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Decrease in the resistance level of *Blattella germanica* (Linnaeus) (Blattodea: Ectobiidae) to insecticides after being reared without selection pressure for ten years

Penurunan tingkat resistensi *Blattella germanica* (Linnaeus) (Blattodea: Ectobiidae) terhadap insektisida setelah dipelihara tanpa tekanan seleksi selama sepuluh tahun

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ABSTRACT

This study aims to investigate changes in resistance to insecticides over a ten-year period in five strains of German cockroaches, *Blattella germanica* (Linnaeus), which had previously shown resistance to deltamethrin, propoxur, and fipronil in 2012. The five strains were reared in a laboratory without exposure to insecticides for ten years. In 2022, they were tested for resistance to the same insecticides using a topical application method. The resistance ratio (RR_{50}) was calculated for each strain to determine the level of resistance to each insecticide. The study found that German cockroaches, initially resistant, became less resistant or even susceptible after being reared in a laboratory without insecticide exposure for over ten years. This decrease in resistance was observed in all strains, but the reduction pattern varied, apparently influenced by the type of insecticide. For instance, the MDN2 strain, which initially had a very high level of resistance (RR_{50}: 1019.74 -fold) to deltamethrin, became susceptible (RR_{50}: 1 -fold). Similarly, the ACH2 strain, initially classified as highly resistant to propoxur (RR_{50}: 48.64 -fold), and the strain with high resistance (RR_{50}: 12.21 -fold) to fipronil, both became susceptible. The study also discussed potential mechanisms for the decrease in resistance, including reduced frequency of resistance genes and fitness costs. The findings suggest that rearing German cockroaches in a laboratory without insecticide treatment can lead to a decrease in resistance to commonly used insecticides. These findings can be used to develop more effective methods for controlling German cockroaches.

Key words: *Blattella germanica*, cockroach strain, decrease insecticide resistance

ABSTRAK

Penelitian ini bertujuan untuk mengetahui perubahan resistensi terhadap insektisida selama sepuluh tahun tanpa paparan insektisida pada lima strain lipas jerman, *Blattella germanica* (Linnaeus) yang sebelumnya resisten terhadap deltametrin, propoxur, dan fipronil pada tahun 2012. Kelima strain tersebut dipelihara di laboratorium tanpa paparan insektisida selama sepuluh tahun dan kemudian diuji tingkat resistensinya terhadap insektisida yang sama, menggunakan metode aplikasi topikal pada tahun 2022. Rasio resistensi (RR_{50}) dihitung untuk setiap strain untuk menentukan tingkat resistensi terhadap setiap insektisida. Hasil studi menunjukkan bahwa lipas jerman, yang awalnya resisten terhadap insektisida, menjadi kurang resisten atau bahkan rentan setelah dipelihara di laboratorium tanpa perlakuan insektisida selama lebih dari sepuluh tahun. Penurunan resistensi

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diamati pada semua strain, dengan pola penurunan yang tidak sama yang tampaknya dipengaruhi oleh jenis insektisida. Misalnya strain MDN2 yang awalnya memiliki tingkat resistensi yang sangat tinggi (RR_{50}: 1019,74 kali lipat) terhadap deltametrin, menjadi rentan (RR_{50}: 1 kali lipat). Demikian pula, strain ACH2, yang awalnya diklasifikasikan sebagai sangat resisten terhadap propoxur (RR_{50}: 48,64 kali lipat), dan strain dengan resistensi tinggi (RR_{50}: 12,21 kali lipat) terhadap fipronil, keduanya menjadi rentan. Studi ini juga membahas kemungkinan mekanisme penurunan resistensi, termasuk penurunan frekuensi gen resistensi dan "*fitness cost*". Hasil penelitian menunjukkan bahwa memelihara lipas jerman di laboratorium tanpa perlakuan insektisida dapat menyebabkan penurunan resistensi terhadap insektisida yang biasa digunakan. Temuan ini dapat digunakan untuk mengembangkan metode yang lebih efektif untuk mengendalikan lipas jerman.

