment was taken as day 1. For adult males, the ICI susceptible strain showed an earlier maturation period than the field collected strains (Fig. 1). All field collected strains showed emergence of their first adult males only five days after the emergence of the first adult male from the ICI strain. The maturation pattern for the field collected strains also ranged widely, indicating that more time was needed for total emergence of adult males than that of the ICI strain. The last male nymph, which was from the Lumut strain, matured 20 days after the emergence of the first adult male from the ICI strain.

For female nymph maturation, the first adult to emerge was from the Subang strain (Fig. 2). All female nymphs from the ICI strain matured into adults within five days with 35% (cockroaches) maturing within one day (at day 3 after the emergence of the first adult female). One field collected strain, Melia I, showed a maturation pattern similar to that of the ICI strain except for its first and last nymphal maturation. Other field collected strains (GoldenSand, Kuantan, Lumut and Subang) showed heterogenous maturation patterns which took 16-27 days for total maturation of nymphs since the emergence of first nymph from each respective strain. The last female nymph to mature in this study was from GoldenSand strain, maturing 30 days later after the emergence of first adult female.

Preoviposition and incubation periods

Differences in preoviposition and incubation periods were found among the strains studied (Table 3). The ICI strain had the shortest preoviposition period (mean period = 9.2 ± 0.1 days). This period was similar to that observed by Abd-Elghafar and Appel [18] (8.2 ± 1.1 days) and slightly longer than that of Archbold *et al.* [17] (7.1 ± 0.4) and Willis *et al.* [19] (7.8 ± 0.3 days). Different nymphal development periods might be due to strain, food and experimental temperature differences. In this study, cockroaches were reared at 26°C, while in Archbold *et al.* [17] and Willis *et al.* [19], the insects were cultured at 30°C.

Variations in preoviposition period were observed in field-collected cockroaches especially in the Subang strain. In this strain, the preoviposition periods for the first and second oothecae were significantly longer

Table 3. Mean preoviposition period (days) for the first and consecutive oothecae in susceptible and field-collected strains of the German cockroach.

Oothecal no.	Strain	n	mean ± S.E.[1] (days)
1	ICI	20	8.4 ± 0.2 *a*
	GoldenSand	20	9.8 ± 0.3 *c*
	Kuantan	20	9.2 ± 0.3 *abc*
	Melia I	20	9.0 ± 0.2 *ab*
	Lumut	20	8.8 ± 0.3 *a*
	Subang	20	9.6 ± 0.4 *bc*
2	ICI	20	9.2 ± 0.3 *a*
	GoldenSand	20	10.9 ± 0.3 *b*
	Kuantan	20	10.0 ± 0.3 *ab*
	Melia I	20	10.5 ± 0.4 *b*
	Lumut	20	10.3 ± 0.6 *b*
	Subang	19	10.1 ± 0.4 *b*
3	ICI	17	9.2 ± 0.4 *a*
	GoldenSand	13	9.8 ± 0.4 *ab*
	Kuantan	17	9.3 ± 0.4 *a*
	Melia I	20	10.6 ± 0.4 *b*
	Lumut	16	10.3 ± 0.6 *ab*
	Subang	15	10.3 ± 0.4 *ab*
4	ICI	17	9.2 ± 0.3 *a*
	GoldenSand	6	10.8 ± 0.7 *b*
	Kuantan	8	10.8 ± 0.9 *b*
	Melia I	14	10.6 ± 0.4 *b*
	Lumut	12	9.4 ± 0.4 *ab*
	Subang	9	9.3 ± 0.6 *ab*
5[2]	ICI	14	9.9 ± 0.4 *a*
	Kuantan	4	9.3 ± 0.3 *a*
	Melia I	6	9.5 ± 0.8 *a*
	Lumut	7	11.1 ± 0.7 *a*
	Subang	4	9.3 ± 0.5 *a*
6[3]	ICI	6	9.7 ± 0.5 *a*
	Melia I	1	9.0*
	Lumut	3	10.3 ± 1.9 *a*
	Subang	3	8.3 ± 0.3 *a*
7[3]	ICI	1	12.0

[1] Mean values followed by different letters within the same oothecal number are significantly different ($P < 0.05$; LSD test).

