Transfer of Ingested Insecticides Among Cockroaches: Effects of Active Ingredient, Bait Formulation, and Assay Procedures

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ABSTRACT Foraging cockroaches ingest insecticide baits, translocate them, and can cause mortality in untreated cockroaches that contact the foragers or ingest their excretions. Translocation of eight ingested baits by adult male *Blattella germanica* (L.) was examined in relation to the type of the active ingredient, formulation, and foraging area. Ingested boric acid, chlorpyrifos, fipronil, and hydramethylnon that were excreted by adults in small dishes killed 100% of first instars within 10 d and >50% of second instars within 14 d. Residues from these ingested baits were also highly effective on nymphs in larger arenas and killed 16–100% of the adults. However, when the baits and dead cockroaches were removed from the large arenas and replaced with new cockroaches, only residues of the slow-acting hydramethylnon killed most of the nymphs and adults, whereas residues of fast acting insecticides (chlorpyrifos and fipronil) killed fewer nymphs and adults. Excretions from cockroaches that ingested abamectin baits failed to cause significant mortality in cockroaches that contacted the residues. These results suggest that hydramethylnon is highly effective in these assays because cockroaches that feed on the bait have ample time to return to their shelter and defecate insecticide-laden feces. The relatively high concentration of hydramethylnon in the bait (2.15%) and its apparent stability in the digestive tract and feces probably contribute to the efficacy of hydramethylnon. To control for differences among baits in inert ingredients and the amount of active ingredient, we compared 1% chlorpyrifos with 1% hydramethylnon in identical baits. Again, hydramethylnon residues provided greater secondary kill, but the results highlighted the importance of the inert ingredients. We conclude that, in the absence of cannibalism and necrophagy, translocation of baits and secondary kill are most effective with slow acting insecticides in palatable baits that can traverse the digestive tract and be deposited within and around the cockroach aggregation.

KEY WORDS *Blattella germanica*, coprophagy, horizontal toxicant transfer, bait

THE DEPLOYMENT OF bait formulations to control infestations of the German cockroach, *Blattella germanica* (L.), is not a new concept, as reports of inorganic compounds, including phosphorus, boric acid, and sodium fluoride date back to the 1860s (Mallis 1969). The efficacy of these 'homemade' formulations, however, was highly variable because they were hand-mixed by pest control operators in small batches with a variety of common foods (Rust et al. 1995). Organophosphate- and carbamate-based bait formulations offered greater stability, safety, and much faster mortality than earlier baits, but insecticide resistance and repellency precluded their widespread adoption in cockroach control. The discovery of hydramethylnon in the early 1980s and subsequent improvements in the formulation, its delivery, and deployment have ushered in a new era of pest control technology offering greater efficacy, safety, reduced nontarget exposure to insecticides, long residual activity, low odor, and utility in "insecticide-sensitive" areas (Milio et al. 1986; Koehler and Patterson 1989; Appel and Abd-Elghafar 1990; Appel 1990, 1992; Cochran 1990; Ross 1993; Appel and Benson 1995; Koehler et al. 1996; Kaakeh et al. 1997).

Feeding, foraging, and reproductive behavior of *B. germanica* have also been extensively studied in efforts to improve the performance of baits (Rust et al. 1995). Baits ought to be effective at suppressing cockroach populations because all mobile life stages must feed before they molt and adult females must eat to reproduce (Kunkel 1966, Schal et al. 1997). However, certain stages of the German cockroach may transiently escape the effect of baits. For example, females carry oothecae for the vast majority of their adult life and feed little and only intermittently during this time (Cochran 1983, Hamilton and Schal 1988). Similarly, early instars appear to forage little and therefore are less likely to encounter baits (Cloarec and Rivault 1991, Kopanic and Schal 1999).