Kata kunci: *Blattella germanica*, resistensi insektisida, strain lipas

INTRODUCTION

The German cockroach, *Blattella germanica* (Linnaeus) (Blattodea: Ectobiidae) is a residential pest insect found in almost all parts of the world where humans live and carry out activities. Its presence in residential areas, hotels, restaurants, kitchens, the food industry, modes of transportation, and similar environment is highly disturbing and detrimental. The German cockroach can act as a disease vector and allergen, and it can also cause economic, aesthetic, and psychological harm (Schal & DeVries 2021). Due to its damaging effects, various efforts have been made to control it, primarily through the use of insecticides (Hu et al. 2020). However, the continuous use of insecticides has led to the development of resistance in German cockroach worldwide, including in Indonesia (Fardisi et al. 2019; Lee et al. 2022; Rahayu et al. 2012).

While there have been several reports on the resistance of German cockroaches to synthetic pyrethroids in Indonesia (Ahmad et al. 2009; Rahayu et al. 2012), residual sprays using synthetic pyrethroids are still the primary choice by pest management professionals (PMP). Hariani (2013) reported cases of *B. germanica* resistance to insecticides from 33 cities across Indonesia. The results indicated very high resistance levels against deltamethrin (highest RR_{50}: 1462 -fold), chlorpyrifos (highest RR_{50}: 317 -fold), and propoxur (highest RR_{50}: 58 -fold).

Additionally, the relatively new insecticide fipronil, which has been used since the early 2000s, showed the highest RR_{50} of 21.28-fold in strain JKT2. These findings suggest that German cockroach resistance has spread to many parts of Indonesia.

Resistance occurs due to continuous selection pressure from insecticides, resulting in the elimination of insects without resistant genes. After several generations, the percentage of insects with resistant genes increases (IRAC 2011). However, without selection pressure, resistant insect populations tend to lose their resistance within a few generations. For example, Cochran (1993) and Strong et al. (1997) reported that certain German cockroach strains that were previously resistant to pyrethroids showed decreased resistance after being reared in a laboratory without exposure to insecticides. The resistance ratio to cypermethrin decreased from 169-fold to 50-fold after 30 months of rearing without selection pressure (Strong et al. 1997).

A better understanding of the occurrence of resistance and the rate at which resistance decreases to insecticides is critical. This knowledge can be utilized to design more effective cockroach control programs, including studying the mechanism of resistance and strategy to reduce resistance. By doing so, insecticides can be used for longer durations while remaining effective. The rate of decline in resistance to insecticides has been reported in other insects. For example, Vera-Maloof et al. (2020) reported a general decrease in the frequency of pyrethroid-resistance alleles in *Aedes aegypti* (Linnaeus) when they were no longer exposed to pyrethroid pressure in the laboratory. Parrella & Trumble (1989) also reported a decline in resistance in *Liriomyza trifolii* (Burgess) in the absence of insecticide selection pressure. However, there is still limited information regarding the German cockroach.

This study aims to investigate changes in resistance levels among several strains of the German cockroach, *B. germanica*, which were previously found to be resistant to deltamethrin, propoxur, and fipronil in 2012. These strains were subsequently reared in a laboratory without exposure to insecticides for ten years until 2022. The study will determine if and how resistance levels have changed over time.

MATERIAL AND METHOD

Experimental insects

The German cockroach, *B. germanica*, used in the insecticide resistance reduction test, was obtained from various locations as listed in Table 1.

All cockroach strains were previously reared in plastic containers without insecticide selection pressure for over ten years. The rearing and experimental conditions in the laboratory of Entomology at SITH-ITB included temperatures ranging from 23–30 °C, relative humidity of 55 to 95%, a photoperiod of 12:12, and access to water and a mixture of fish feed and dog food. The rearing methods were similar to those described by Noland et al. (1949) described. The VCRU insecticide-susceptible strain of cockroaches was obtained from the Vector Control Research Unit (VCRU) at Universiti Sains Malaysia and has been reared in our laboratory since 2007.

Hariani (2013) tested the resistance levels of all cockroach strains included in this study in 2012, and the results are listed in Tables 2, 3, and 4.