[2] GoldenSand not included because no 5th ootheca was produced.

[3] GoldenSand and Kuantan not included because no 6th. oothecae were produced or all the cockroaches had died.

* Not included in statistical analysis because only one ootheca hatched.

($P < 0.05$) from that of the susceptible strain, but at the third and fourth oothecae, the periods became comparable to that of the susceptible strain. The GoldenSand strain had the longest preoviposition period for the first and second oothecae while Melia I possessed the longest preoviposition period for the third ootheca. The Kuantan and Lumut strains generally had similar preoviposition period to that of the ICI susceptible strain, except for the second and fourth oothecae for Lumut and Kuantan, respectively. The longest preoviposition period seen in this study was 15 days, which was observed in Melia I and Lumut, both at the third ootheca.

The trends seen in the incubation period were quite similar to that observed for the preoviposition period (Table 4). The ICI susceptible strain showed the shortest incubation period (mean = 25.0 ± 0.2 days) ranging from 19 (one at the seventh ootheca) to 30 days (one at the first ootheca). Conversely, both Melia I and GoldenSand had the longest incubation periods (29.6 ± 0.2 and 29.9 ± 0.2 days, respectively); these differred significantly ($P < 0.05$) from the susceptible and other field collected strains. The last ootheca produced from GoldenSand had the longest incubation period in this study (4th ootheca; 35 days). The Subang, Lumut and Kuantan strains showed similar incubation periods to that of the susceptible strain (except for the second and fourth oothecae for Subang and Kuantan, respectively). Contrasting results in incubation periods of field collected/resistant strains as compared to susceptible strains had been reported earlier. Ross [3] observed that resistant strains needed longer time between the hatch of successive oothecae than their susceptible counterparts. However, Wright [11] did not find any difference in oothecal incubation periods between chlordane-susceptible and -resistant strains of the German cockroach.

Table 4. Mean incubation period (days) for first and consecutive oothecae in susceptible and field-collected strains of the German cockroach.

Oothecal no.	Strain	n	mean ± S.E.[1] (days)
1	ICI	19	25.3 ± 0.5 *ab*
	GoldenSand	16	29.6 ± 0.3 *c*
	Kuantan	19	25.8 ± 0.6 *b*
	Melia I	14	29.0 ± 0.3 *c*
	Lumut	16	24.6 ± 0.3 *a*
	Subang	17	25.6 ± 0.2 *ab*
2	ICI	19	24.6 ± 0.5 *a*
	GoldenSand	18	30.0 ± 0.4 *d*
	Kuantan	17	26.0 ± 0.4 *bc*
	Melia I	20	30.0 ± 0.4 *d*
	Lumut	16	24.9 ± 0.3 *ab*
	Subang	15	26.2 ± 0.4 *c*
3	ICI	17	25.5 ± 0.4 *a*
	GoldenSand	8	29.8 ± 0.3 *b*
	Kuantan	16	26.3 ± 0.5 *a*
	Melia I	16	29.9 ± 0.4 *b*
	Lumut	11	26.0 ± 0.3 *a*
	Subang	12	25.4 ± 0.5 *a*
4	ICI	16	25.8 ± 0.4 *a*
	GoldenSand	1	35.0*
	Kuantan	6	27.7 ± 1.1 *bc*
	Melia I	9	29.2 ± 0.4 *c*
	Lumut	7	26.7 ± 0.6 *ab*
	Subang	4	25.0 ± 0.7 *a*
5[2]	ICI	11	24.2 ± 0.4 *a*
	Kuantan	2	24.5 ± 1.5 *a*
	Melia I	4	29.3 ± 0.8 *b*
	Lumut	3	25.7 ± 0.7 *a*
6	ICI	2	24.5 ± 0.5
7	ICI	1	19.0

[1] Mean values followed by different letters within the same oothecal number are significantly different ($P < 0.05$; LSD test).