Active translocation of baits to the cockroach aggregation may figure prominently in the efficacy of baits. Foraging cockroaches can translocate the bait to other members of their aggregation, which in turn contact the bait or ingest insecticide-laden feces (coprophagy), other excretions, or dead and dying insects (necrophagy and cannibalism). Coprophagy by first instars appears to be an important mechanism underlying the horizontal transmission of hydramethylnon,

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Table 1. Baits and active ingredients used in translocation studies and their toxicity to adult male *B. germanica*

Bait	Formulation	% (AI)	Manufacturer	Slope ± SEM	LT_{50} (95% FL)
Avert PT310	Powder	0.05 abamectin	Whitmire Micro-Gen, St. Louis, MO	9.4 ± 0.9	18.7 (17.9–19.5)
Avert Formula3	Gel	0.05 abamectin	Whitmire Micro-Gen, St. Louis, MO	12.4 ± 1.4	13.8 (13.2–14.4)
Maxforce bait station	Block	2.00 hydramethylnon	Clorox, Oakland, CA	15.3 ± 1.6	44.4 (43.4–45.5)
Maxforce gel	Gel	2.15 hydramethylnon	Clorox, Oakland, CA	19.0 ± 1.6	41.4 (40.7–42.1)
Maxforce FC bait station	Block	0.05 fipronil	Clorox, Oakland, CA	14.0 ± 1.1	3.6 (3.5–3.7)
Maxforce FC gel	Gel	0.01 fipronil	Clorox, Oakland, CA	11.2 ± 0.8	3.4 (3.3–3.5)
MRF 2000	Paste	33.33 boric acid	Blue Diamond Exterminating, Rogersville, TN	10.1 ± 0.6	45.8 (44.8–46.8)
Raid Max Roach bait	Block	0.528 chlorpyrifos	S. C. Johnson & Son, Racine, WI	5.8 ± 0.4	5.5 (5.3–5.7)

All baits, except Raid Max were purchased from a pesticide distributor in Raleigh, NC. Raid Max was purchased at a local grocery market. Data were analyzed by probit analysis (SAS Institute, 1997). LT_{50} values reported in h. None of the control males died.

a slow-acting insecticide (Silverman et al. 1991, Kopanic and Schal 1997, 1999). The aim of our research was to determine which bait formulations retained insecticide activity in excretions, including feces, and to ascertain what factors contribute to differences among the baits. Our results demonstrate that translocated hydramethylnon residues cause the highest mortality in nymphs and adults. We further show that properties of the formulation, speed of the active ingredient, and proximity of the bait to the shelter can affect the horizontal transmission of the bait and therefore its overall performance.

Materials and Methods

Insects. Cockroaches were an insecticide-susceptible strain that originated from an American Cyanamid (Princeton, NJ) stock. Insects were reared at 27 ± 1°C, ambient relative humidity, and a photoperiod of 12:12 (L:D) h, and provided with water and Purina Rat Chow #5012 (Purina Mills, St. Louis, MO) ad libitum. In all experiments, first and second instars were used within 12 h of ecdysis, before their peak feeding period (Valles et al. 1996, Young and Schal 1997).

Insecticide Baits. Eight different baits (Table 1) were examined in various experiments and their oral toxicity was characterized in dish bioassays. Fourteen-day-old adult males were starved for one scotophase (12 h) in dishes 150 mm diameter by 25 mm high while provided with water. The next day, the males were provided a bait that, after 24 h, was replaced with rat chow for the duration of observations. Two replications of 25 males were performed with each bait.

Technical grade chlorpyrifos (99% [AI], SC. Johnson & Son, Racine, WI) and hydramethylnon (98% [AI], Clorox, Oakland, CA) were dissolved in acetone and thoroughly mixed with rat chow or inert Maxforce gel (gift from Clorox) to make 1% (AI) (wt:wt) baits. The acetone was evaporated for 24 h in a fume hood before the baits were used. Rat chow and inert Maxforce gel, similarly treated with acetone, were fed to control insects.

Small Foraging Arena. To determine which baits retained their toxicity to first and second instars after being ingested and excreted by adults, we exposed nymphs to excreted residues. Ten adult males, 14 d old, were starved for one scotophase, but provided with water, as above, then fed a bait for 2 h and immediately transferred without anesthesia to clean 150 mm diameter by 25 mm high polystyrene dishes. Dead males were removed daily and after all males died 20 first or second instars were added to each dish containing the adult residues, a rat chow pellet, and water. Mortality was recorded and dead insects were removed daily from the dish for 2 wk. Because dead adults were excluded from these bioassays and all nymphs were accounted for, these experiments do not consider the role of cannibalism in secondary kill.

