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Research

Insecticide Resistance, and Its Effects on Bait Performance in Field-Collected German Cockroaches (Blattodea: Ectobiidae) From Taiwan

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Abstract

Insecticide resistance in the German cockroach, *Blattella germanica* (L.), is a significant challenge to the pest management professionals worldwide. We collected 24 field populations of *B. germanica* from different localities in Taiwan island, reared them for one to two generations, and evaluated them for their resistance to deltamethrin, propoxur, and fipronil using the surface-contact method. Results showed that deltamethrin resistance ratio ranged from 1.5 to 817.5×. Among the strains, TC Supermarket, TC Sanshang Logistics, TC THSR, and TC 1Taichungsteak strains showed very high resistance to deltamethrin, which mortality ranged between 0 and 33% at 7-d post-treatment. On the other hand, resistance to propoxur and fipronil RR were 0.70–7.13× and 1.67–3.72×, respectively. Synergism studies using piperonyl butoxide (PBO) and *S,S,S*-tributylphosphorotrithioate (DEF) suggested the major involvement of cytochrome P450 monooxygenase and minor involvement of esterases. However, deltamethrin resistance in two strains (i.e., TC Supermarket and TC THSR) was not affected by both PBO and DEF, indicating that other mechanisms are involved in the resistance, including *kdr* resistance. Evaluation of the field strains using commercial gel baits containing fipronil, imidacloprid, hydramethylnon, and indoxacarb for up to 7 d resulted in 24.4–100%, 11.3–78.5%, 15.8–75.5%, and 63.3–100% mortality, respectively. We found that high deltamethrin resistance in some strains could affect the performance of fipronil, imidacloprid, and indoxacarb baits, indicating the potential involvement of cytochrome P450 monooxygenase in reducing the effectiveness of the bait toxicants.

Key words **Cross-resistance, cytochrome P450 monooxygenase, esterases, *kdr* resistance**

The German cockroach, *Blattella germanica* (L.), is one of the most important urban insect pests in the world. Besides serving as a mechanical vector of pathogenic diseases, this species is a major nuisance in restaurant kitchens, hotels, public, and residential premises (Peterson and Shurdut 1999, Mullen and Durden 2009). Insecticides remain as one of the most convenient and effective methods to manage German cockroach populations. However, heavy reliance and frequent usage of insecticides have led to the development of insecticide resistance in the German cockroach (Chai and Lee 2010, Fardisi et al. 2019).

To date, the German cockroach has been reported to develop resistance toward 42 insecticides (Zhu et al. 2016). Resistance mechanisms found in the German cockroach include metabolic resistance, reduced penetration, target-site insensitivity, and behavioral resistance (glucose aversion) with metabolic resistance being the most common mechanism (Siegfried and Scott 1992, Bull and Patterson 1993, Anspaugh et al. 1994, Valles 1998, Wu et al. 1998, Lee et al. 2000, Valles et al. 2000, Chai and Lee 2010, Fardisi et al. 2019).

In Taiwan, residual insecticide sprays are the mainstay of cockroach treatment strategy. In some situations, treatment with gel baits is carried out, especially when treatment failure with sprays was experienced. In recent years, there have been anecdotal reports that field bait performance against German cockroaches are declining. We hypothesize that physiological resistance in some strains may have affected the performance of field bait performance. Earlier, Pai et al. (2005) collected and evaluated German cockroaches from hospitals and homes and reported resistance toward organophosphates, carbamates, and pyrethroids. At present, little is known on the status of insecticide resistance in the German cockroaches, and its effects on the performance of gel bait toxicants.

In this study, we collected German cockroaches from 24 localities in Taiwan island and evaluated their resistance status to

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several commonly used insecticides (i.e., deltamethrin, propoxur, and fipronil) using surface-contact method. Next, we determined the possible resistance mechanisms using synergists such as piperonyl butoxide (PBO) and *S,S,S*-tributylphosphorotrithioates (DEF). Finally, we tested the performance of several common gel baits against the field-collected strains and determined the relationship between pyrethroid resistance and bait performance.

Materials and Methods

Insects

Blattella germanica was collected from 24 premises from three cities in Taiwan: Taipei (5 strains), Taichung (18 strains), and Kaohsiung (1 strain; Table 1) between July 2017 and April 2018. These premises were a restaurant, supermarket, meat shop, train station, and shopping mall and were subjected to residual insecticide spray either on a monthly basis or once every 3–5 mo (see Supp Information [online only]). Gel baits were used whenever there were callbacks after residual insecticide treatments. A laboratory-susceptible strain (EHI), which was obtained from the Vector Control Research Unit, Universiti Sains Malaysia, was used for comparison. All strains were reared in round polyethylene containers (24 cm diameter × 32 cm height) and provided with corrugated cardboard harborage, dog food (RT-Mart chicken flavor dog food, Hsinchu, Taiwan), and water ad libitum. Cockroaches were kept in the insectarium under laboratory conditions of 25 ± 1°C, 50 ± 5% RH, and a 12-h photoperiod. Before the test, we collected the adult males and acclimatized them in a polyethylene cup with a piece of dog food and water in cotton bung for 24 h.

Insecticide Resistance Bioassays

Technical grade insecticides deltamethrin (98%, Tagros Chemicals India Ltd., Chennai, India), propoxur (99.3%, Sigma–Aldrich Corporation, Saint Louis, MO) and fipronil (98%, Toronto Research Chemicals, Inc., North York, Canada) were used in this study. Stock solutions of the aforementioned chemicals were prepared in acetone (Union Chemical Works Ltd., Hsinchu, Taiwan). An amount of 1-ml diluted insecticides was applied to the base of a glass jar (surface area = 28.27 cm^2) to prepare test concentrations (deltamethrin: 0.001 mg/cm^2; propoxur: 0.025 mg/cm^2, and fipronil: 0.001 mg/cm^2). The test concentration is based on the LC_{95} of the respective insecticide when tested on the EHI-susceptible strain. The inner wall surface was lined with a thin layer of petroleum jelly to prevent test cockroaches from escaping. Ten cockroaches were introduced into the insecticide-treated glass jar, and mortality was recorded at selected time intervals up to 7-d post-treatment or when 95% mortality was achieved. The survivors in the jar were provided with food and water 24 h after treatment.

Gel Bait Evaluation

Four commercial gel baits were evaluated in this study: Jin-Li-Hai Ultra Max cockroach gel bait containing 0.05% fipronil (Kukbo Science Co., Ltd, Cheongju-si, Korea), Premise cockroach gel bait containing 2.15% imidacloprid (Bayer AG, Petaling Jaya, Malaysia), Pu-Jhang gel bait containing 2% hydramethylnon (Chung Hsi Chemical Plant, Ltd, Hsinchu, Taiwan), and Advion cockroach gel containing 0.6% indoxacarb (Syngenta AG, Singapore). The cockroaches were acclimatized with only water for 48 h before the experiment. Ten each of adult males, nongravid females, and mid-instars were introduced into a polyethylene container (36 × 28 × 12 cm) with dried dog food, harborage, water, and 1 g of gel bait ad libitum. The mortality and bait consumption of the cockroaches were recorded daily up to 7 d. Gel bait and food were replenished when they were 70% consumed. Four replicates were done for each strain.