[2] GoldenSand and Subang not included because none of their fifth oothecae hatched.

* Not included in statistical analysis because only one ootheca hatched.

Oothecal production and hatchability

The susceptible strain (ICI) produced a mean total oothecae of 4.8 ± 0.3 with percentage hatchability of 87.5% (Table 5). This value was much higher than that observed in the VCRU strain (CY Lee, unpublished data) with an oothecal production of 3.2 ± 0.4 and percentage hatchability of 78.1%. In a susceptible strain (AC strain), Abd-Elghafar and Appel [18] reported oothecal production of 3.6 ± 0.9 with only 66.7% of them hatching.

In field collected strains, a favourable hatchability rate was only observed in the Kuantan strain (85.7%),

Table 5. Mean total oothecal production and hatch in susceptible and field-collected strains of the German cockroach.

Strain	n	Total oothecae produced per female (mean ± S.E.)[1]	Total hatched oothecae per female (mean ± S.E.)[1]
ICI (susceptible)	20	4.8 ± 0.3 *a*	4.2 ± 0.3 *a*
GoldenSand	20	3.0 ± 0.2 *c*	2.2 ± 0.2 *d*
Kuantan	20	3.5 ± 0.2 *bc*	3.0 ± 0.2 *bc*
Lumut	20	4.0 ± 0.3 *b*	2.7 ± 0.4 *bcd*
Melia	20	4.1 ± 0.2 *ab*	3.2 ± 0.2 *b*
Subang	20	3.5 ± 0.3 *bc*	2.4 ± 0.3 *cd*

[1] Means followed by different letters within the same column are significantly different ($P < 0.05$; LSD test).

while other strains demonstrated percentage hatchability lower than 80% (GoldenSand = 73.3%; Melia I = 78.0%; Subang = 68.8%; Lumut = 67.5%). Although the Kuantan strain had the highest percentage hatchability of oothecae among the field strains, its total oothecal production was still much lower than that of the Melia I strain due to the higher oothecal production by the latter strain. The lowest oothecal production and oothecal hatch were observed in the GoldenSand strain; however, the latter parameter did not differ significantly from that of the Lumut and Subang strains.

The viability of the first and subsequent oothecae was compared among the six strains. The frequency distribution of non-viable oothecae in all strains was seen to skew to the right, indicating a higher tendency towards oothecal abortion or towards non-viability with increasing oothecal number (Fig. 3). The GoldenSand strain had the highest non-viable oothecae; this number constituted an average of 38% of the total oothecae produced by this strain (from first to fourth oothecae), compared with only 4% in the ICI susceptible strain for the same oothecal numbers. All the sixth oothecae produced by the resistant strains (Melia I, Lumut and Subang) were not viable. It was also observed in this study that after the non-viable oothecae were aborted or dropped, most females died shortly thereafter. This phenomenon had also been reported earlier by Atkinson *et al.* [20] and was proposed to be due to the poor physiological condition of the female cockroaches after oothecal abortion.

Nymphal production, sex ratios and % attaining adulthood

All field collected strains demonstrated lower fecundity than the susceptible strain (Table 6). The three strains with the lowest fecundity (GoldenSand, Lumut and Subang) produced only 46.3%, 44.6% and 36.2%, respectively, of the total offsprings produced by the ICI susceptible strain. The Kuantan strain had the highest total number of nymphs produced per female among

