BEHAVIORAL MODIFICATIONS AND THEIR IMPLICATIONS FOR COCKROACH RESISTANCE TO TOXIC BAITS

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Abstract—Inter-strain variation of German cockroaches in response to several commercial baits and their potential to develop resistance to the baits was investigated. Late instars were given a choice between the bait and an alternate food source (dog chow). Survivors were saved and choice tests repeated. Tests were done on fourth or fifth generation progeny in selected strains except with Raid Max. Relative attractancy/ repellency was estimated on basis of percentage bait consumption (amount of bait consumed divided by total food consumption).

The greatest inter-strain variation was with Baygon bait and Raid Max. It was associated with physiological resistance, but a behavioral component also affected the response to Raid Max. Avoidance and physiological resistance increased significantly in one strain following two generations of selection with Raid Max. Baygon bait was repellent to all strains. Low levels of physiological resistance had major effects on bait efficacy. Abamectin baits (Roach Ender and WIT gel) and, in tests with insecticide susceptible strains, Raid Max, were highly attractive. Avoidance was increased in two strains selected with abamectin baits. Strong behavioral resistance developed in strains selected with Stapleton's Magnetic Roach Food. The implications of the above for pest management are discussed.

INTRODUCTION

Laboratory studies revealed differences between the behavior of susceptible and resistant German cockroaches exposed to vapors and residues of various pyrethroids (Wooster and Ross, 1989; Ross 1992, 1993; Ross and Cochran, 1992). Whether and to what extent these differences affect the efficacy of insecticides used in the field is uncertain. Zungoli (1990) questioned whether repellency of an insecticide really has an impact in the field. One problem, generally overlooked, in attempting to address this question is a lack of information on physiological and/or behavioral resistance of the particular field population. In any case, when it comes to toxic baits, there is little argument that repellency affects their efficacy.

Appel (1990) suggested that toxicity and repellency of active ingredients in baits "are probably the most important factors affecting bait performance". This implies recognition of the effects of both physiological and behavioral factors. Nevertheless, Appel's statement needs to be expanded to include repellency of inert ingredients. Avoidance can develop as a result of selection for aversion to ingredients of a bait base, as in the case of glucose (Silverman and Biemen, 1993, Silverman and Ross, 1994). A control failure in the field was due to selection for a semi-dominant gene (*Glu*) that causes an aversion to glucose.

In spite of numerous studies on bait and bait technology, little is known concerning inter-strain variation in the response of German cockroaches to commercial baits or their potential to develop resistance to the baits Experiments were undertaken to address these questions because of the increasing importance of baits in pest management strategies for cockroach control. Part of the work presented here is a continuation of experiments done by a graduate student (Negus and Ross, unpubl.).

Behavioral responses to the baits were evaluated on basis of percentage bait consumption (amount of bait consumed divided by total food consumption) when cockroaches were given a choice between the bait and dog chow. If <50%, it is assumed that the bait was repellent; if >50%, that the bait was attractive. An increase in avoidance coupled with slower kill and at least a trend towards reduced mortality in selected strains is interpreted as indicative of the development of behavioral resistance. Learning might also affect response to a bait (Reierson, 1995), but this should not be confused with heritable differences in avoidance behavior.

The effects of physiological resistance on the results of experiments with Raid Max and Baygon Bait were assessed in strains resistant to chlorpyrifos and propoxur, respectively.

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MATERIALS AND METHODS

Nymphs were drawn from two insecticide susceptible strains, Navy 3 (N3) and Fairbanks (FBK). Other strains were resistant to various insecticides. They included the Jacksonville (Jax), Forest Green (FG), Puerto Rico (PR), and Las Palms (LP).