Synergist Bioassays

Synergism studies were carried out using PBO (97%, Chem Service, Inc., West Chester, PA) and DEF (97%, Chem Service, Inc.). One microliter of PBO solution (100 µg/insect) or DEF (30 µg/insect) was applied on the first abdominal sternite of each cockroach using a microapplicator (Burkard Scientific Ltd., Middlesex, United Kingdom) approximately 1 h before being introduced into a deltamethrin-treated glass jar. For fipronil, only two strains, i.e., TP Center Mall and TC Vimilan Restaurant that showed relatively high resistance to fipronil (Table 3), were subjected to synergism test. Control cockroaches were treated with acetone or acetone + synergist. All tests were replicated three times.

Data Analysis

Mortality data were pooled and subjected to probit analysis to determine the LT_{50} values. Resistance ratio (RR_{50}) was calculated by dividing the LT_{50} value of field strain with corresponding susceptible strain, and the synergist ratio (SR_{50}) was generated by dividing the LT_{50} using insecticide alone with insecticide + synergist. The significant difference of insecticide susceptibility between strains was determined based on the nonoverlapping 95% fiducial limit.

For gel bait evaluation, the mean survival time of each strain for each treatment was estimated using Kaplan–Meier analysis. The log-rank test was employed to examine whether the mean survival time of each strain significantly differed from that of the EHI-susceptible strain. The percentage of mortality at 7 d were arcsine square-root transformed before analysis of variance (ANOVA), and means were separated using Tukey HSD. The performance of gel baits against field-collected cockroaches was visualized in terms of % mortality, bait consumption, and mean survival time using canonical discriminant analysis (JMP 7, SAS Institute Inc.). The relationships between deltamethrin resistance ratio and mean survival time, and between deltamethrin resistance ratio and % mortality at 7-d post-baiting were analyzed by linear regression. All analyses were conducted using SPSS analysis version 11.0 (SPSS Inc., Chicago, IL) at $\alpha = 0.05$ unless otherwise specified.

Results

Insecticide Resistance Status

Deltamethrin resistance in field-collected populations of *B. germanica* ranged from 1.5 to >817.5× (Table 1). Four strains (TC Supermarket, TC Sanshang Logistics, TC THSR, and TC 1Taichungsteak) showed very high resistance to deltamethrin, which in these strains, the LT_{50} values were undetermined as the % mortality after 7-d exposure ranged from 0 to 33%.

Most strains demonstrated no to low resistance to propoxur, which RR_{50} ranged from 0.90 to 4.13×; Table 2). Only the KS Wufu Road strain showed moderate resistance to propoxur (RR_{50} = 7.13×). On the other hand, all strains were found to have no or low resistance to fipronil (1.47–3.76×; Table 3).

Bait Evaluation

The mean consumption ± SE of fipronil, imidacloprid, hydramethylnon, and indoxacarb gel baits were 167.5 ± 9.1, 85.0 ± 4.4, 56.8 ± 2.1, and 397.7 ± 16.6 mg, respectively (Table 4).

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Table 1. Toxicity and synergism of deltamethrin using PBO and DEF on field strains of German cockroaches in Taiwan using surface-contact method

