

Behavioral Resistance of Field-Collected German Cockroaches (Blattodea: Blattellidae) to Baits Containing Glucose

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ABSTRACT German cockroaches, *Blattella germanica* (L.), collected from a number of field locations, ranging from Florida to South Korea, displayed an avoidance behavior to a bait formulation. Cockroaches collected from locations that had a history of treatment with this formulation demonstrated bait avoidance, whereas laboratory and field strains with no prior exposure ingested and were susceptible to the toxic bait. Thus, behavioral resistance had evolved in these insects. Selection experiments showed that several susceptible strains were potentially capable of developing behavioral resistance. Strains that avoided ingesting bait also displayed an aversion to glucose, which is a component of the bait that is typically phagostimulatory. Substitution of fructose for glucose in toxic baits significantly improved bait efficacy.

KEY WORDS *Blattella germanica*, behavioral resistance, glucose aversion

IN A REVIEW ARTICLE on urban integrated pest management (IPM), Schal and Hamilton (1990) emphasized the need for research in a number of areas before sound IPM practices can be established for cockroach control. Like other researchers (Appel 1990, Koehler et al. 1991), they recognized the value of baits for cockroach control. Excellent results in laboratory and field tests have been obtained with baits containing hydramethylnon (Appel 1990, McDonald et al. 1987, Mileo et al. 1986), and no indication of physiological resistance to hydramethylnon was found in field-collected *B. germanica* (L.) (Schal 1992).

Recently, Silverman & Bieman (1993) identified a field location where hydramethylnon bait performance against *B. germanica* had declined over several years. The decline in bait performance was caused in large part by behavioral resistance, specifically aversion to glucose, a component of the bait matrix. Behavioral resistance has received little attention to date. Sparks et al. (1989) challenged the interpretation of many resistance studies by offering behavioral explanations for responses to toxicants attributed to physiological and biochemical mechanisms. Strain differences in the behavioral response of German cockroaches to insecticide deposits (Ross & Cochran 1992), vapors of commercial propoxur formulations (Wooster & Ross 1989), and the vapors of the inert in pyrethroid formulations (Ross 1992) illustrate the importance of behavior in resistance management. The present

study was undertaken to examine behavioral resistance to glucose in *B. germanica* collected over a broad geographic area from locations with and without prior hydramethylnon bait treatment and to assess the potential for the development of behavioral resistance through selection experiments.

Materials and Methods

Materials. Hydramethylnon bait (1.65%, Clorox, Pleasanton, CA) was used in all experiments. Fructose/glucose corn syrup (CornSweet 55) was obtained from Archer Daniels Midland (Cedar Rapids, IA), and fructose corn syrup (Krystar) was supplied by A. E. Staley (Decatur, IL). Crystalline D-glucose and D-fructose were obtained from Sigma Chemical (St. Louis, MO). Agar (Bacto) was supplied by Difco (Detroit, MI). Untreated food used in bait choice tests was Purina dog chow (Ralston Purina, St. Louis, MO).

Cockroach Strains. Strains used, their origin, and year of collection were the following: Forest Green (T-164) strain, Gainesville, FL, 1989; Hawthorne strain, Gainesville, FL, 1989; Lincoln Terrace strain, Roanoke, VA, 1990; Opelika strain, Opelika, AL, 1991; Jacksonville strain, Jacksonville, FL, 1988; Miami, Miami, FL, 1990; K-851, Muldraugh, KY, 1986; Fairbanks strain, Fairbanks, AK, 1985; Navy 3, Norfolk VA, 1987; NYC, New York City, 1990; Torrance, Torrance, CA, 1991; 6133, Gainesville, FL, 1991; Seoul, Seoul, South Korea, 1992; and two standard susceptible strains in culture for >40 yr, VPI and Orlando normal. The T-164, Hawthorne, NYC, Torrance, 6133, and Seoul strains were from populations where hydramethylnon bait had become

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less effective. The Opelika, Lincoln Terrace, and Jacksonville strains were from locations where hydramethylnon bait had been used with no apparent decrease in effectiveness. Because the experiments were conducted in different laboratories, not all of the above strains were included in all the studies.

Tests with Whole Baits. Choice experiments on nine strains were conducted in 5 gal aquaria.