Table 1 lists baits and the duration of each experiment. Roach Ender and Raid Max baits were removed from bait stations immediately before use. Twenty nymphs (10 males, 10 females) were given a choice between a bait and dog chow. Sixth instars were used in experiments of short duration (abamectin and chlorpyrifos baits); 4–5th instars were used in work with the Magnetic Roach Food and Baygon bait. Mortality was recorded during the experiment and after cockroaches were removed to clean containers until at least 2 d passed with no further kill in any of the replicates (6–10 per strain). Probit analysis was used to compare LT_{50}s. Bait and dog food consumption was determined by weighing the materials before and at the end of each experiment. The gel bait and Magnetic Roach Food were dried before use (preliminary experiments indicated no loss of attractancy). If necessary, consumption was adjusted based on percentage weight change in controls (jars with bait, dog chow, and water). Percentage bait consumption was estimated as described above.

Strains were kept under selection pressure by repeatedly saving survivors of the choice experiments, mating them, and testing the progeny. With Roach Ender, the WIT gel bait, and Stapleton's Magnetic Roach Food, selections were limited to strains that had apparently been modified by three prior generations of selection (Negus and Ross, unpubl.). Experiments with Raid Max were begun recently and only F_1 and F_2 data are available. The effects of selection were assessed from simultaneous tests on the selected strain and the unselected parent stock.

RESULTS

Abamectin baits. No deleterious effects on reproduction with the abamectin baits (Cochran, 1985) were observed, suggesting that survivors were cockroaches that fed mostly, if not entirely, on dog food. Kill was slow. Mortality was not complete until 7–10 days after survivors were placed in clean containers. Among six strains tested with Roach Ender, no single strain differed significantly from the other five in either mortality or percentage bait consumption (Negus and Ross, unpubl.). The greatest inter-strain variation was between the PR and Jax strains, in both mortality and attractancy (Table 2, initial tests). Low mortality in the PR strain was associated with a lower percentage bait consumption than in the Jax strain. With the WIT gel, mortality in the PR strain was also low, but percentage bait consumption was high. Table 2 shows results from the PR and a second strain, the FG strain, that was typical of other strains tested with the WIT gel. Percentage bait consumption was high. Low mortality in tests of the PR strain with both abamectin baits suggests a low level of physiological resistance.

After three generations of selection, percentage bait consumption in two strains selected with Roach Ender and one with the WIT gel bait was lower and kill slower than in the parent stocks (Ross and Negus, unpubl.). Only one of the strains selected with Roach Ender, the Jax, showed a further change from the F_3. Percentage bait consumption was 25% lower than in the parent stock

Table 1. Baits and times used in choice experiments with German cockroaches

Bait	Time
Roach Ender (0.05% abamectin)	3d*
WIT gel** (0.05% abamectin)	3d*
Raid Max (0.5% chlorpyrifos)	5d***
Baygon Bait (2% propoxur)	14d
Stapleton's Magnetic Roach Food (33.3% boric acid)	14d

*Increased to 4 d in some selection experiments.
**Whitmire gel bait, not commercially available .
***Increased to 14 d in one resistant strain.

(Table 2, selection experiments). It was 18% lower than in the F_3. LT_{50} data indicated that the behavioral modification apparently resulted in slower kill. Mean mortality was lower in the selected strain than in the parent stock, but the difference was not statistically significant. With the gel bait, trends in the F_3 of the PR strain were the most strongly suggestive of incipient change. By the 5th generation, the strain differed markedly from the parent stock (Table 2). The complicating factor was that the stock itself had apparently changed. In initial tests with both the gel bait and Roach Ender, mortalities were 38%-39%, but 9–12 mo later, mortalities in the stock were >60% in tests with both baits.

Baygon Bait. Mortalities in the Jax and LP strains were lower than in the susceptible strains (Table 3). Mortalities corresponded to levels of physiological resistance of 1.8x in the Jax and 15.0x in the LP, both of which differed significantly from the VPI susceptible strain (jar-type test, Cochran, 1989). Low percentage bait consumption indicates that the bait was highly repellent. Three generations of selection did not result in significant changes from parental stocks. No further selections were done.