	Insecticide alone				Insecticide + PBO					Insecticide + DEF				
Strains	*N*	LT_{50} (95% FL; min)	Slope ± SE	RR_{50}[b]	*N*	LT_{50} (95% FL; min)	Slope ± SE	RR_{50}[b]	SR_{50}[c]	*N*	LT_{50} (95% FL; min)	Slope ± SE	RR_{50}[b]	SR_{50}[c]
EHI	30	12.33 (12.15–12.52)	14.65 ± 0.95		30	10.76 (10.56–10.96)	11.96 ± 0.81		1.15	30	9.16 (8.75–9.55)	6.46 ± 0.45		1.35
TP Ce Zi Restaurant	30	117.46 (106.73–129.39)	2.27 ± 0.15	9.53	30	19.76 (19.21–20.33)	7.70 ± 0.53	1.84	5.94	30	53.24 (48.01–59.19)	2.48 ± 0.16	5.81	2.21
TP Center Mall	30	2,061.58 (1,764.89–2,568.72)	2.37 ± 0.25	167.20	30	27.27 (26.52–28.04)	7.80 ± 0.48	2.53	75.59	30	269.66 (229.60–317.65)	1.37 ± 0.10	29.44	7.65
TP AP Bar	30	279.39 (257.15–302.99)	2.65 ± 0.18	22.66	30	17.40 (17.24–17.57)	22.78 ± 1.44	1.62	16.05	30	118.87 (109.34–128.66)	3.61 ± 0.24	12.98	2.35
TP Hotpot Restaurant	30	843.51 (655.46–1,172.85)	1.15 ± 0.13	68.41	30	28.20 (26.83–29.76)	4.52 ± 0.38	2.62	29.91	30	248.98 (213.98–295.63)	1.58 ± 0.14	27.18	3.39
TP Daan Restaurant	30	560.43 (484.17–645.32)	1.51 ± 0.10	45.45	30	24.58 (23.56–25.63)	5.10 ± 0.31	2.28	22.80	30	75.40 (65.66–86.54)	1.55 ± 0.10	8.23	7.43
TC Supermarket	30	0%[a]	—	>817.52	30	3%[a]	—	>936.64	—	30	0%[a]	—	>1,100.44	—
TC Vimilan Restaurant	30	3,019.44 (2,098.23–6,701.47)	1.59 ± 0.33	244.89	30	116.37 (98.42–139.25)	1.32 ± 0.10	10.81	25.95	30	800.33 (714.72–917.59)	2.21 ± 0.22	87.37	3.77
TC Dali Restaurant	30	261.63 (236.93–288.70)	2.21 ± 0.14	21.22	30	18.10 (17.72–18.50)	10.13 ± 0.65	1.68	14.45	30	25.02 (19.98–33.08)	2.99 ± 0.26	2.73	10.46
TC Johan Restaurant	30	612.47 (534.69–707.07)	1.60 ± 0.12	49.67	30	20.12 (19.74–20.51)	11.33 ± 0.74	1.87	30.44	30	89.57 (77.30–103.36)	1.81 ± 0.11	9.78	6.84
TC UniqueInn	30	75.65 (68.44–83.66)	2.15 ± 0.13	6.14	30	24.92 (20.13–29.59)	9.81 ± 0.63	2.32	3.04	30	133.13 (126.03–140.51)	3.96 ± 0.24	14.53	0.57
TC Birosabakery	30	81.74 (68.66–98.38)	1.27 ± 0.10	6.63	30	24.53 (21.84–28.02)	3.03 ± 0.26	2.28	3.33	30	109.67 (92.80–131.17)	1.35 ± 0.11	11.97	0.75
TC Dasanyuan Restaurant	30	194.56 (167.62–227.01)	1.47 ± 0.11	15.78	30	25.35 (24.62–26.07)	7.63 ± 0.50	2.36	7.68	30	232.73 (215.17–252.22)	2.81 ± 0.20	25.41	0.84
TC Hanjiayuan Restaurant	30	220.37 (187.54–261.89)	1.38 ± 0.11	17.87	30	19.55 (18.73–20.45)	7.45 ± 0.53	1.82	11.27	30	132.99 (106.63–174.89)	1.18 ± 0.12	14.52	1.66
TC Sanshang Logistics	30	33%[a]	1.07 ± 0.26	>817.52	30	58.48 (51.73–67.19)	1.89 ± 0.17	5.43	—	30	1,293.47 (1,139.77–1,638.42)	3.94 ± 0.70	141.21	—
TC Taixi Restaurant	30	61.43 (50.91–76.03)	2.01 ± 0.17	4.98	30	27.94 (27.04–28.91)	6.80 ± 0.54	2.60	2.20	30	57.85 (54.48–61.53)	3.63 ± 0.26	6.32	1.06
TC 2Tasty Restaurant	30	78.97 (69.79–89.36)	1.75 ± 0.11	6.40	30	22.44 (21.72–23.17)	6.72 ± 0.42	2.09	3.52	30	26.99 (24.19–30.26)	3.80 ± 0.28	2.95	2.93
TC Meatshop	30	18.03 (17.59–18.48)	8.79 ± 0.57	1.46	30	15.11 (14.56–15.66)	5.94 ± 0.37	1.40	1.19	30	24.04 (23.10–25.06)	9.19 ± 0.72	2.62	0.75
TC Beitun Bento	30	71.57 (61.26–83.88)	1.38 ± 0.09	5.80	30	20.55 (20.32–20.79)	18.75 ± 1.17	1.91	3.48	30	37.34 (33.21–45.06)	3.45 ± 0.41	4.08	1.92
TC THSR	30	0%[a]	—	>817.52	30	537.38 (342.50–1,124.75)	0.86 ± 0.13	49.93	—	30	27%[a]	—	>1,100.44	—
TC 1Taichungsteak House	30	0%[a]	—	>817.52	30	102.93 (98.56–107.45)	5.04 ± 0.31	9.56	—	30	620.15 (597.04–644.24)	5.77 ± 0.43	67.70	—
TC Nantun Bakery	30	1,665.54 (1,505.25–2,245.88)	7.44 ± 1.97	135.08	30	169.41 (156.53–182.70)	3.45 ± 0.24	15.74	9.83	30	356.21 (347.83–364.84)	9.18 ± 0.61	38.89	4.68
TC Steak Restaurant	30	152.74 (142.58–163.31)	3.21 ± 0.20	12.39	30	24.32 (23.89–24.73)	13.01 ± 0.90	2.26	6.28	30	69.74 (62.42–77.66)	1.99 ± 0.13	7.61	2.19
TC Pizza	30	145.87 (137.20–155.03)	3.57 ± 0.23	11.83	30	33.96 (32.91–35.03)	6.89 ± 0.42	3.16	4.30	30	44.56 (43.23–45.91)	7.21 ± 0.44	4.86	3.27
KS Wufu Road	30	28.06 (27.19–28.97)	6.91 ± 0.46	2.28	30	16.26 (15.95–16.57)	11.50 ± 0.77	1.51	1.73	30	12.34 (12.17–12.53)	14.87 ± 0.91	1.35	2.27

[a]The percentage of mortality at 7 d.

[b]RR_{50}, LT_{50} of field strain/LT_{50} of EHI strain.

[c]SR_{50}, LT_{50} of insecticide only/LT_{50} of insecticide with synergist.

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Table 2. Toxicity of propoxur on field strains of German cockroaches in Taiwan using surface-contact method

Strains	*N*	LT_{50} (95%FL; min)	Slope ± SE	χ^2 (df)	RR_{50}[b]
EHI	30	23.41 (23.14–23.68)	18.76 ± 1.23	5.92 (28)	
TP Ce Zi Restaurant	30	23.62 (23.35–23.89)	19.22 ± 1.26	8.97 (28)	1.01
TP Center Mall	30	36.77 (35.48–38.08)	6.15 ± 0.38	9.49 (28)	1.57
TP AP Bar	30	21.02 (20.78–21.25)	19.47 ± 1.19	9.69 (28)	0.90
TP Hotpot Restaurant	30	21.79 (21.40–22.18)	12.28 ± 0.85	16.45 (28)	0.93
TP Daan Restaurant	30	50.54 (47.01–54.85)	3.31 ± 0.29	7.16 (21)	2.16
TC Supermarket	30	60.98 (57.39–64.75)	3.62 ± 0.24	8.59 (27)	2.60
TC Vimilan Restaurant	30	61.18 (58.96–63.54)	6.00 ± 0.46	5.95 (24)	2.61
TC Dali Restaurant	30	55.34 (53.5–57.24)	6.51 ± 0.45	7.72 (26)	2.36
TC Johan Restaurant	30	48.26 (45.53–51.24)	3.83 ± 0.31	12.01 (24)	2.06
TC UniqueInn	30	71.52 (69.29–73.77)	6.98 ± 0.49	16.58 (27)	3.06
TC Birosabakery	30	96.63 (93.54–100.54)	8.01 ± 0.81	9.84 (19)	4.13
TC Dasanyuan Restaurant	30	67.52 (64.60–70.65)	4.99 ± 0.37	6.21 (25)	2.88
TC Hanjiayuan Restaurant	30	21.58 (20.92–22.25)	7.05 ± 0.46	8.77 (28)	0.92
TC Sanshang Logistics	30	36.57 (34.97–38.23)	4.86 ± 0.30	14.04 (28)	1.56
TC Taixi Restaurant	30	22.86 (21.74–24.09)	5.51 ± 0.39	43.14 (28)	0.98
TC 2Tasty Restaurant	30	48.51 (46.65–50.44)	6.59 ± 0.42	35.98 (28)	2.07
TC Meatshop	30	16.35 (15.97–16.73)	9.41 ± 0.61	3.21 (28)	0.70
TC Beitun Bento	30	15.40 (15.13–15.66)	12.69 ± 0.83	10.93 (28)	0.66
TC THSR	30	86.74 (81.56–94.38)	5.08 ± 0.61	3.81 (16)	3.71
TC 1Taichungsteak House	30	22.86 (22.34–23.38)	9.51 ± 0.60	20.71 (28)	0.98
TC Nantun Bakery	30	32.80 (31.48–34.25)	5.52 ± 0.45	6.95 (23)	1.40
TC Steak Restaurant	30	21.16 (20.44–21.90)	6.29 ± 0.39	13.20 (28)	0.90
TC Pizza	30	23.08 (22.50–23.65)	8.74 ± 0.57	21.72 (28)	0.99
KS Wufu Road	30	166.84 (154.14–181.13)	2.76 ± 0.20	22.62 (25)	7.13

[a]% mortality at 7 d.