A harborage (10 cm by 4 cm by 0.8 cm high), open at each end, was placed at one end of the aquarium. Twenty late instars (most in the sixth stadium) were released into each aquarium and allowed to settle for 2–2½ h before water and food were placed into the aquarium. Water was supplied from a sponge-stoppered vial that was placed at the opposite end of the aquarium from the shelter. Food was in two small dishes (2 cm diameter) placed in the center of the aquarium, at approximately two-thirds of the distance between the shelter and the opposite end of the aquarium. One dish contained dog food pellets (Ralston Purina); the other, hydramethylnon bait (15.4% fructose, 11.8% glucose). Both were broken up into small pieces (0.1–5 mm). Consumption was determined by weighing each food-filled dish before and after each experiment (48 h). Mortality data were gathered daily during the 48-h exposure period. Afterwards, cockroaches were removed to clean jars and daily counts continued until it was apparent that mortality was complete. Each day, cockroaches were put in clean containers with fresh harborages (folded strips of screen wire). This was necessary to avoid toxicity from feces contaminated with hydramethylnon (Silverman et al. 1991). Strains were reared at 24°–27°C, and tested at 27°C and 55–60% RH, with a 10:14 (L:D) h photoperiod.

roach with both toxic bait and alternate food continuously for 52 wk. The T-164 strain was not assayed for bait aversion after each generation but was assayed for glucose aversion ≈1 y after selection.

Tests with Corn Syrup and Components. The corn syrup present in hydramethylnon bait was avoided by T-164 cockroaches (Silverman & Bieman 1993). It (CornSweet 55) consisted of 55% fructose, 42% glucose, and 3% higher saccharides. Diets consisting of sugar concentrations similar to the levels in the hydramethylnon baits (1 M glucose [18% wt/vol], 1 M fructose [18% wt/vol], corn syrup [40% wt/vol]) were evaluated against the Hawthorne, Torrance, 6133, Miami, Orlando normal, and T-164 strains. The sugar diets were prepared by bringing 1% agar to a boil, allowing it to cool to ≈60°C, and then adding glucose, fructose, or corn syrup. The diets were dispensed in dishes (34 cm³) and allowed to solidify. Dishes with plain 1% agar were also prepared. Diet pairs (sugar/agar and plain agar) were preweighed and placed into plastic containers (20 cm diameter by 20 cm height) with established populations of 1,000–2,000 mixed age/sex *B. germanica*. The cockroaches were deprived of food and water for 48 h before feeding trials to facilitate a rapid response to the diets and thereby minimize diet weight loss caused by evaporation. Diets kept apart from cockroaches served as water-loss controls. The diet pairs were left with the insects for 2 h. Four replicates were performed per strain per sugar. Consumption of each sugar/agar pair was determined gravimetrically, correcting for water loss. The feeding index was calculated to determine stimulation, nondetection, or aversion as follows:

$$\text{Feeding index} = \frac{\text{sugar-agar diet consumed (mg)} - \text{agar-only diet consumed (mg)}}{\text{sugar-agar diet consumed (mg)} + \text{agar-only diet consumed (mg)}}$$

Selection Experiments. Choice experiments were also used to investigate the potential for the development of resistance by selection-experiments on four strains (Lincoln Terrace, Jacksonville, Opelika, and Hawthorne). Survivors of choice experiments were mated and choice experiments repeated on their progeny. Three generations were tested in each strain. In each generation, experiments with 20 late instars (10 males, 10 females) were replicated six to 10 times.

The T-164 strain was also selected for bait aversion in the laboratory by introducing hydramethylnon bait for 2 d of each week for 28 wk in the continuous presence of alternate food (dog chow). Selection pressure was subsequently increased by confining surviving T-164 cock-

roaches with positive, zero, and negative feeding indices reflect stimulatory, neutral (no detection), and deterrent responses, respectively, to each sugar diet. A feeding index of 1 = 100% consumption of the sugar-containing agar, whereas an index of -1 = 100% consumption of plain agar.

Cockroaches from each of the same six strains were evaluated for hydramethylnon bait susceptibility to determine if a relationship existed between sugar acceptance and LT-50. Twenty male *B. germanica* from each of the above containers (six strains by four repetitions) were placed in 39.0 cm by 27.0 cm by 27.0 cm plastic containers provisioned with dog chow, water, and harborage. After the insects had acclimated for 3 d, an unbroken hydramethylnon bait was placed along the side of the container opposite the harborage.