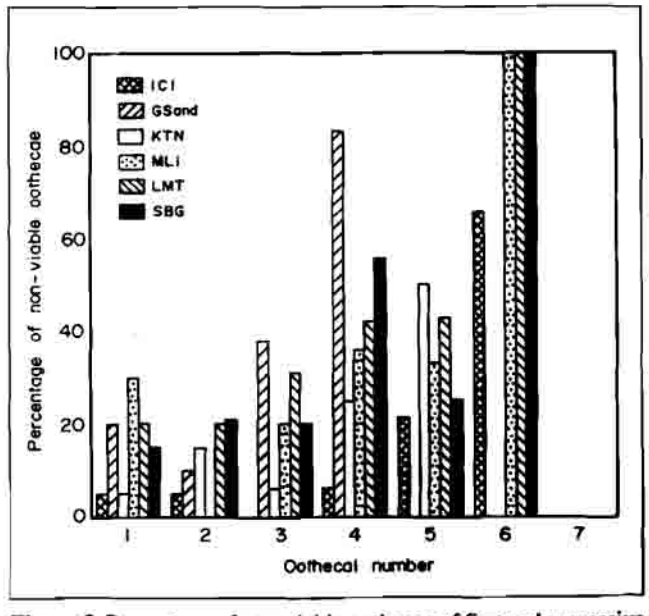

Figure 3. Percentage of non-viable oothecae of first and successive oothecae in laboratory and field-collected strains of the German cockroach.

Table 6. Mean total number of offsprings produced per female in susceptible and field-collected strains of the German cockroach.

Strain	n[1]	Mean ± S.E.[2]	% nymphs reaching adulthood
ICI (susceptible)	20	139.4 ± 8.0 *a*	90.9 ± 0.3 *a*
GoldenSand	20	74.8 ± 5.7 *d*	87.2 ± 1.0 *bc*
Kuantan	20	106.5 ± 6.7 *b*	89.1 ± 1.0 *ab*
Lumut	20	88.9 ± 11.1 *bcd*	90.1 ± 0.8 *ab*
Melia	20	99.3 ± 7.0 *bc*	89.2 ± 0.9 *a*
Subang	20	77.2 ± 8.3 *cd*	85.8 ± 1.6 *c*

[1] Number of female cockroaches observed in this study.
[2] Means followed by different letters within the same column are significantly different ($P < 0.05$; LSD test).

the resistant strains; however, its mean value did not differ significantly from that of the Lumut and Melia I strains.

Mean total nymphal production per female of the ICI strain was 139.4 ± 8.0, much higher than that observed in the VCRU strain (CY Lee, unpublished data) (109.3 ± 10.6) and in the AC strain [18] (69.0 ± 7.3), but less than that in the VPI normal strain (163 ± 5.4) [21].

In terms of mean nymphal production per female at each consecutive oothecal number (Table 7), the Kuantan strain had results comparable to that of the ICI strain throughout the first five oothecae. Melia I, GoldenSand and Subang had significantly lower number of offsprings per female than the susceptible strain. Comparing the number of nymphs produced per female at the first three oothecae, the field collected strains used in this study showed greater mean fecundity (>30 nymphs) than that reported by Ross [3] where mean nymphal production per female per ootheca was <25 nymphs. The highest number of offsprings produced per ootheca was observed in the ICI and Lumut strains at the first oothecal number where 48 nymphs were produced in each strain. Conversely, the lowest number recorded was 12 nymphs (in the ICI strain at the seventh ootheca).

Overall, the number of offsprings produced per female per ootheca decreased with each succeeding oothecal number. In the ICI strain, this number of offsprings decreased linearly with increasing oothecal number [$y = (47.4 \pm 1.6) - (5.0 \pm 0.4).x$; $R^2 = 0.9742$; $x \geq 1$], where y = the number of offsprings produced per female per ootheca and x = oothecal number. A similar trend was also observed for all the field collected strains — GoldenSand: $y = (41.7 \pm 0.6) - (3.9 \pm 0.2).x$, $R^2 = 0.9930$, $x \geq 1$; Kuantan: $y = (43.0 \pm 1.6) - (3.3 \pm 0.5).x$, $R^2 = 0.9433$, $x \geq 1$; Melia I: $y = (38.7 \pm 0.9) - (2.9 \pm 0.3).x$, $R^2 = 0.9768$, $x \geq 1$; Lumut: $y = (44.2 \pm 0.8) - (4.6 \pm 0.2).x$, $R^2 = 0.9925$, $x \geq 1$ and Subang: $y = (42.1 \pm 0.6) - (4.8 \pm 0.2).x$, $R^2 = 0.9961$, $x \geq 1$. Based on the regression slope from each relationship, it can be predicted that the number of offsprings produced per female per ootheca declined faster in some strains (ICI, Lumut and Subang) than in the other strains (GoldenSand, Kuantan and Melia I).