Large Foraging Arena. Lucite sections were assembled into rectangular cages (117 by 15 by 15 cm high). The inner lower 10 cm of each wall was coated with petroleum jelly to prevent cockroaches from escaping. The floor of each cage was lined with absorbent disposable paper (Labmat, Bel-Art Products, Pequannock, NJ). A section of cardboard egg carton served as a shelter at one end of the cage, between two water vials. To ensure that introduced cockroaches would remain in this shelter rather than aggregating elsewhere in the cage, the egg carton was placed in a cockroach colony for 7 d, a procedure that results in the deposition of aggregation pheromone on the egg carton (Ishii 1970). Fecal particles were removed from the shelter before it was used in assays.

To prevent nymphs from gaining access to the bait we used a "moat-bait," as described by Kopanic and Schal (1997). A small cup, which contained the bait was fastened in the center of a larger cup, and the space between the two cups was filled with mineral oil to create a moat; adult insects easily traversed the moat to feed on the bait, but first and second instars were physically excluded from the bait. This bait was placed at a corner diagonally across from the shelter (>117 cm), 15 cm away from a 1.5 cm cup containing finely ground rat chow in the adjacent corner. Each assay consisted of two parts. The first was designed to determine the magnitude of horizontal transfer of each bait shortly after adults ingested the bait. A cockroach population consisting of 20 adult females, 20 adult males, 30 first instars, and 30 second instars, all 1 d after ecdysis, was monitored for 5 d, mortality was recorded and dead insects were removed twice daily. This assay was followed by a second assay that examined the effect of fecal and other residues on a new population of cockroaches in the same cage. On day 6

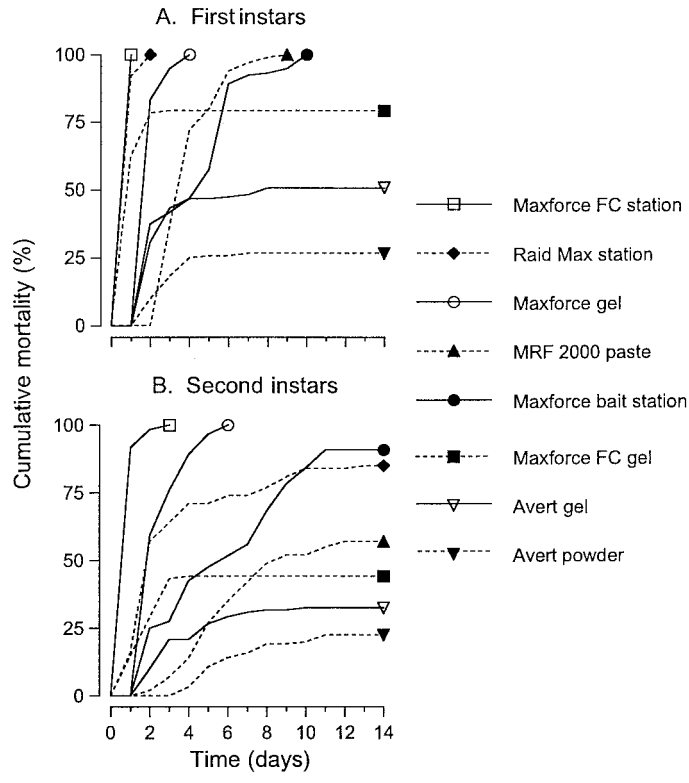

Fig. 1. Mean cumulative daily secondary mortality of first and second instar *B. germanica* ($n = 6$; 20 insects of each stage) exposed in 150 by 25 mm round dishes to the residues of various baits deposited by adult males.

of the experiment the bait and any remaining live insects from the first assay were removed from the cage. A new population of cockroaches, consisting of the same number and age as before, was again monitored for 5 d, with mortality checked and dead insects removed twice daily.

The large cages were also used to determine the distribution of dead males and their feces in fipronil- and hydramethylnon-fed cockroaches. Thirty adult males were placed in a large cage and allowed to acclimate for 2 d. On day 3, the floor of the cage was swept of all fecal residues and a bait and ground rat chow (≈1 g each) were positioned at the two corners opposite from the shelter. The males had unrestricted access to the bait and rat chow. We recorded the distribution of dead cockroaches and feces (by mass) in each of five sections of the cage.