Insecticide resistance bioassay

The study utilized technical-grade insecticides, namely deltamethrin (98%, PT. Gelpi Kurnia Lestari), propoxur (99.25%, PT. Inti Everspring), and fipronil (88.2%, PT. Sanova). Adult German cockroaches were used to evaluate the resistance levels of five strains. These cockroaches were previously tested for their resistance to the same insecticides in 2012 and were subsequently reared without exposure to insecticides for ten years. To

Table 1. Experimental insects

Strain	Collection location	Collection year
VCRU (Laboratory susceptible strain)	Laboratory USM, Penang Malaysia	2007
ACH2	Restaurant, Banda Aceh	2010
JKT2	Restaurant, Jakarta Barat	2011
MDN2	Restaurant, Medan	2010
KLT1	Traditional market, Samarinda	2010

Table 2 Toxicity of deltamethrin applied topically to cockroaches (Hariani 2013*)*

N	Strain	Insecticide	LD_{50} (μg/g)	Slope ± SE	RR_{50}
180	VCRU	Deltamethrin	0.114	1.536 ± 0.148	1.00
180	ACH2		61.004	1.578 ± 0.204	535.12
210	JKT2		122.25	1.647 ± 0.150	1072.37
180	MDN2		116.25	1.986 ± 0.432	1019.74
180	KLT1		1.28	1.602 ± 0.420	11.23

RR: resistance ratio; LD: lethal dose.

Table 3 Toxicity of propoxur applied topically to cockroaches (Hariani 2013)

N	Strain	Insecticide	LD_{50} (μg/g)	Slope ± SE	RR_{50}
210	VCRU	Propoxur	0.61	2.884 ± 0.080	1.00
210	ACH2		29.77	2.046 ± 0.199	48.64
200	JKT2		27.21	1.647 ± 0.150	44.46
180	MDN2		27.65	1.986 ± 0.432	45.17
150	KLT1		0.65	1.602 ± 0.420	1.05

RR: resistance ratio; LD: lethal dose.

Table 4 Toxicity of fipronil applied topically to cockroaches (Hariani 2013)

N	Strain	Insecticide	LD_{50} (µg/g)	Slope ± SE	RR_{50}
200	VCRU	Fipronil	0.04	2.884 ± 0.080	1.00
200	ACH2		0.46	2.046 ± 0.199	12.21
210	JKT2		0.83	1.647 ± 0.150	21.82
150	MDN2		0.22	1.986 ± 0.432	5.76
200	KLT1		0.04	1.602 ± 0.420	1.11

RR: resistance ratio; LD: lethal dose.

measure the changes in resistance levels, a topical test method was conducted, and the LC_{50} (lethal concentration for 50% mortality) was determined for each insecticide and strain. The resistance ratios were then calculated by dividing the LC_{50} values for each strain by the LC_{50} value for the VCRU susceptible reference strain.

The test utilized 10 adult cockroaches from each strain with 3 replications for each insecticide. The procedure for the test followed the methods described by Lee et al. (1996). It involved applying an insecticide solution, using a micro syringe, to the first abdominal sternite of each anesthetized cockroach. The treated cockroaches were then placed in a plastic jar with food, water, and harborage. The mortality rate was observed 48 hours after treatment.

Statistical analysis

The mortality rate of the treated cockroaches was analyzed using a probit analysis. This analysis was used to calculate the lethal dose of the insecticide required to kill 50% of the population (LD_{50}). To determine the resistance ratio, we compared the LD_{50} of each field strain to the LD_{50} of a susceptible strain (VCRU). Insecticide resistance was classified based on the LD_{50} value, using the methods described by Lee & Lee (2004) and Rahayu et al. (2012).

RESULT

Based on data obtained in 2012 (Hariani 2013), and 2022, this information can be used to compare the effectiveness of insecticides against cockroaches in these two periods and assess any changes in the resistance level. In general, the results showed a decrease in the resistance ratio in cockroaches that were initially resistant, including those with very high resistance (RR_{50} > 1000 -fold) in 2012. After the colonies were reared without selection pressure for ten years (2022), these cockroaches became not resistance or even susceptible. For example, the MDN2 strain decreased its resistance to deltamethrin from very high resistance (RR_{50}: 1019.74 -fold) to susceptible (RR_{50}: 1 -fold), and the ACH2 strain decreased its resistance to propoxur from high resistance (RR_{50}: 48.64 -fold) to susceptible. Similalrly, the resistance ration of the ACH2 strain to fipronil decreased from high resistance (RR_{50}: 12.21 -fold) to susceptibility (RR_{50}: 1 -fold). However, there was no decrease in resistance for fipronil in the KLT1 strain, and the RR_{50} increased from 1.11 -fold (2012) to 3.0 -fold (2022). The complete findings of the study on the alteration of the resistance level of *B. germanica* in 2022 and data obtained in 2012 can be found in Tables 5, 6, and 7.