The percentage of nymphs reaching adulthood was comparable among the ICI, Kuantan, Lumut and Melia strains (~ 90%) (Table 6). The GoldenSand and Subang strains had a significantly lower rate of maturation when compared with these strains. Archbold *et al.* [17] reported 87% of the nymphs achieving maturation in the UCR susceptible strain.

A hundred nymphs of each strain from each of the first, second and third oothecae were sexed; the male to female ratio did not deviate from 1:1 in all strains, based on a χ^2 test at $\alpha = 0.05$ (Table 8). Similar observations were also reported by other researchers [3,11,17].

Adult longevity

Ross [3] found a highly resistant strain which possessed a shorter longevity than the susceptible strain. Two other resistant strains, however were found to have lifespans comparable to that in the susceptible strain. Perkins and Grayson [2] reported three resistant strains having longer female longevity than the susceptible strain. This was also observed by Wright [11]. In this study, how-

Table 7. Mean number of offsprings produced per female at first and consecutive oothecae in susceptible and field-collected strains of the German cockroach.

Oothecal no.	Strain	n	mean ± S.E.[1]
1	ICI	18	40.5 ± 1.0 *a*
	GoldenSand	16	37.4 ± 0.7 *b*
	Kuantan	19	39.6 ± 0.7 *a*
	Melia I	14	34.9 ± 1.0 *c*
	Lumut	16	39.7 ± 0.9 *a*
	Subang	17	37.1 ± 0.5 *bc*
2	ICI	19	36.9 ± 0.9 *a*
	GoldenSand	18	34.5 ± 0.9 *bc*
	Kuantan	17	37.3 ± 0.6 *a*
	Melia I	20	33.9 ± 0.9 *bc*
	Lumut	16	35.2 ± 1.0 *ab*
	Subang	15	32.4 ± 0.7 *c*
3	ICI	17	34.3 ± 1.0 *a*
	GoldenSand	8	30.1 ± 1.5 *bc*
	Kuantan	16	32.8 ± 0.7 *ab*
	Melia I	16	30.2 ± 1.4 *bc*
	Lumut	11	30.8 ± 1.1 *bc*
	Subang	12	28.2 ± 0.7 *c*
4	ICI	16	30.1 ± 1.3 *a*
	GoldenSand	1	26.0 *
	Kuantan	6	27.8 ± 0.8 *ab*
	Melia I	9	27.0 ± 1.6 *ab*
	Lumut	7	24.9 ± 2.1 *b*
	Subang	4	22.5 ± 2.9 *b*
5[2]	ICI	11	22.6 ± 1.4 *a*
	Kuantan	2	27.8 ± 0.8 *a*
	Melia I	4	23.8 ± 1.3 *a*
	Lumut	3	22.0 ± 4.0 *a*
6[3]	ICI	2	15.5 ± 2.5
7[3]	ICI	1	12.0

[1] Mean values followed by different letters within the same oothecal number are significantly different ($P < 0.05$; LSD test).

[2] GoldenSand and Subang strains were not included because none of their oothecae hatched.

[3] Other strains were not included because none of their oothecae hatched or all their cockroaches had died.

* Not included in statistical analysis because only one ootheca hatched.

Table 8. Sex ratios of offsprings emerging from oothecae produced by susceptible and field-collected strains of the German cockroach.