[b]RR_{50}, LT_{50} of field strain/LT_{50} of EHI strain.

The mean % mortality of German cockroach ranged from 8.5 ± 5.4 to 98.4 ± 0.9%, after 7-d exposure to fipronil bait (Fig. 1a). Post hoc analysis revealed that the mean mortalities of TP Center Mall, TP Daan Restaurant, TC Vimilan Restaurant, TC Dali Restaurant, TC Johan Restaurant, TC Birosabakery, TC Dasanyuan Restaurant, TC Hanjiayuan Restaurant, TC Sanshang Logistic, TC 2Tasty Restaurant, TC 1Taichungsteak House, TC Nantun Bakery, and KS Wufu Road were significantly lower than that of EHI-susceptible strain (F = 37.5; df = 24; P < 0.05). The mean survival time of the field strains was significantly longer than the susceptible strains (Table 5).

There were 66% of field strains with the mean % mortality (43.3 ± 2.0%) that were significantly lower than that of EHI-susceptible strain (F = 10.6; df = 24; P < 0.05) after 7-d imidacloprid bait exposure (Fig. 1b). The mean survival time of overall populations was 4.67 ± 0.05 d, but TP Center Mall, TC Vimilan Restaurant, TC Johan Restaurant, TC Hanjiayuan Restaurant, and TC THSR strains required >6 d to achieve 20% mortality (Table 5).

Hydramethylnon bait was least effective among all the baits tested. Even the EHI-susceptible strain only had 53.6 ± 9.2% mortality at 7-d post-exposure (Fig. 1c). The strain with the highest mortality was TC Birosabakery, with 75.5 ± 6.9% mortality, whereas TP AP Bar only recorded 15.8 ± 7.5% mortality. In general, the mean survival time was 5.71 ± 0.03 d, indicating its relatively slow action among the tested baits. For indoxacarb bait, the mean mortality of TP Hotpot Restaurant, TC Supermarket, TC Johan Restaurant, TC Birosabakery, TC Dasanyuan Restaurant, TC Sanshang Logistic, TC THSR, and TC Nantun Bakery was significantly lower than that of EHI-susceptible strain, registering 63–80% mortality at 7-d exposure (F = 14.0; df = 24; P < 0.05; Fig. 1d). Indoxacarb exposure of field strains of the German cockroach resulted in significantly prolonged mean survival times of 2.58 ± 0.04 d (Table 5). TC Supermarket, TC THSR, and TC Birosabakery had prolonged survival time after indoxacarb treatment (3.92–4.13 d).

Canonical discriminant functions showed differential gel bait performance against field-collected German cockroach (Fig. 2). There are two discriminant functions. The first discriminant function accounted for 82.8% of the total variance and was mainly associated with bait consumption at day one exposure, while the second discriminant function accounted for 16.4% of the total variance, which was correlated with mean survival time of German cockroach and % mortality at 7-d exposure. High bait consumption rate significantly differentiated indoxacarb gel bait from other gel baits. However, we are unable to differentiate the performance of fipronil and indoxacarb baits (based on mean survival time of German cockroach and % mortality at 7-d exposure) due to the fast action of both baits (Table 4). The results also demonstrated that the performance of fipronil bait was inconsistent among tested strains, possibly due to physiological resistance. For example, 75 mg killed 95.9% test insects in TC Pizza (Fig. 2), whereas 66.3 mg only caused 8.5% mortality in TC 2Tasty Restaurant. The bait consumption rates of imidacloprid and hydramethylnon were low, but the performance of imidacloprid could be distinguished from hydramethylnon, which generally resulted in a lower mortality rate of the test cockroaches.

Regression of Toxicity of Deltamethrin and Baits

There was a significant positive correlation between deltamethrin resistance and mean survival time after being exposed to fipronil bait, but the association with % mortality after 7 d was not significant (P = 0.0632; Table 6). The resistance levels of deltamethrin significantly influenced the mean % mortality and the mean survival time

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Table 3. Toxicity of fipronil on field strains of German cockroaches in Taiwan using surface-contact method

Strains	*N*	LT_{50} (95% FL; min)	Slope ± SE	χ^2 (df)	RR_{50}[b]
EHI	30	370.62 (354.16–387.35)	5.72 ± 0.35	36.34 (28)	
TP Ce Zi Restaurant	30	786.22 (771.81–800.89)	11.81 ± 0.76	3.54 (28)	2.12
TP Center Mall	30	1,353.07 (1,332.73–1,373.65)	14.45 ± 1.00	14.99 (27)	3.65
TP AP Bar	30	666.73 (654.02–679.45)	11.45 ± 0.74	15.66 (28)	1.80
TP Hotpot Restaurant	30	1,076.00 (1,052.53–1,099.60)	10.00 ± 0.67	13.88 (28)	2.90
TP Daan Restaurant	30	952.95 (910.63–993.97)	8.94 ± 0.61	17.89 (26)	2.57
TC Supermarket	30	1,094.88 (1,069.17–1,121.68)	9.13 ± 0.62	11.79 (27)	2.95
TC Vimilan Restaurant	30	1,201.98 (1,160.88–1,245.41)	6.27 ± 0.44	11.28 (26)	3.24
TC Dali Restaurant	30	1,292.11 (1,270.84–1,313.38)	13.24 ± 0.85	13.05 (28)	3.49
TC Johan Restaurant	30	1,330.18 (1,319.24–1,340.96)	26.75 ± 1.80	18.31 (28)	3.59
TC UniqueInn	30	1,192.41 (1,167.43–1,217.56)	10.38 ± 0.67	13.74 (28)	3.22
TC Birosabakery	30	966.89 (953.32–980.47)	15.58 ± 1.05	14.70 (28)	2.61
TC Dasanyuan Restaurant	30	1,393.83 (1,345.69–1,442.16)	6.24 ± 0.39	33.06 (28)	3.76
TC Hanjiayuan Restaurant	30	710.18 (694.52–726.17)	9.76 ± 0.70	26.29 (28)	1.92
TC Sanshang Logistics	30	1,379.00 (1,348.85–1,410.31)	9.82 ± 0.72	33.71 (27)	3.72
TC Taixi Restaurant	30	558.58 (544.86–572.86)	8.64 ± 0.55	20.19 (28)	1.51
TC 2Tasty Restaurant	30	1,289.45 (1,260.22–1,319.12)	9.50 ± 0.58	10.00 (28)	3.48
TC Meatshop	30	777.68 (766.58–788.67)	15.45 ± 1.00	9.85 (27)	2.09
TC Beitun Bento	30	545.43 (534.31–556.63)	10.67 ± 0.70	9.52 (28)	1.47
TC THSR	30	620.29 (604.25–637.06)	8.21 ± 0.54	20.72 (28)	1.67
TC 1Taichungsteak House	30	910.82 (888.70–932.74)	9.05 ± 0.60	21.13 (28)	2.46
TC Nantun Bakery	30	1,277.32 (1,243.64–1,311.73)	8.15 ± 0.50	8.92 (28)	3.45
TC Steak Restaurant	30	653.42 (641.39–665.49)	11.79 ± 0.76	16.36 (28)	1.76
TC Pizza	30	729.24 (717.26–741.46)	13.09 ± 0.82	9.91 (28)	1.97
KS Wufu Road	30	794.84 (774.65–815.43)	8.48 ± 0.53	7.55 (28)	2.14