Table 1. Food consumption and mortality in choice tests on bait preference of field-collected strains of *B. germanica*

Strain ^a	n ^b	Food consumption, $\bar{x} \pm \text{SEM}^c$		% Mortality, $\bar{x} \pm \text{SEM}^c$
		Total mg ^d	% Bait ^e	
Miami**	4	48.1 \pm 1.12a	38.1 \pm 3.96abc	88.8 \pm 3.96a
Linc T*	10	48.5 \pm 2.37a	40.1 \pm 3.46ab	81.0 \pm 4.35ab
Jax*	6	49.3 \pm 3.45a	47.6 \pm 2.78a	78.5 \pm 3.68abc
Navy 3**	7	23.3 \pm 2.41b	29.2 \pm 6.32bcd	69.7 \pm 10.2bcd
Fairbanks**	8	23.3 \pm 2.42b	20.1 \pm 2.69de	69.4 \pm 3.46bcd
K 851**	8	30.8 \pm 1.90b	19.8 \pm 3.20de	62.0 \pm 3.38cde
Opelika*	6	32.3 \pm 2.46b	25.6 \pm 4.92cd	56.8 \pm 5.53de
NYC*	8	54.1 \pm 6.21a	18.8 \pm 2.28de	47.1 \pm 5.56e
Hawthorne*	8	50.0 \pm 2.37a	11.0 \pm 0.93e	45.9 \pm 4.28e

^a Jax, Jacksonville strain; Linc T, Lincoln Terrace strain; *, strain from field location with hydramethylnon bait treatment history; **, strain from field location with no known history of hydramethylnon bait treatment.

^b Number of replicates (20 nymphs per replicate, except adjusted for 20 from 15 nymphs in Navy 3 strain).

^c Final mortality (7 to 10 d after 48-h exposure). Numbers in columns followed by the same letter are not significantly different ($P > 0.05$; Duncan's multiple range test [SAS Institute 1985]).

^d Total amount of food consumed (bait plus dog food).

^e Hydramethylnon bait (1.65%).

Mortality was assessed daily and an LT-50 was calculated. Feeding indices were plotted against the LT-50 for each strain.

Response to Glucose and Fructose. We determined the approximate frequency of glucose avoiders from each of seven *B. germanica* field-collected and two lab strains. Individual male cockroaches ($n = 100$ per strain) were secured dorsally to adhesive strips (10 strips and 10 per strip). The strips were positioned under a stereozoom microscope and a single 1- μ l droplet of either 1 M glucose or 1 M fructose was placed on the mouthparts of each male using a hand-held pipet fitted with a finely tapered disposable tip. Each male received both solutions ≈ 1 h apart. The solutions were administered randomly. A positive response was recorded if the sugar droplet was imbibed within 5 s. Rejected droplets were removed with a tissue.

Efficacy of Low-Glucose Baits. Experiments were conducted to determine whether reduction of glucose in hydramethylnon baits would improve performance. We prepared two proprietary hydramethylnon bait compositions, which shared only 25% of the inert components including corn syrup. Each composition was prepared with either a fructose/glucose corn syrup (Corn-Sweet 55; total in bait = 15.4% fructose, 11.8% glucose) or a 100% fructose corn syrup (Krystar; total in bait = 27.2% fructose). The T-164 strain was chosen for this study because it responded poorly to the original hydramethylnon bait used in field trials and it demonstrated the strongest aversion to glucose. Four replicates of 20 males each were provided each of the baits (two compositions by two corn syrups) along with dog chow, water, and harborage. Mortality was assessed daily.

Statistical Analyses. Analysis of variance followed by Duncan's multiple-range test was used for comparison of bait consumption and mortality. Probit analysis was used to compare mortality from bait formulations with and without glu-

cose (SAS Institute 1985). Analysis of variance and Fisher's LSD and *t*-tests were used to compare feeding responses of cockroaches fed 1 M glucose and fructose solutions. Correlation analysis was performed to determine if a relationship occurred between sugar consumption and hydramethylnon bait LT-50. A line was fitted for each sugar/LT-50 strain response (BBN Software Products 1988).

Results

Whole Bait Studies. Significant differences in total consumption (treated and untreated foods), treated food as a percentage of total consumption, and mortality in choice experiments occurred among field-collected strains (Table 1). Mortality was clearly related to percentage bait consumption but not total food consumption. The highest mortalities occurred in the three strains with highest percentage bait consumption: Miami, Lincoln Terrace, and Jacksonville. As a result of the comparatively high total food consumption and percentage bait consumption, the amounts of bait consumed were also relatively high (18–23 mg). Lowest mortalities and percentage bait consumption occurred in the Hawthorne and NYC strains. Bait consumption in the Hawthorne strain (5.5 mg) was similar to consumption in the Navy 3, Fairbanks, and K-851 strains (4.7–6.8 mg), yet mortality was significantly less than in the Navy 3 and Fairbanks strains. Total food consumption was not related to mortality. For example, total food consumption was significantly lower in the Navy 3, Fairbanks, K-851, and Opelika strains than in the other strains but percentage mortalities were intermediate.