Raid Max. In 5 d choice experiments, mortalities and percentage bait consumption were high in susceptible strains (Table 4, Fbk and N3). Mortality was lower in the PR strain. The strain is characterized by a low but significant degree of physiological resistance (1.3x). Percentage bait consumption (50%) indicates that the PR nymphs were less attracted to the bait than those of the susceptible strains. Physiological resistance in the LP strain (4.4x) was higher than in the PR strain. No mortality occurred in 5 d tests. After lengthening the choice test to 14 d, mortality and percentage bait consumption were still lower than in the other strains.

Table 2. Choice experiments with abamectin baits*

Strain and Bait	Total Food (mg)	% Bait Eaten**	% Mortality	LT_{50} (95% C.I.) days
Roach Ender				
Initial tests (3d):				
Jax	11.2	76.1a	66.0a	3.7 (3.3–4.3)
PR	12.6	51.7b	39.1b	13.5 (7.8–23.2)
*Selection (4d)****:				
Jax	18.7	83.6a	77.2a	3.5 (3.1–3.9)
Jax F_4	21.9	58.5b	69.4a	5.1 (4.7–5.6)
WIT gel				
Initial tests (3d):				
FG	36.6	77.3a	53.1a	3.1 (2.7–3.6)
PR	44.4	79.1a	38.0b	4.2 (3.8–4.7)
*Selection (4d)****:				
PR	46.4	65.2a	69.3a	3.7 (3.1–4.4)
PRc F_5	41.2	41.1b	38.1b	10.5 (5.9–19.0)

*Pairs in columns followed by the same letter are not significantly different (P>0.05, Tukey's Studentized (HSD) Range test).
**Bait consumption divided by total food consumption (bait + dog chow).
***Parent stocks tested simultaneously with selected strains.

Table 3. Choice tests with Baygon bait (14 d)

Strain	Total Food mg	% Bait Eaten	% Mortality	LT_{50} (95% C.I.) days
Fbk (S)	251.4	10.5a	59.4a	11.8 (10.5–13.2)
N3 (S)	219.8	5.2b	51.9a	13.3 (12.0–14.8)
Jax	278.8	8.4ab	35.6b 22.3	(16.9–29.4)
LP	358.6	6.5b	3.1c	

Numbers in columns followed by the same letter are not significantly different (P>0.05).

The LP strain has only been selected for one generation. The results in the F_1 suggest a decrease in mortality (Table 4), but the parent strain was not re-tested. Percentage bait consumption was like the initial test on the parent stock (35.4 and 33.9%, respectively). With the PR strain, one selection had relatively little effect on mortality or percentage bait consumption. In the F_2, mortality and percentage bait consumption were lower than in the parent stock (Table 4). Physiological resistance was tested to determine whether the lower mortality was due entirely to a lesser attraction to the bait. Resistance in the selected strain was 1.4x that in the parent stock (no overlap of 95% C.I.s).

Stapleton's Magnetic Roach Food. Mortality in experiments with Stapleton's Magnetic Roach Food was usually complete within 5–6 days after cockroaches were removed from the bait. In initial tests on four strains, mortality ranged from 46 to 62%. The differences were not significant. Percentage bait consumption was not estimated because of weight loss in the controls. Subsequent work with more thoroughly dried bait suggested a slight repellency. Percentage bait consumption ranged from 35 to 43% in stocks tested in conjunction with selection experiments (Table 5, Fbk, PR, and Jax). Mortalities were generally similar to those of the initial experiments, ranging from 50.0 to 66.9%

Significant changes in mortalities and percentage bait consumption occurred in the F_3 of strains selected with Stapleton's Magnetic Roach bait. Selection of three strains for a fourth generation resulted in major differences in mortality and percentage bait consumption between the selected strains and the parent stocks (Table 5). Mortality of cockroaches in the parent stocks was more rapid than in the selected strains. For this reason, and because of the relatively long duration of the experiments, total food consumption was higher in the selected strains than in the parent stocks. The difference in percentage bait consumption between parent stocks and selected strains did not