Statistical Analysis. Preliminary analysis (PROC CATMOD, SAS Institute 1997) revealed differential survivorship of the four groups (males, females, first, and second instars) of *B. germanica* on the eight baits. Contingency table analysis (PROC FREQ, SAS Institute 1997) was then performed to detect differences in the survivorship rates on the eight baits. When significant chi-square values were obtained ($P < 0.05$), posthoc Z-tests (Marascuilo and McSweeney 1977) were performed on the proportions of dead cockroaches to identify treatments that differed significantly. Two samples were compared using the Mann-Whitney U test (StatView 1998). The distributions of dead males and their feces were compared in fipronil- and hydramethylnon-fed cockroaches using Student's t-test (SAS Institute 1997). All statistical analyses were conducted at the $\alpha = 0.05$ level of significance and data are presented as means ± SEM.

Results and Discussion

Comparison of Baits. In all assays in small dishes (177 cm^2) all the adult males died, regardless of which bait they ingested; LT_{50} values are reported in Table 1. However, residues that dying males excreted caused varying levels of secondary mortality (Fig. 1), suggesting that secondary kill was related to a complex interaction among the mode and speed of action of the insecticide, its metabolism in the alimentary canal, and the quality and palatability of the bait formulation. All first instars died within 10 d of exposure to residues from five baits, and their rate of death was affected largely by the speed of action of the insecticide (Maxforce FC bait station > Raid Max station > Maxforce gel > MRF 2000 paste > Maxforce bait station) (Fig. 1A). Residues from adults that ingested Avert powder and gel (with abamectin, a relatively slow-acting active ingredient; Table 1), however, failed to kill >38% of the first instars during the 14 d assay. A similar pattern emerged with second instars, but only residues of Maxforce FC bait station (with fast acting fipronil;

Table 2. Mean ± SEM cumulative percentage mortality of adults and nymphs of *B. germanica* in sequential assays in large cages

Bait	Initial 5 d (first population)[a]				Next 5 d (second population)[b]			
	Adult males	Adult females	First instars	Second instars	Adult males	Adult females	First instars	Second instars
Maxforce gel	100 ± 0.0a	100 ± 0.0a	100 ± 0.0a	100 ± 0.0a	66 ± 17.3a	41 ± 18.5a	97 ± 3.3a	95 ± 5.3a
Maxforce station	88 ± 10.8ab	94 ± 6.0a	100 ± 0.0a	97 ± 2.7a	6 ± 2.9bc	5 ± 0.0bc	81 ± 6.9ab	56 ± 3.4b
Maxforce FC gel	100 ± 0.0a	100 ± 0.0a	100 ± 0.0a	100 ± 0.0a	1 ± 1.0c	1 ± 1.0c	79 ± 3.9b	45 ± 4.4b
Maxforce FC station	100 ± 0.0a	100 ± 0.0a	100 ± 0.0a	100 ± 0.0a	15 ± 3.2b	17 ± 2.6b	81 ± 3.9ab	50 ± 3.0b
Avert Formula3	100 ± 0.0a	100 ± 0.0a	36 ± 6.2c	19 ± 1.3c	0 ± 0.0c	0 ± 0.0c	15 ± 1.7c	7 ± 1.9c
Avert PT 310	16 ± 7.0c	35 ± 13.9b	26 ± 10.1c	22 ± 9.0c	1 ± 1.0c	1 ± 1.0c	13 ± 5.5c	5 ± 2.3c
MRF 2000	16 ± 8.9c	7 ± 4.6c	87 ± 3.9b	62 ± 11.0b	2 ± 1.2bc	1 ± 1.0c	21 ± 7.1c	11 ± 5.4c
Raid Max	69 ± 5.3b	94 ± 2.9a	96 ± 1.9ab	95 ± 3.3a	3 ± 2.0bc	0 ± 0c	11 ± 8.1c	4 ± 1.3c

Means with different letters within each column are significantly different based on a Z-test ($\alpha = 0.05$, $n = 5$).
[a] During the first 5 d, adults ingested baits from which nymphs were physically excluded. Rat chow was available in all cages.
[b] On day 6 of the assay the baits were removed and new adults and nymphs were added and monitored for 5 d.

Table 1) and Maxforce gel (with slow acting hydramethylnon; Table 1) killed 100% of the second instars, whereas secondary mortality was lower and delayed with all other baits (Fig. 1B).