Based on the value of the resistance ratio, a loss of very high ($50 < RR_{50} \leq 1000$) and high ($10 < RR_{50} \leq 50$) resistance levels occurred in all strains for the insecticides deltamethrin, propoxur, and fipronil. These strains became susceptible ($RR_{50} \leq 1$) or had low resistance ($1 < RR_{50} \leq 5$). The highest decrease occurred in strains that initially had a very high level of resistance to deltamethrin (Table 5), namely ACH2 (from 532.12 -fold to 1.00 -fold, susceptible); JKT2 (from 1072.37 -fold to 2.00 -fold), and MDN2 (from 1019.74 -fold to 1.00-fold, susceptible).

DISCUSSION

It is widely known that insects can evolve resistance to insecticides through natural selection. When exposed to insecticides as selection pressure, some insects may possess genetic variations that

Table 5. Comparison of the topical toxicity of deltamethrin in 2022 and resistance ratio (RR) data obtained in 2012 for the German cockroach

Strain	Insecticide	LD_{50} (µg/g)	Slope ± SE	RR_{50} 2022	RR_{50} 2012	Decrease in resistance (%)
VCRU	Deltamethrin	0.001	2.064 ± 1.940	1.00	1.00	
ACH2		0.001	1.231 ± 0.329	1.00	532.12	99.81
JKT2		0.001	0.455 ± 0.235	2.00	1072.37	99.80
MDN2		0.001	0.702 ± 0.269	1.00	1019.74	99.90
KLT1		0.004	4.057 ± 3.102	4.00	11.23	64.38

Note: the number of insects per strain for testing in 2022 is 30.

Table 6. Comparison of the topical toxicity of propoxur in 2022 and resistance ratio (RR) data obtained in 2012 for the German cockroach

Strain	Insecticide	LD_{50} (µg/g)	Slope ± SE	RR_{50} 2022	RR_{50} 2012	Decrease in resistance (%)
VCRU	Propoxur	0.035	2.725 ± 5.906	1.00	1.00	
ACH2		0.035	2.725 ± 5.906	1.00	48.64	97.94
JKT2		0.111	4.250 ± 7.789	3.17	44.46	92.87
MDN2		0.080	3.716 ± 7.799	2.29	45.17	94.93
KLT1		0.035	2.725 ± 5.906	1.00	1.05	4.76

Note: the number of insects per strain for testing in 2022 is 30.

Table 7. Comparison of the topical toxicity of fipronil in 2022 and resistance ratio (RR) data obtained in 2012 for the German cockroach

Strain	Insecticide	LD_{50} (µg/g)	Slope ± SE	RR_{50} 2022	RR_{50} 2012	Decrease in resistance (%)
VCRU	Fipronil	0.001	2.064 ± 1.940	1.00	1.00	
ACH2		0.001	2.064 ± 1.940	1.00	12.21	91.80
JKT2		0.002	1.201 ± 0.302	2.00	21.82	90.83
MDN2		0.001	2.191 ± 1.527	1.00	5.76	82.64
KLT1		0.003	3.572 ± 3.549	3.00	1.11	-

Note: the number of insects per strain for testing in 2022 is 30.

protect them from toxic effects. These insects are more likely to survive and reproduce, passing their protective genes to their offspring. As a result, the proportion of resistant insects increases in the population over time, leading to the entire population becoming resistant to the insecticide. However, in the absence of selection pressure, resistant insect populations tend to lose their resistance within a few generations (Cochran 1993).

This study demonstrates that even highly resistant cockroaches, such as JKT2 and MDN2, which exhibited more than a 1000-fold resistance to deltamethrin in 2012, can become susceptible again if they are reared without insecticide selection pressure. In other words, the level of resistance can decrease to such an extent that these cockroaches become susceptible once again.