Strain[1]	male : female	χ^2
ICI	0.90 : 1	2.18
GoldenSand	1.05 : 1	0.43
Kuantan	1.14 : 1	3.41
Lumut	1.10 : 1	1.52
Melia	0.94 : 1	0.69
Subang	0.88 : 1	2.64

[1] total number of nymphs sexed per strain = 300 (100 nymphs each from first, second and third oothecae).

ever, the susceptible strain demonstrated a longevity period longer than the field collected strains (Table 9). In the adult males of field-collected strains, both the Subang and GoldenSand strains had the lowest mean longevity; however, this value did not differ significantly from that of the Kuantan and Lumut strains. Female longevity in field-collected strains ranged from 52-206 days and 40-160 days in adult males. GoldenSand had the lowest longevity among the adult females; it was approximately 34.3% lower than that of the susceptible strain.

The longevity of susceptible adult male ranged from 54 to 179 days with a mean of 115.1 ± 7.4 days, while female longevity ranged from 78 to 247 days (mean ± S.E.M. = 165.8 ± 10.3 days). The results obtained were comparable with those obtained earlier on susceptible adult males by Archbold *et al.* [17] (122.8 ± 3.0 days) and Willis *et al.* [19] (128 ± 8 days). For adult females, the longevity period recorded did not differ much from that reported by Abd-Elghafar and Appel [18] (157.0 ± 24.5 days), Willis *et al.* [19] (153 ± 9 days), Hamilton and Schal [21] (176 ± 5.7 days) and Archbold *et al.* [17] (181.5 ± 2.4 days).

Intrinsic rate of increase (r_n)

The ICI susceptible strain demonstrated a significantly higher ($P < 0.05$) r_n value than the GoldenSand strain; however, this value was comparable to that of the Melia I strain (Table 10). The r_n value calculated for the ICI susceptible strain was similar to that generated by Grothaus *et al.* [22] where they obtained an r_n of 0.045. However, this value was much higher in Lim [16] (r_n = 0.03) and Reid [23] (r_n = 0.023), but lower than that

Table 9. Longevity period of susceptible and field-collected strains of the German cockroach.

Strain	n	Mean ± S.E. (days)[1]			
		Male	range	Female	range
ICI (susceptible)	20	115.1 ± 7.4 *a*	54 - 179	165.8 ± 10.3 *a*	78 - 247
GoldenSand	20	82.2 ± 7.0 *c*	40 - 139	108.9 ± 7.6 *c*	59 - 170
Kuantan	20	94.6 ± 5.5 *bc*	55 - 149	122.0 ± 7.7 *bc*	66 - 190
Lumut	20	92.4 ± 5.2 *bc*	60 - 140	127.3 ± 8.9 *bc*	78 - 201
Melia	20	104.0 ± 7.3 *ab*	57 - 160	141.2 ± 7.7 *b*	87 - 206
Subang	20	82.2 ± 6.0 *c*	45 - 140	126.5 ± 7.8 *bc*	52 - 188

[1] Means followed by different letters within the same column are significantly different ($P < 0.05$; LSD test).

Table 10. Intrinsic rate of increase (r_n) of susceptible and two field-collected strains of the German cockroach.

Strain	N_t	days after establishment	replicate	N_{t+1}	r_n	mean r_n ± S.E.[1]
ICI (sucp.)	10	70	1	297	0.0484	
	10	70	2	344	0.0505	
	10	70	3	370	0.0516	
	10	140	4	5525	0.0451	
	10	140	5	4095	0.0430	
	10	140	6	3798	0.0424	0.0468 ± 0.0016 ***a***
G-Sand	10	70	1	189	0.0420	
	10	70	2	244	0.0456	
	10	70	3	171	0.0406	
	10	140	4	2432	0.0392	
	10	140	5	2977	0.0407	
	10	140	6	3085	0.0409	0.0415 ± 0.0009 ***b***
Melia I	10	70	1	288	0.0480	
	10	70	2	301	0.0486	
	10	70	3	197	0.0426	
	10	140	4	3874	0.0426	
	10	140	5	2976	0.0407	
	10	140	6	3176	0.0411	0.0439 ± 0.0014 ***ab***