[a]% mortality at 7 d.
[b]RR_{50}, LT_{50} of field strain/LT_{50} of EHI strain.

Table 4. The mean of % mortality, survival time, and bait consumption in gel bait evaluations

	Fipronil			Imidacloprid			Hydramethylnon			Indoxacarb				
	N	Mean	SE	*N*	Mean	SE	*N*	Mean	SE	*N*	Mean	SE	*F*	*P* value
Mortality at 7 d (%)	100	62.11	2.92	100	43.28	2.04	100	46.6	1.97	100	87.15	1.17	26.6	<0.01
Mean survival time (d)	100	3.98	0.05	100	4.67	0.05	99	5.71	0.03	100	2.58	0.04	30.52	<0.01
Consumption (mg)	100	167.49	9.1	100	84.97	4.42	100	56.84	2.06	100	397.69	16.57	71.55	<0.01

at post-treatment of imidacloprid bait (Table 6). We also found that there was a significant correlation between mean survival time after indoxacarb bait treatment and % mortality at 7 d associated with deltamethrin resistance level (Table 6). However, in hydramethylnon bait test, neither % mortality nor mean survival time was correlated with deltamethrin resistance (Table 6).

Synergist Treatment

Synergism studies using PBO significantly reduced deltamethrin resistance in most field strains (Table 1). Several strains (TP AP Bar, TP Hotpot restaurant, TP Daan Restaurant, TC Dali Restaurant, TC Johan Restaurant, TC Dasanyuan Restaurant, TC Hanjiayuan, TC Steak Restaurant, and TC Pizza) that registered high deltamethrin resistance showed a drastic reduction in resistance level on treatment with PBO. The deltamethrin resistance levels for three strains, i.e., TP Center Mall, TC Sanshang Logistics, and TC 1Taichungsteak, reduced from 167.2 to 2.5×, >817.5 to 141.2×, and >817.5 to 67.7×, respectively, after PBO treatment. However, the resistance levels of TC Vimilan Restaurant, TC THSR, and TC Nantun Bakery only were partially decreased and remained high (RR ranged from 10.8 to 49.9) after PBO pretreatment. The deltamethrin resistance of TC Supermarket strain remained unaffected even after the PBO pretreatment (Table 1).

DEF synergism on deltamethrin significantly reduced the resistance of TP Ce Zi Restaurant, TP Center Mall, TP AP Bar, TP Hotpot Restaurant, TP Daan Restaurant, TC Dali restaurant, TC Johan Restaurant, TC 2Tasty Restaurant, TC Beitun Bento, TC Nantun Bakery, TC Steak Restaurant, TC Pizza, and KS Wufu Road strains (SR ranged from 2.2 to 10.5), but the resistance levels remained high in some strains (TC Vimilan Restaurant, TC Sanshang Logistics, and TC 1Taichungsteak; Table 1), indicating that DEF only partially negated deltamethrin resistance in these strains. On the other hand, DEF failed to reduce the resistance levels of TC Supermarket and TC THSR strains (Table 1).

Discussion

The present study demonstrated a varying degree of deltamethrin resistance (ranging from low to very high resistance) and suggested the possible involvement of metabolic resistance (cytochrome P450 monooxygenase) and target-site insensitivity (*kdr* resistance) as resistance mechanisms. We also found that the performance of three

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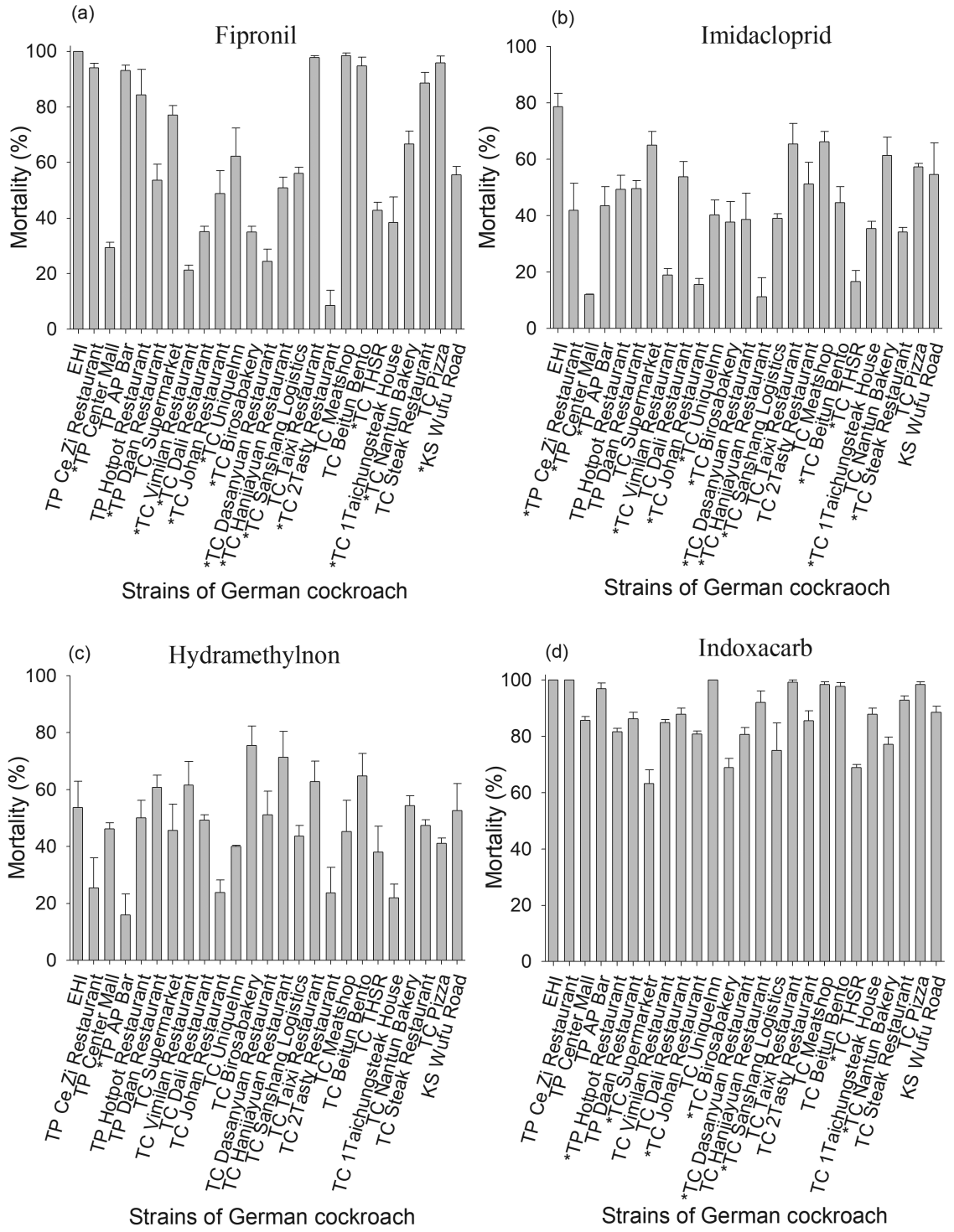