Changes in the resistance of German cockroaches to deltamethrin have not been reported previously. This study is fascinating because two strains, namely JKT2 and MDN2, displayed a very high resistance ratio to deltamethrin in 2012, with values of 1072 -fold and 1019 -fold, respectively. However, after being reared without exposure to insecticides, the RR_{50} values in 2022 decreased to 2.00 -fold and 1.00, respectively, indicating susceptibility. This represents an extraordinary drop in the resistance level, from over 1000 -fold, and to susceptible (1 -fold). It is worth noting that according to Hariani (2013), the high level of resistance in these two strains to deltamethrin was observed because the cockroaches (JKT2 and MDN2) were collected from restaurants and bakeries that conducted routine and intensive pest control every two months. At times, control measures were increased at the request of consumers, occasionally with higher doses.

Reduced resistance to deltamethrin has been reported in other insects besides cockroaches. For example, Ahmad et al. (2007) reported a decrease in resistance of *Spodoptera litura* (Fabricius) from the 3rd generation resistance ratio (RR) of 63-fold to RR: 60 -fold in the 8th generation. *Plutella xylostella* (Linnaeus) showed a decrease in resistance from RR_{50}: 507 -fold in the second generation to RR_{50}: 29 -fold in the ninth generation (Sayyed et al. 2005). However, neither of these studies explained the mechanism behind the decrease in resistance to deltamethrin. In the case of German cockroaches, known to be resistant to pyrethroids, it is suspected that the reduction in resistance is due to a decrease in the frequency of resistance genes (Cochran 1993). For instance, Lee et al. (1996) reported a decrease in resistance of *B. germanica* in the Melia strain from Kuala Lumpur, Malaysia, after two generations without propoxur selection pressure, with the RR_{50} decreasing from 66-fold to 54-fold. This decrease in resistance is believed to be a result of the reduced frequency of resistance genes and coadaptation with fitness costs (Tang et al. 1990), where the benefits of resistance are outweighed by the costs of carrying resistance genes. However, a study by Wirth & Georghiou (1999) on *Ae. aegypti* from Tortola found no significant difference in resistance ratio between those exposed to propoxur and those not subjected to propoxur selection pressure for 13 generations.

In addition to deltamethrin, research on changes in the resistance ratio of German cockroaches after being reared in the laboratory for several generations without fipronil selection pressure has not been reported before. However, several studies have reported a decrease in fipronil resistance in other insects. For instance, Sayyed et al. (2005) observed a reduction in resistance of *P. xylostella* to fipronil, from an initial RR of 398 -fold to becoming susceptible after seven generations without exposure to fipronil selection. Abbas et al. (2016) reported that the Fipro-SEL strain exhibited 181.94 -fold resistance to fipronil compared to the UNSEL strain. However, this resistance was found to be unstable and decreased after five generations without selection.

However, this study observed an interesting phenomenon: an increase in the resistance ratio (RR_{50}) in the KLT1 strain from 1.11 -fold to 3 -fold, although it was still classified as low resistance. A similar increase in the resistance ratio was reported in a study by Cochran (1993) on German cockroaches without cypermethrin selection pressure, there the resistance ratio data in the sixth generations was RR: 1.3-fold and in the eighth generation RR: 3.7 -fold. Although no explanation was provided for why this occurred, Cochran (1993) mentioned that an error in sampling the test cockroaches could have caused the increase in RR. In our study, no errors were identified, but as noted by Strong et al. (1997), it is possible that the resistance level did not decrease after being reared without selection pressure due to the presence of resistance genes in the population. Furthermore, Lucas et al. (2015) stated that in certain cases, the resistance level in a species is initially significant, making the species inherently resistant. This could possibly explain the slight decrease or even increase in resistance level observed in the KLT1 strain to deltamethrin and fipronil after being reared for ten years without insecticide selection (see Tables 5 and 7).

This phenomenon is intriguing because the KLT1 strain showed a decrease in resistance to deltamethrin of only 64.38%, while other strains showed reductions ranging from 99.80% to 99.90%. Moreover, the reduction in resistance to propoxur in the KLT1 strain was only 4.76%, significantly different from the reductions observed in other strains, which ranged from 92.87% to 97.94%. Interestingly, the resistance ratio to fipronil increased from 1.11-fold in 2012 to 3.0-fold in 2012. Since all insects were raised in a laboratory, external factors such as gene flow between populations and environmental influences were not present. Therefore, it is likely that the factors influencing resistance are genetic factors and the specific resistance mechanisms within the insects.