Table 4. Choice tests with Raid Max*

Strain	Total Food mg	% Bait Eaten	% Mortality	LT_{50} (95% C.I.) days
Initial tests:				
Fbk (S)	31.9	75.2a	91.7a	2.4 (1.8–3.3)
N3 (S)	28.2	82.5a	88.3a	1.3 (0.8–2.2)
PR	27.0	64.2b	50.0b	7.1 (2.3–22.4)
LP**	327	33.9c	38.0c	29.2 (17.3–49.1)
Selections:				
LP F_1**	350	35.4	21.7	54.0 (16.5–176.8)
PR***	50.2	67.2a	62.5a	3.6 (1.8–5.0)
PR F_2	76.8	54.2b	44.1b	9.5 (2.7–33.5)

*Numbers in columns under "Initial tests" and under "Selection" followed by the same letter are not significantly different (P>0.05).
**14 instead of 5 d choice experiment.
***PR stock tested simultaneously with the selected strain.

Table 5. The results of four generations of selection with Stapleton's Magnetic Roach Food (14 d choice experiments)

Strain	Total Food mg	% Bait Eaten	% Mortality	LT_{50} (95% C.I.) days
Fbk	94.7	41.6a	66.9a	14.2 (13.7–14.8)
Fbk F_4	226	13.3b	16.3b	49.6 (29.3–84.2)
PR	113.2	43.3a	63.1a	15.0 (14.2–15.9)
PR F_4	234.b	12.0b	26.3b	30.6 (26.2–35.7)
Jax	145.9	34.5a	50.0a	19.6 (18.3–21.0)
Jax F_4	238.3	17.8b	25.1b	45.4 (26.9–75.6)

*F_4s tested simultaneously with the corresponding parent strain.
**Different letters indicate significant differences between each parent stock and the corresponding F_4 (P<0.05).

appear to be exaggerated by higher consumption of dog chow among survivors present during the latter parts of the experiments. In the Fbk F_4, bait consumption by cockroaches of the parent stock was 3.6x that of selected strain cockroaches at 6 d, compared with 3.1x at the end of the choice experiment (14d).

DISCUSSION

A toxic bait should not be used in a pest management program without a clear understanding of its characteristics. Of those studied here, only the abamectin baits might conceivably be useful for a "saturation" approach (Georghiou, 1994) to resistance management, in the sense that resistance would, at the most, be slow to develop. There were no indications of high level resistance, similar to physiological resistance in the Colorado potato beetle or house flies (Clark *et al.*, 1994). Rather, the results on non-selected strains were similar to those of Cochran (1990), who found basically no evidence of physiological resistance to abamectin.

With few exceptions (see below), the abamectin baits were attractive. Presumably this was due to ingredients of the bait bases. Although a saturation approach would be unlikely to foster the development of significant levels of resistance, the most attractive use of the baits would be in a rotational scheme. The primary purpose would not be to avoid development of resistance, as proposed for most rotational schemes, but rather because baits share a major limitation. Apparently they are not capable of eradicating established populations (Reierson, 1995), although abamectin baits can reduce populations (Appel and Benson, 1995).

The increase in avoidance behavior coupled with slower kill found in one strain selected for four generations with Roach Ender and another with the WIT gel indicated behavioral modifications. Further selection with Roach Ender might well result in a significant difference between mortalities in the selected strain and stock, especially since there was a tendency in this direction (mortality after cessation of lethal effects of the toxicant). Otherwise, a modification resulting only in slower kill probably has little practical importance. In the strain selected with the WIT gel, mortality was significantly lower than in the stock (Puerto Rico stock). However, these data were complicated by an apparent change in the stock itself during approximately 9–12 mo between initial tests and those conducted simultaneously with tests on the selected strains. It is doubtful that four, rather than three day tests with the selected strains can account for the higher mortality in the later tests. Selection appears to have merely maintained a trait present in the original stock. Whether the relatively low mortality (38%) would affect the efficacy of the bait in the field probably depends on conditions in the particular field situation.