Fig. 1. Mortality of the German cockroach at 7-d post-treatment with gel baits. The asterisk (*) indicates significant difference ($P < 0.05$) when compared with EHI strain using one-way ANOVA.

gel baits (fipronil, imidacloprid, and indoxacarb) was correlated with the deltamethrin resistance level. It is possible that metabolic resistance has an influence on the mean survival time, whereas at the same time, reduced mortality of fipronil, imidacloprid, and indoxacarb gel baits because of bait consumption level (bait palatability and bait aversion behavior) also could be a contributing factor. The TC Supermarket and TC THSR that showed very low mortality after 7-d exposure to deltamethrin may possess *kdr* resistance that reduced their susceptibility toward indoxacarb gel bait.

The point mutation in voltage-gated sodium channel (*kdr* resistance), cytochrome P450 monooxygenases and esterases, have been reported to be main mechanisms of pyrethroid resistance in German cockroaches (Pridgeon et al. 2002, 2003; Liu et al. 2006; Zhu et al. 2016; Tang et al. 2018). Our results showed that 33% of the field

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Table 5. Mean survival time (day) of German cockroach after exposure to four gel baits

Strains	Fipronil		Imidacloprid		Hydramethylnon		Indoxacarb	
	Mean (SE)	95% FL	Mean (SE)	95% FL	Mean (SE)	95% FL	Mean (SE)	95% FL
EHI	1.05 (0.02)	1.00–1.09	2.70 (0.21)	2.28–3.12	5.85 (0.13)	5.59–6.11	1.05 (0.02)	1.02–1.09
TP Ce Zi Restaurant	1.60 (0.13)*	1.34–1.86	4.52 (0.25)*	4.03–5.00	6.36 (0.13)*	6.11–6.60	1.13 (0.04)	1.05–1.20
TP Center Mall	6.07 (0.15)*	5.78–6.36	6.40 (0.15)*	6.11–6.68	5.64 (0.15)	5.35–5.92	2.73 (0.21)*	2.32–3.14
TP AP Bar	1.98 (0.14)*	1.70–2.25	4.71 (0.24)*	4.24–5.18	6.58 (0.10)*	6.39–6.78	1.98 (0.14)*	1.70–2.25
TP Hotpot Restaurant	3.54 (0.18)*	3.19–3.90	4.37 (0.24)*	3.90–4.84	5.81 (0.14)	5.55–6.07	3.31 (0.22)*	2.88–3.73
TP Daan Restaurant	4.78 (0.21)*	4.37–5.18	4.24 (0.26)	3.74–4.75	5.21 (0.17)	4.88–5.53	2.80 (0.20)*	2.41–3.19
TC Supermarket	2.92 (0.21)*	2.52–3.32	3.44 (0.25)*	2.95–3.94	5.71 (0.15)	5.42–6.01	3.92 (0.23)*	3.47–4.38
TC Vimilan Restaurant	6.32 (0.13)*	6.06–6.58	6.20 (0.17)*	5.86–6.53	5.41 (0.15)	5.12–5.71	2.76 (0.21)*	2.35–3.16
TC Dali Restaurant	5.63 (0.18)*	5.28–5.99	4.27 (0.26)*	3.76–4.78	5.68 (0.15)	5.39–5.96	2.52 (0.19)*	2.14–2.89
TC Johan Restaurant	4.82 (0.21)*	4.41–5.23	6.23 (0.18)*	5.88–6.58	6.75 (0.06)*	6.64–6.87	3.64 (0.22)*	3.21–4.07
TC UniqueInn	4.05 (0.21)*	3.64–4.46	4.80 (0.25)*	4.31–5.28	6.05 (0.12)*	5.81–6.29	1.20 (0.05)*	1.10–1.30
TC Birosabakery	5.66 (0.18)*	5.32–6.01	5.17 (0.22)*	4.73–5.61	4.96 (0.14)*	4.68–5.24	4.13 (0.21)*	3.72–4.54
TC Dasanyuan Restaurant	6.01 (0.17)*	5.68–6.34	3.03 (0.34)	2.36–3.69	5.39 (0.16)	5.08–5.70	2.82 (0.21)*	2.41–3.22
TC Hanjiayuan Restaurant	4.60 (0.24)*	4.13–5.06	6.32 (0.18)*	5.97–6.67	5.02 (0.15)*	4.72–5.31	2.36 (0.18)*	2.01–2.72
TC Sanshang Logistics	4.67 (0.20)*	4.28–5.06	5.38 (0.20)*	4.99–5.76	5.91 (0.14)	5.64–6.18	3.35 (0.22)*	2.91–3.78
TC Taixi Restaurant	1.51 (0.11)*	1.29–1.73	3.46 (0.26)*	2.94–3.98	5.51 (0.14)	5.24–5.78	1.25 (0.06)*	1.12–1.37
TC 2Tasty Restaurant	6.79 (0.08)*	6.64–6.94	4.15 (0.27)*	3.62–4.67	6.49 (0.11)*	6.28–6.70	2.94 (0.21)*	2.52–3.35
TC Meatshop	1.74 (0.11)*	1.52–1.95	2.77 (0.29)	2.20–3.34	5.76 (0.15)	5.47–6.05	1.55 (0.10)*	1.36–1.73
TC Beitun Bento	2.06 (0.16)*	1.76–2.37	4.71 (0.25)*	4.23–5.19	4.94 (0.17)*	4.61–5.27	1.65 (0.12)*	1.41–1.89
TC THSR	5.37 (0.19)*	4.99–5.75	6.08 (0.18)*	5.72–6.44	6.16 (0.12)*	5.92–6.39	4.12 (0.22)*	3.69–4.54
TC 1Taichungsteak House	5.59 (0.17)*	5.24–5.93	4.95 (0.24)*	4.48–5.43	6.52 (0.11)*	6.30–6.74	2.71 (0.20)*	2.32–3.10
TC Nantun Bakery	4.24 (0.19)*	3.87–4.60	3.90 (0.25)*	3.42–4.39	5.43 (0.16)	5.12–5.74	3.40 (0.22)*	2.97–3.82
TC Steak Restaurant	2.44 (0.18)*	2.09–2.79	5.33 (0.22)*	4.90–5.77	5.59 (0.15)	5.30–5.88	2.54 (0.18)*	2.20–2.89
TC Pizza	2.00 (0.16)*	1.69–2.31	3.64 (0.26)*	3.12–4.15	5.57 (0.17)	5.24–5.89	1.66 (0.11)*	1.45–1.88
KS Wufu Road	4.19 (0.25)*	3.70–4.68	4.40 (0.25)*	3.91–4.90	4.38 (0.24)	3.91–4.85	3.07 (0.20)*	2.69–3.45
Overall	3.98 (0.05)	3.89–4.07	4.67 (0.05)	4.57–4.76	5.71 (0.03)	5.65–5.77	2.58 (0.04)	2.50–2.66