Selection Experiments. Two strains with high mortality, Lincoln Terrace and Jacksonville, one with intermediate mortality, Opelika, and one with low mortality, Hawthorne, were selected for avoidance of the bait. Following the first se-

Table 2. Effects of selection on bait consumption and mortality of German cockroach field strains

Strain ^a	Observed ^b , %	Group selected ^c		
		F ₁	F ₁	F ₂
Linc T	Mortality	81.0 ± 4.35a	41.7 ± 6.67b	44.8 ± 2.48b
	Bait eaten	40.1 ± 3.46a	6.7 ± 1.76b	11.5 ± 2.47b
Jax	Mortality	78.5 ± 3.68a	54.2 ± 3.52b	30.0 ± 5.45c
	Bait eaten	47.6 ± 2.78a	14.5 ± 3.11b	9.2 ± 3.06b
Opelika	Mortality	56.8 ± 5.53a	62.4 ± 11.75a	70.5 ± 11.7a
	Bait eaten	25.6 ± 4.92a	17.5 ± 5.60a	27.0 ± 2.36a
Hawthorne	Mortality	45.9 ± 4.28a	12.3 ± 2.07b	10.0 ± 2.83b
	Bait eaten	11.0 ± 0.93a	3.7 ± 1.06b	3.1 ± 1.20b

^a Linc T, Lincoln Terrace strain; Jax, Jacksonville strain.

^b % Bait eaten = amount of bait eaten (mg) divided by the total amount of food consumed (bait + dog chow).

^c Means ± SEM. F₁, initial test; F₁, test on survivors of P₁; F₂, tests on survivors of F₁. Numbers in rows followed by the same letter are not significantly different ($P > 0.05$; Duncan's multiple range test [SAS Institute 1985]).

lection, mortality and percentage bait consumption were reduced significantly in all strains except the Opelika (Table 2, F₁). No significant changes occurred in percentage bait consumption or mortality in the Opelika strain following either the first or second selection (Table 2, F₁ and F₂). However, increases occurred in total food consumption (from 32.2 to 58.5 and 61.5 mg in the F₁ and F₂, respectively) and in bait consumption (from 8.2 to 10.3 and 16.6 mg in the F₁ and F₂, respectively). Total food consumption in the other strains was relatively high in the initial experiments (Table 1, Lincoln Terrace, Jacksonville, and Hawthorne) and remained high following selection. The Jacksonville strain was the only strain in which mortality decreased significantly following the second selection (Table 2, F₂). Bait consumption dropped from 14.5 to 9.2% but the difference was not significant.

Role of Sugars. A strong negative correlation was established for corn syrup feeding index and hydramethylnon bait LT-50 ($r = -0.99$, $P < 0.05$) (Fig. 1). Those cockroach strains demonstrating the greatest aversion to CornSweet 55 corn syrup (negative feeding index) also revealed the longest LT-50s. Some of these insects survived up to 2 mo in the presence of bait. The feeding index versus LT-50 relationship was identical for glucose ($r = -0.99$, $P < 0.05$) and corn syrup, while feeding on fructose was poorly correlated with bait efficacy ($r = -0.79$, $P > 0.05$). Therefore, glucose acceptance varied by cockroach strain and directly affected bait efficacy. The frequency of glucose avoiders within a strain was ascertained in single-insect assays. The proportion of insects accepting glucose and fructose was equal in lab strains with no prior exposure to hydramethylnon bait and field-collected insects from locations never treated with hydramethylnon bait. However, significantly fewer cockroaches from locations previously treated with hydramethylnon bait accepted glucose than fructose (Table 3).

Effect of Corn Syrup on Bait Efficacy. Efficacy improved significantly against the T-164 strain following substitution of 100% fructose corn

syrup (LT₅₀ [95% CI], bait 1 = 3.87 [1.92–5.08], bait 2 = 4.08 [1.85–5.41]) for corn syrup with fructose and glucose (LT₅₀ [95% CI], bait 1 = 14.01 [11.42–23.90], bait 2 = 16.46 [12.73–45.36]) (Fig. 2). Baits without glucose provided 100% mortality by day 10; however, baits with glucose never killed more than 40% of the insects throughout the 14-d study.