Each of the other baits studied had at least one major problem. The one least likely to be effective was the Baygon bait. Repellency to all strains was undoubtedly the reason it took two weeks to kill approximately 50% of the susceptible populations. Furthermore, mortality was significantly decreased in strains with physiological resistance. **A very low level of physiological resistance had a major effect on the effectiveness of the bait.**

A high percentage bait consumption in choice tests with Raid Max indicates that the bait was highly attractive to chlorpyrifos-susceptible strains. Also, mortality of susceptible strain cockroaches was high. The bait should be effective on populations that are susceptible to chlorpyrifos and, in this case, useful in a rotational scheme. The increase in physiological resistance following two generations of selecting the Puerto Rico strain demonstrated that physiological resistance increased rapidly, in spite of the presence of an alternate food source. The speed with which resistance would develop if the bait was used in a rotational scheme would depend on characteristics of the target population.

With Raid Max, similarly to Baygon bait, a low level of physiological resistance was associated with a lower mortality than in susceptible strains. A lower preference for the bait also contributed to low mortalities in resistant strains. Apparently resistant strain cockroaches did not respond positively to an ingredient(s) of the bait base that made it highly attractive to susceptible strain cockroaches. At the higher levels of resistance (ca. <3.0x), cockroaches avoided the bait. Perhaps avoidance is an ancillary effect of one or more of the genetic factors that control chlorpyrifos resistance (Siegfried *et al.*, 1990). Linkage of an avoidance-controlling gene with a chlorpyrifos resistance gene is another possibility. An interesting question for future exploration is why resistant cockroaches avoided a chlorpyrifos bait but not vapors or residues of chlorpyrifos insecticides (Ross and Cochran, 1992).

LT_{50}s of 14–20 d in unselected strains indicated that kill with Stapleton's Magnetic Roach Food was slow. Kill was slower than with two other commercial boric acid baits (Appel 1990), but the latter experiments were done in Ebeling choice boxes. Strong *et al.*'s (1993) choice tests with dry and wet mixtures of boric acid with rat chow were more similar than choice box experiments to the present tests. Their results indicated a greater repellency than found here with Stapleton's Magnetic Roach Food. Enough of the Roach Food was eaten to kill $\geq$50% of the test populations (unselected), compared with no kill in Strong et al.'s (1993) experiments. Apparently, repellency of boric acid was at least partially overcome by a highly attractive bait base in Stapleton's Magnetic Roach Food.

Selection with Stapleton's Magnetic Roach Food resulted in the only occurrence of behavioral resistance equal to that which caused a loss of control due to the inclusion of glucose in a hydramethylnon bait (Silverman and Bieman, 1993, Silverman and Ross, 1994). Perhaps we are again dealing with a single, at least partially dominant gene, similar to *Glu* (Ross and Silverman, 1995). The relatively rapid development of behavioral resistance in all the selected strains suggests that Stapleton's Magnetic Roach Food should only be used for short periods, possibly in rotational schemes.

In conclusion, the most promising baits for long term control were the abamectin baits, Roach Ender and the WIT gel. The greatest inter-strain variation was between insecticide susceptible and physiologically resistant strains. Low levels of physiological resistance were associated with large decreases in mortality. A highly attractive bait base may overcome repellency of active ingredients in some instances, but it would be exceedingly difficult to overcome the effects of physiological resistance. The response to Raid Max was complex. Avoidance was associated with chlorpyrifos resistance. Prolonged use of Stapleton's Magnetic Roach Food will almost certainly result in a control failure. If behavioral resistance is due to an ingredient of the bait base, rather than the A.I., the problem may be corrected, as in the case of Maxforce (Ross, 1996).

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