*Significant difference from EHI ($P < 0.05$) by log-rank test.

populations showed RR_{50} more than 50×. Of the 33% field populations, four strains (TC Supermarket, TC Sanshang Logistics, TC THSR, and TC 1Taichungsteak; 16.7%) have a very limited number of mortality (<33%) after 7-d exposure to deltamethrin. We found that the deltamethrin resistance levels in this study were higher than those reported earlier by Pai et al. (2005) in field German cockroaches collected from Kaohsiung, Taiwan (RR_{50} = 1.95–27.35×).

PBO suppressed the deltamethrin resistance levels of most strains, including TC Sanshang Logistics and TC 1Taichungsteak. In contrast, pretreatment of DEF only partially reduced the deltamethrin resistance level with SR < 5. The present results suggested the involvement of cytochrome P450 monooxygenases in deltamethrin resistance in most German cockroach strains, but the contribution of hydrolytic enzymes toward deltamethrin resistance is limited. Most other studies reported earlier demonstrated the involvement of both cytochrome P450 monooxygenases and esterases in pyrethroid-resistant German cockroaches (Pridgeon et al. 2002, Chai and Lee 2010).

Because neither PBO nor DEF pretreatment could increase the toxicity of deltamethrin in TC Supermarket strain, this ruled out the involvement of metabolic resistance, indicating *kdr* resistance and other mechanisms, i.e., reduced cuticular penetration (Chen et al. 2020) might be involved in the strain. As for the TC THSR strain, although pretreatment of PBO decreased the RR value (to 49.9×), its resistance level was not entirely negated by the synergists. Both *kdr* resistance and oxidative metabolism are likely involved in the resistance. The involvement of multiple resistance mechanisms had been reported in other earlier studies, especially on pyrethroid-resistant *B. germanica* (Scott et al. 1990, Valles and Yu 1996, Wei et al. 2001, Pridgeon et al. 2002) and in Iran (five out of seven strains, Limoee et al. 2007), Singapore (8 out of 22 strains, Chai and Lee 2010) and Malaysia (4 out of 53 strains, Lee and Lee 2004).

All field strains showed a low level of resistance to propoxur (0.90–4.13×), except for KS Wufu Road strain (7.13×). Pai et al. (2005) reported propoxur resistance in German cockroaches collected from hospital and residential areas in Kaohsiung, with RR values registering 2.86–30.86× and 6.93–62.50×, respectively. Increased hydrolytic activity due to elevated esterases contributed toward propoxur resistance (Siegfried and Scott 1991).

The fipronil resistance level in the field strains was relatively low when tested using surface-contact method. However, evaluation using fipronil gel bait revealed that % mortality of German cockroach up to 7 d was moderate (62.11 ± 2.92%). The *rdl* mutation involves the replacement of amino acid alanine to serine (A302S) due to mutation encoded by the γ-amino butyric acid-gated chloride channel subunit gene that confers resistance to fipronil and dieldrin (Kristensen et al. 2005, Gondhalekar and Scharf 2012, Ang et al. 2013). Ang et al. (2013) selected fipronil-resistant *B. germanica* using fipronil gel bait up to F_5 generation and observed high frequencies of individuals possessing the *rdl* mutation. In this study, we rule out the possible involvement of *rdl* mutation-associated resistance in the field strains, and we found that the pretreatment of PBO antagonized fipronil toxicity in TP Center Mall and TC Vimilan Restaurant. The possible involvement of bait aversion is also excluded as the cockroaches readily feed on the bait, as demonstrated from bait consumption results.

Gondhalekar and Scharf (2012) reported that metabolic resistance played a significant role in fipronil resistance in the German cockroach. The role of metabolic resistance in fipronil resistance was further supported by Valles et al. (1997), who reported that the

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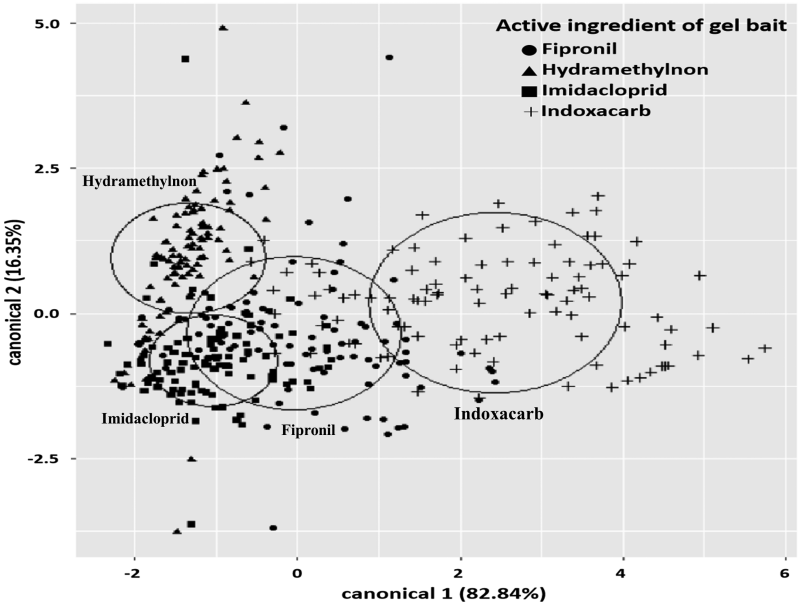

Fig. 2. Canonical discriminant functions showed differential gel bait efficacy against field-collected German cockroach. The ellipses indicate 50% confidence region of each bait formulation.