[1] Mean values followed by different letters in the same column are significantly different ($P < 0.05$; LSD test).

reported by Archbold *et al.* [17] ($r_n = 0.052$). Differences in r_n values might be due to strain differences, rearing conditions (temperature, humidity, rearing chamber, food, stress), number of insects used, age/stages used for establishment and sampling time. In this study, all strains registered higher r_n values at 70 days than at 140 days post-establishment. It can be seen from this study that for a more accurate estimate of the r_n, cockroaches should be established for a longer period of time, provided that at the time of sampling, the population is still below its carrying capacity.

DISCUSSION

The F_1 or F_2 generation was chosen for this study instead of the parental generation to prevent the possibility of using cockroaches which had been exposed to insecticides in the field prior to collection. These survivors will undergo changes in their physiology and may affect the validity of the results [18].

Many previous studies have shown that field collected strains were mostly resistant to insecticides and were reduced in fitness. Roush and Plapp [9] studied

the biotic potential of house flies carrying resistant (R) and susceptible (S) genotypes (RR, RS and SS) and found that those carrying the RR gene had reduced biotic potential of 11-43% when compared to the SS strain. This reduced fitness was due to reduced fecundity and longer nymphal development in all R strains. However, the biotic potential of RS was similar to that of the SS strain. Roush and Plapp [9] concluded that the R-gene was dominant for the expression of resistance, but recessive for adverse effects on biotic potential. It was not possible to compare Roush and Plapp's [9] finding with the present study because the genotype and resistant genotype frequency of different strains used in this study are unknown.

In this study, however, the Melia I strain with a higher resistance level than the GoldenSand strain was shown to be fitter than the latter for survival under insecticide-free laboratory environment. On the other hand, the Kuantan strain was shown to have biological fitness that was comparable to that of the susceptible strain. Recently, Cochran [24] reported varying results while working on the resistance gene frequencies of some field collected strains. He found that in the absence of insecticide selection, some strains had increase in gene frequencies while some others had decreases in or similar gene frequencies. In addition, Ross [3] also found a highly resistant strain which had fitness similar to a susceptible strain, while two others were found with fitness disadvantages. These findings seem to be in contrast with the previous hypothesis that resistant strains usually have reduced fitness when compared to susceptible strain.

One possible explanation to these disparities is the phenomenon of co-adaptation which is defined as "the selection and integration of resistance genes with other loci that ameliorate the deleterious effects of resistance" [25]. It is possible that genes or modifier that might improve the fitness disadvantages were present in the Kuantan and Melia I strains, but not in the GoldenSand and Subang strains. These might be due to differences in genetic background of the strains.

Although all cockroaches examined are of the same species, their genetic background may differ because of origin differences. Amin and White [5] earlier reported that if a chlorpyrifos-resistant strain of *Culex quinquefasciatus* which had a lower biological fitness was backcrossed with a laboratory susceptible strain for five generations, the resistant strain would have biological fitness similar to the susceptible strain. The authors concluded that the reduced fitness was due to the genetic background of the resistant strain rather than to its resistant gene.

This present study demonstrates a direction for further investigation. German cockroaches of known genotypes (SS, RS and RR) should be studied to determine how their fitness differ from each other. If fitness disadvantages occur in resistant insects when compared to that of the susceptible strain, it would be of interest to confirm whether it is due solely to the resistant gene or under the influence from other genes associated with the resistant gene. This can be done by backcrossing the resistant strain with their susceptible counterpart for several generations in order to increase the genetic relatedness of the two strains, and then subjecting the offsprings to several generations of insecticide selection. Only when this stage is reached, can a proper comparison of biological parameters between the resistant and susceptible cockroaches without the influence of background genetic differences be made.

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