Strains with greater genetic diversity, such as ACH2, JKT2, and MDN2 may exhibit a faster decrease in resistance due to increased recombination, while strains with lower genetic diversity, such as possibly KLT1, could show a slower decline. Additionally, the specific resistance mechanism (such as metabolic resistance, target site insensitivity, behavioral resistance, or reduced penetration) can also influence the rate of resistance reduction (Fardisi et al. 2019). Certain mechanisms might incur higher fitness costs or be more prone to reversal mutations, leading to a more rapid decline in resistance.

In this 2022 study, the decrease in resistance is believed to occur because the resistant cockroach population has a fitness disadvantage, resulting in lower quality and reproductive rates (Cai et al. 2020). For example, Grayson (1953) reported that insecticide-resistant cockroaches have a lower number of nymphs and smaller ootheca compared to susceptible ones. Similarly, Lee et al. (1996) found that insecticide-resistant cockroaches exhibited reduced fecundity and a longer nymph development period compared to susceptible ones. Rahayu (2011) reported that susceptible cockroaches had a lower fitness cost for reproduction compared to resistant ones. For instance, resistant field strain cockroaches had a 46.67% chance of having no offspring after mating, while susceptible strains had only a 13.04% chance. This phenomenon seems to have occurred in a recent study where initially insecticide-resistant cockroaches were reared without insecticide selection pressure for more than ten years, resulting in a gradual dominance of susceptible cockroaches and a decrease in the resistance ratio. Another example is the study by Roush & Plapp (1982) reporting a decrease in biotic potential (length of development period and fecundity) ranging from 11%-43% in organophosphate-resistant strains of *Musca domestica* Linnaeus compared to susceptible strains. Similarly, Abbas et al. (2016) found that the offspring of the Fipro-SEL strain, which had a resistance ratio of 181.94-fold to fipronil, exhibited a lower biotic potential compared to the susceptible strain (UNSEL) of the same species. Their findings indicated that resistance to fipronil is associated with high fitness costs in *M. domestica.* However, Ang & Lee (2011) reported different findings, stating that insecticide-resistant German cockroaches did not exhibit any fitness costs compared to susceptible cockroaches. Almost all insecticide-resistant German cockroach strains showed no significant difference in terms of the incubation period, nymphal development, production of nymphs, and ootheca when compared to the susceptible ones.

Given the differing opinions on the relationship between fitness and resistance to insecticides in German cockroaches, Cochran's (1993) study provides valuable insights. The study found that German cockroaches reared in a laboratory setting without pyrethroid selection pressure experienced a decrease in resistance after six generations or approximately two years, transitioning from high resistance (RR: >140-fold) to susceptibility due to a reduction in the frequency of resistance genes. However, conflicting research suggests that German cockroaches reared in the laboratory for two years without insecticide selection pressure may maintain their resistance, as the resistant gene is not adversely affected by laboratory conditions (Atkinson et al. 1991). Furthermore, the recent study by Scharf et al. (2022) sheds new light on the development of insecticide resistance in cockroaches, showing a link between selection for resistance and the elimination of commensal, pathogenic, and/or parasitic microbes. Specifically, gregarine infections in lab-cultured cockroaches may contribute to the buildup or reduction of resistance levels. Therefore, the observed reduction in resistance levels in this study may also be influenced by the presence of gregarine infections during the rearing of cockroaches in the laboratory. Furthermore, it is important to note that different strains exhibit varying patterns of decline, as illustrated by the case of the KLT1 strain. Even among pyrethroid-resistant *Ae. aegypti*, the extent of reduced resistance was found to depend on the specific strain, as observed by Vera-Maloof et al. (2020).

In addition, from the perspective of pest management, the development of cockroach resistance to insecticides is an inevitable occurrence. Therefore, when controlling cockroaches, the use of insecticides will still be necessary. We recommend employing a rotation strategy that involves using insecticides with different active ingredients if resistance to certain insecticides is encountered. This approach aims to achieve effective results in cockroach control. While this method may eventually lead to resistance in the target insects, it is possible to implement a control approach that does not rely solely on insecticides or aligns with the principles of integrated pest management. Such an approach can provide reasonable cockroach control over an extended period.

CONCLUSION

The results of this study and previous studies indicate that insect populations will decrease in resistance, either disappearing or exhibiting reduced resistance levels over several generations in the absence of insecticide selection. However, the way the decline occurs seems to vary based on the particular strain. Pest management professionals can utilize this information to design effective cockroach control programs.

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