Table 6. Regression of deltamethrin resistance ratio and bait performance

Insecticides	Independent variable	Dependent variable	df	*F*	R^2	*P*
Fipronil	Deltamethrin RR_{50} (Log)	Mortality (%)	19	3.89	0.17	0.06
		Mean survival time	19	6.62	0.26	0.02
Imidacloprid	Deltamethrin RR_{50} (Log)	Mortality (%)	19	8.90	0.32	0.01
		Mean survival time	19	8.97	0.32	0.01
Hydramethylnon	Deltamethrin RR_{50} (Log)	Mortality (%)	19	<0.01	<0.01	0.99
		Mean survival time	19	0.19	0.01	0.67
Indoxacarb	Deltamethrin RR_{50} (Log)	Mortality (%)	19	6.60	0.26	0.02
		Mean survival time	19	6.30	0.25	0.02

fipronil toxicity decreased by 2.2–3.0 times in *B. germanica* after pretreatment with PBO and DEF compared with treatment with fipronil alone. Similarly, house flies with high deltamethrin resistance survived longer after exposure to fipronil than that of less resistant ones (Liu and Yue 2000). However, several studies showed mixed results. For instance, Wei et al. (2001) tested on a pyrethroid-resistant German cockroach and observed that the cockroach did not show cross-resistance to fipronil. Holbrook et al. (2003) reported that males of *B. germanica* that were tolerant of cypermethrin were susceptible to fipronil. Similar results were reported by Wu and Appel (2017) that pyrethroid-resistant German cockroaches with elevated cytochrome P450 monooxygenases activity were susceptible to fipronil.

Besides fipronil, correlation between deltamethrin resistance level and the imidacloprid bait performance was detected. The mean survival time after imidacloprid bait exposure increases with deltamethrin resistance level, whereas % mortality after treatment with imidacloprid bait decreases with resistance level. Imidacloprid is an agonist of insect nicotinic acetylcholine receptors (Matsuda et al. 2001, Tomizawa and Casida 2005). This compound has a rapid knockdown effect on German cockroaches (Chai and Lee 2010; Zhu et al. 2016). The cross-resistance due to the overexpression of cytochrome P450 monooxygenase detoxification has been demonstrated in not only German cockroach but a wide array of insects (Wen and Scott 1997, Liu and Yue 2000, Wei et al. 2001). In this study, the TP Center Mall, TP Daan Restaurant, TC Vimilan Restaurant, TC Dali Restaurant, TC Johan Restaurant, TC Hanjiayuan Restaurant, and TC THSR strains with possible high cytochrome P450 monooxygenase activity (SR from 11.27 to 75.59) showed low mortality after treatment with imidacloprid. Besides that, the bait palatability or bait aversion issues in the imidacloprid bait formulation may also be a contributing factor as the mortality of the susceptible EHI strain was <80% after 7-d exposure to the imidacloprid bait.

Resistance to indoxacarb has been documented in the German cockroach (Gondhalekar et al. 2011). Ko et al. (2016) reported that nymphs that were repeatedly selected using indoxacarb bait for 2 yr had significantly extended survival time compared with those unselected and susceptible strains. To date, indoxacarb bait has not been registered and used for German cockroach management in Taiwan, which may explain why the indoxacarb gel bait performance was the highest among the four baits tested. However, there are two interesting observations: 1) the TC Supermarket and TC THSR strains that possibly possessed other mechanisms of resistance (other than cytochrome P450 monooxygenases and hydrolases), including *kdr* resistance showed that the mean survival time of German cockroach was >3.9× longer than the susceptible

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EHI strain at 7-d indoxacarb bait post-treatment. Indoxacarb is an oxadiazine insecticide, which inhibits insect neuronal voltage-dependent sodium channels (Wing et al. 1998, Lapied et al. 2001). Although the action of target-sites is not entirely similar (Lapied et al. 2001), the cross-resistance between pyrethroid-associated *kdr* resistant to indoxacarb is possible (Chai and Lee 2010). Earlier, Ang et al. (2014) demonstrated that both LD_{50} and RR_{50} values for deltamethrin and indoxacarb were positively correlated. 2) A positive linear correlation between deltamethrin resistance level, and mean % mortality at 7-d exposure to indoxacarb and mean survival time after indoxacarb exposure. The unexpectedly low mortality and prolonged survival upon exposure in several strains may be due to enhanced metabolic detoxification. Also, the combined effects of metabolic resistance and target-site insensitivity may also lead to unidirectional cross-resistance, as reported by Liang et al. (2017) that exposure to fipronil bait may increase cross-resistance to indoxacarb but not vice versa. However, the speculation on the effect of *kdr* mutations in sodium channels on indoxacarb susceptibility in German cockroaches warrants further investigation.

Hydramethylnon, an inhibitor of mitochondrial respiration that blocks the electron transport chain (Hollingshaus 1987), works as ingestion toxicant against a range of insects (Koehler and Patterson 1991). Hydramethylnon bait has been shown to provide excellent performance against German cockroach (Appel 1992, Lee 1998), especially managing pyrethroid-resistant German cockroaches (Lee 1998, Sitthicharoenchai et al. 2006). In 1990s, the incidence of hydramethylnon associated resistance was rare (Koehler and Patterson 1991) but the resistance has more recently been documented and likely is more common than presently believed. A German cockroach population from Puerto Rico was shown to have 4× resistance to hydramethylnon when compared with susceptible strain (Ko et al. 2016). The resistance level subsequently increased to 351-fold after artificial selection for 2 yr (Ko et al. 2016). In the present study, we detected no correlation between RR of deltamethrin, and mean % mortality and mean survival time after hydramethylnon treatment. However, hydramethylnon bait was least effective among all bait tested. This ineffectiveness could be explained by poor bait palatability of hydramethylnon bait or bait aversion behavior, judging from the moderate performance of the EHI-susceptible strain (<60%). Further investigation on the bait palatability is urgently required.

In summary, we demonstrated the pyrethroid resistance status and the performance of several gel baits against *B. germanica* in Taiwan. Synergism studies using PBO and DEF suggested the involvement of cytochrome P450 in conferring pyrethroid resistance in many strains, and other mechanisms, including *kdr* resistance and elevated esterases in fewer strains. We also found that deltamethrin resistance level correlated with mean survival time after exposure to fipronil, imidacloprid, and indoxacarb in gel baits. A negative correlation was found between deltamethrin resistance level and % mortality at 7 d after exposure to these gel baits. In addition, bait consumption level and mean survival time are main functions that accounted for the majority of variability in the analysis of different factors contributing to bait resistance. It is important to note that the results obtained from this laboratory study only suggest the possible presence of insecticide resistance development in the field populations; our results do not indicate total control failure of the insecticides used in the field. This is because the field-collected strains that were tested were based on progenies of field insect samples that were collected and bred under the laboratory conditions for several generations. Only when control failure is similarly experienced in the field can such a statement be made.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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