Effective translocation of hydramethylnon was not surprising because secondary kill had been amply demonstrated to occur through coprophagy and not through contact with contaminated feces (Silverman et al. 1991; Kopanic and Schal 1997, 1999). Yet, in the dish assays, residues of fipronil and chlorpyrifos, both fast-acting contact neurotoxins (Table 1), resulted in the fastest secondary mortality of first instars (Fig. 1A), and relatively rapid death of second instars (Fig. 1B). These insecticides could be transferred by either coprophagy or by contact with dying cockroaches or their excretions. Because nymphs were constrained on the insecticide residues in the small dishes, we repeated these assays under experimental conditions that allow nymphs to avoid the residues.

In large cages (1,755 cm^2), only adult cockroaches could ingest baits that were positioned 117 cm from the shelter, whereas nymphs were physically excluded from the baits (see Kopanic and Schal 1997). The results generally confirmed those from the small dish assays, although mortality was much lower. Both hydramethylnon baits were highly effective during the first 5 d of the assay, and the hydramethylnon-laden feces retained its toxicity to new nymphs that were introduced on day 6 (Table 2). Notably, however, few adults (<6%) that contacted Maxforce station residues died, compared with >41% mortality of adults exposed to residues from Maxforce gel.

Abamectin gel, also slow-acting (Table 1), caused 100% mortality in adults that ingested the bait while abamectin powder, which contained the same amount of the active ingredients as the gel, surprisingly killed <35% of the adults that could freely ingest it. This suggests that adults preferentially fed on the rat chow and were either repelled or deterred from eating the powder. In repellency assays, a powder formulation of Avert was slightly more repellent to the German cockroach than a gel formulation (Appel and Benson 1995). Despite the fact that Avert gel killed significantly more adults during the first 5 d of the experiment (Mann-Whitney *U* test; $Z = 3.780$; $n = 10$; $P < 0.001$), it did not effect higher secondary mortality in the nymphs. As in the small dish assays, both abamectin baits killed <1% of the adults and <15% of nymphs that were exposed only to abamectin residues deposited by the adults (Table 2). It is not known whether abamectin is metabolized in the digestive tract, not excreted, or excreted but avoided by nymphs. A similar pattern was evident with MRF 2000, a slow-acting boric acid bait. Few adults died, probably because they ingested sublethal dosages or fed on rat chow. Yet, more nymphs that could not directly ingest the bait were killed, ostensibly from ingesting adult feces that contained boric acid.

The fast-acting insecticides, chlorpyrifos and fipronil, were highly effective during the first 5 d of the experiment, but their efficacy dramatically declined on the second population of cockroaches placed into the same arena after the bait and dead cockroaches were removed (Table 2). Residues of chlorpyrifos (Raid Max) were particularly ineffective, killing <11% of nymphs and <3% of adults.

Effect of the Formulation. In both small and large cages, gel formulations resulted in greater secondary mortality than the drier powder or bait block formulations. This trend was especially apparent in a comparison of Maxforce gel and bait station, both of which contained approximately the same amount of hydramethylnon (Table 1) and differed only in the inert formulation. Fecal residues from the gel killed 100% of first instars by day 4 in small dishes, while mortality due to the drier bait was significantly lower, only 47% (Mann-Whitney *U* test; $Z = 2.882$, $n = 6$, $P = 0.004$), and 100% mortality in the latter was not achieved until day 10 (Fig. 1A). The gel killed 100% of second instars by day 6, while mortality due to Maxforce station was only 91% after 14 d (Fig. 1B). Likewise, in the large cages, even as nymphs were prevented from directly contacting the gel, it killed all adults and nymphs within 5 d (Table 2). The excreted gel remained toxic after the dead insects and bait were removed and a new population of adults and nymphs was introduced, causing moderate mortality in the adults (<66%) and high mortality in first (97%) and second (95%) instars. Although the drier Maxforce station was equally effective on the foraging adults, and translocated hydramethylnon killed nearly all the nymphs in the first 5 d of the assay, it killed significantly fewer adults