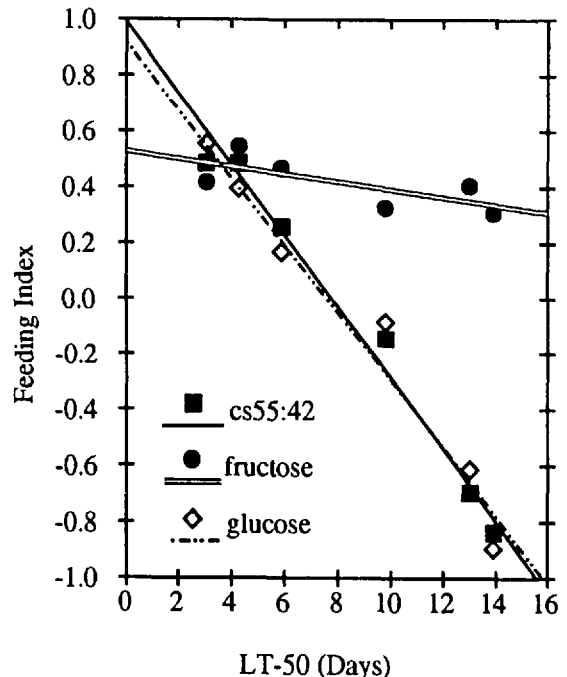


Fig. 1. Relationship of hydramethylnon bait toxicity to sugar consumption in 6 *B. germanica* strains. Positive, zero, and negative feeding indices reflect stimulatory, neutral, and deterrent feeding responses in choice tests, respectively. Strains from lowest to highest LT-50 are Orlando normal, Miami, 6133, Hawthorne, Torrance, and T-164. Linear equations for each sugar are cs55:42 (corn syrup), $y = -0.13x + 0.99$ ($r^2 = 0.98$, $F = 205.1$, $P < 0.0001$); fructose, $y = -0.01x + 0.53$ ($r^2 = 0.62$, $F = 6.6$, $P > 0.05$); glucose, $y = -0.12x + 0.92$ ($r^2 = 0.97$, $F = 110.6$, $P < 0.0005$).

Table 3. Response of individual field-collected and laboratory *B. germanica* males to 1 M glucose and 1 M fructose solutions

Strain	Positive responders, % ± SEM		
	Glucose	P-value, t-test	Fructose
T-164**	8.0 ± 2.91a	0.0001	92.0 ± 3.59a
Hawthorne*	33.0 ± 3.00b	0.0001	94.0 ± 4.00a
Torrance*	33.0 ± 5.39b	0.0001	97.0 ± 1.53a
Seoul*	45.3 ± 3.59c	0.0001	95.9 ± 2.25a
6133*	62.0 ± 4.67d	0.0006	89.0 ± 4.59a
Miami++	88.0 ± 2.00e	0.1743	92.0 ± 2.00a
Orlando+	91.0 ± 2.77e	0.1033	97.0 ± 2.14a
VPI+	92.0 ± 4.17e	0.4073	96.0 ± 2.21a
Fairbanks++	93.0 ± 2.14e	0.7767	93.9 ± 2.24a

*, Field location with hydramethylnon bait treatment history; **, treatment history plus further laboratory selection; +, longstanding lab maintained colony; ++, field location with no history of hydramethylnon bait treatment. Column means followed by same letter are not significantly different ($P > 0.05$; Fisher's LSD).

Discussion

Genetic variability among German cockroach field populations may be far more extensive than generally realized. In addition to the gamut of responses to a toxic bait and glucose in particular, reported here, differences occur in insecticide-induced dispersal (Bret & Ross 1985, Wooster & Ross 1989, Ross 1992), response to dried formulations (Ross & Cochran 1992), and fitness (Ross 1991). These variations have most likely developed as a result of insecticide treat-

ments. The relative roles of physiological and behavioral resistance in control by conventional means is not well understood (Sparks et al. 1989), but the present study suggests that altered behavior may become a major factor in determining the efficacy of baits. Barson (1989) inferred that repeated avoidance of a methomyl commercial bait by a proportion of resistant houseflies indicated a potential for the development of behavioral resistance.

Total amounts of food consumed, in the whole bait assays, were variable, as might be expected. The environment was not perfectly uniform and the nymphs were not precisely the same age nor, in all probability, in the same physiological state. Nevertheless, one group of strains was distinguished from the others by significantly lower food consumption and intermediate bait consumption and mortality. Selection experiments were carried out on only one member of the group, the Opelika strain. Although neither mortality nor percentage bait consumption increased with selection, food consumption did increase. We do not know whether selection would affect other members of the group similarly. However, shared characteristics of the unselected strains suggested genetically controlled differences in physiology. Conceivably, the common characteristics are typical of strains with little or no potential for the development of resistance to hydramethylnon bait. In any case, the results from the Opelika strain indicate that at least some populations would be slow to develop an effective defense mechanism against hydramethylnon bait.

Glucose aversion was demonstrated in field strains with a history of exposure to hydramethylnon bait. A direct relationship was established between hydramethylnon bait efficacy (LT-50) and glucose aversion. In strains with no prior bait exposure, LT-50s were low (<5 d) and the response to glucose and fructose were comparable (>90%). Between-strain variability in the paired sugar-agar feeding assay could be attributed to the ratio of avoiders to nonavoiders within a population or different levels of consumption by individual insects, or both. Single-insect assays revealed glucose avoiders within strains; however, ingested amounts were not quantified. Glucose aversion is controlled by an incompletely dominant gene(s) with heterozygotes ingesting intermediate amounts of glucose (Silverman & Bieman 1993). Therefore, most of the interstrain variability in the sugar-agar feeding assay could be explained by the relative proportion of homozygous glucose acceptors, hybrids, and homozygous avoiders. The results of the selection experiments support the suggestion that single-bait treatments could alter the gene frequency of the aversion behavior and also reduce bait efficacy. These findings agree with Roush and McKenzie's (1987) statement that "field treatment tends to select for major genes

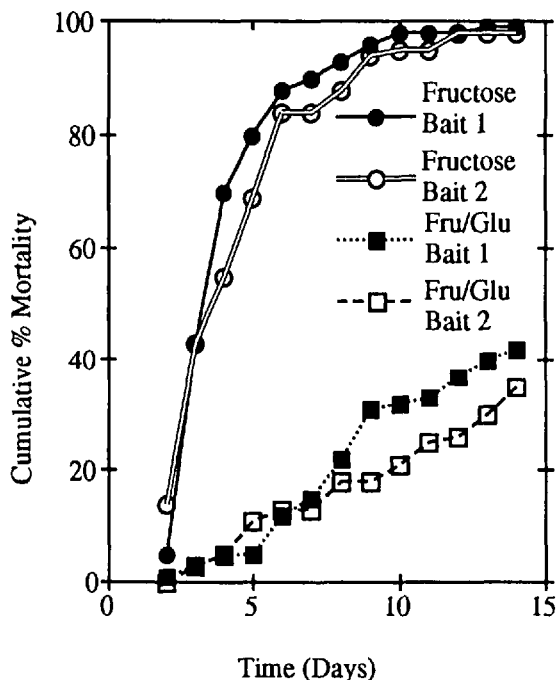


Fig. 2. Performance of two hydramethylnon bait compositions with fructose or fructose/glucose corn syrups against the T-164 strain of *B. germanica*.

that can confer large increases in resistance immediately," although they were referring to the development of physiological resistance. The intensity of selection with baits at the field sites where the strains were collected was not known. Hydramethylnon baits were first field tested in 1980. Baits were not recognized as an effective control strategy before this time, although other insecticidal baits (with or without glucose) may have provided some selection pressure.

The effect of glucose aversion on bait performance was further demonstrated by dramatic efficacy improvements with fructose for glucose substitutions in two distinct bait formulations. The effect of glucose was also evident in field trials because *B. germanica* populations were reduced from 42 to 85% following substitution of fructose for glucose in the hydramethylnon bait matrix (unpublished data).

We propose three explanations for the appearance of glucose aversion over a broad geographic range. First, it evolved independently in many isolated locations. Second, it originated in a few locations and spread elsewhere through commerce. The selective force was probably toxic baits containing glucose in either of these scenarios. Finally, it may have evolved before the cockroach/human association under the selective pressure of allelochemicals; specifically ones containing the glucose molecule, such as glucosinolates or cyanogenic glycosides.

Although the toxic and repellent properties of the active ingredient are extremely important in determining bait efficacy, they may not be the primary factors as suggested by Appel (1990). We have demonstrated that the composition of the bait base may be the most important factor in determining bait efficacy. Glucose is the most abundant monosaccharide in nature, a universal energy source, and a potent feeding stimulant to many insects, including cockroaches (Tsuji 1965). Therefore, the surprising discovery of glucose as the aversive material in the hydramethylnon baits indicates that any component can be responsible for the development of resistance to toxic baits.

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