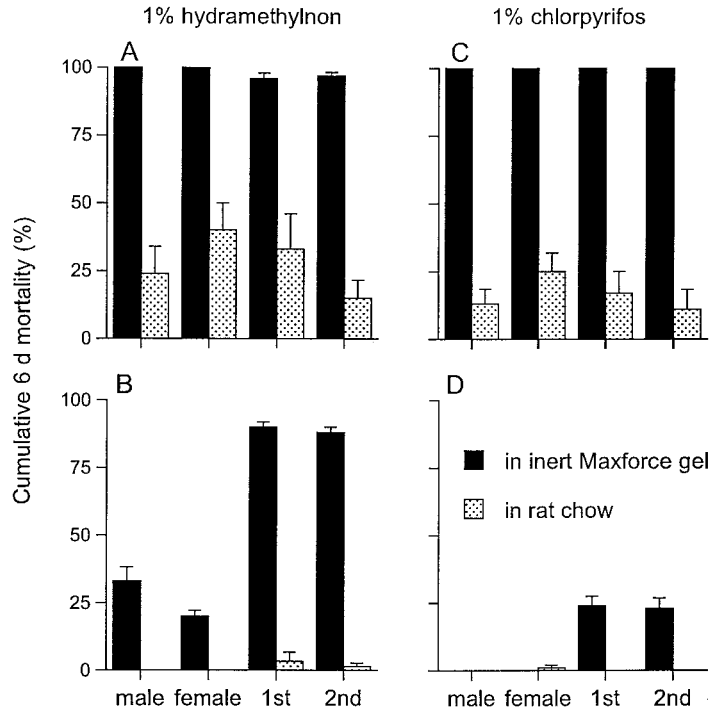

Fig. 2. Mean (± SEM) cumulative 6 d mortality of cockroaches fed 1% hydramethylnon (A) or 1% chlorpyrifos (C) in inert Maxforce gel or in rat chow. In (B) and (D) the baits and dead insects were removed and a second population of nymphs and adults was added to each cage.

(<6%; Mann-Whitney *U* test; $Z = 2.381$, $n = 10$, $P = 0.01$) and nymphs (<81%; $Z = 3.024$, $n = 10$, $P = 0.002$) when new cockroaches were exposed to the residues (Table 2).

Avert powder and Avert gel (both 0.05% abamectin) caused low secondary mortality in nymphs in small dishes (<38%) (Fig. 1) and larger cages (<15%) (Table 2). Yet, residues from Avert gel resulted in slightly but not significantly higher secondary kill (Mann-Whitney *U* test; $Z = 0.038$; $n = 10$; $P > 0.05$). The data for hydramethylnon and abamectin demonstrate that more residues are scattered in cockroach aggregations when foraging cockroaches ingest a gel bait than a drier powder or solid bait formulation. Because moist baits are generally preferred by cockroaches over dry baits (Appel and Benson 1995), more of the active ingredient from gels would be excreted. A different pattern emerged in a comparison of Maxforce FC bait station (0.05% fipronil) and Maxforce FC gel (0.01% fipronil). Translocated residues from the solid bait killed 100% of first and second instars by day 2 of the small dish assay, whereas mortality due to the gel did not exceed 80% after 14 d (Fig. 1). In large cages both baits were equally effective in the first part of the assay, killing all adults and nymphs by day 3 of the assay (Table 2). In the second part of the assay, too, secondary mortality of nymphs was not significantly different for the two baits (Mann-Whitney *U* test; $Z = 0.454$, $n = 10$, $P = 0.65$). Surprisingly, however, the solid bait killed more adults in the second part of the assay (Mann-Whitney *U* test; $Z = 3.780$, $n = 10$, $P = 0.002$), suggesting that it was more effectively translocated than the gel bait. Such a conclusion is confounded, however, because fipronil is active at very low amounts ($LD_{50} = 2.4$ ng per adult male; Buczkowski and Schal 2001a), and the solid bait contained five-fold more fipronil than the gel.

To further demonstrate that both the formulation and type of active ingredient affected secondary kill we designed an experiment in which two different active ingredients (hydramethylnon and chlorpyrifos) were incorporated at equal concentrations into two different bait formulations (inert Maxforce gel and ground rat chow). The gel formulations of both active ingredients killed 100% of the adults that ingested them and >96% of the nymphs, which had no direct access to the baits (Fig. 2 A and C). However, either active ingredient admixed in ground rat chow failed to kill >32% of adults (Mann-Whitney *U* test; $Z = 3.780$, $n = 10$, $P < 0.001$) and >24% of the nymphs ($Z = 3.78$, $n = 10$, $P < 0.001$) within 5 d. Although mortality was lower in a new cockroach population exposed to the same residues, a similar pattern emerged, with the gel significantly outperforming the rat chow bait. The two experiments were closely coupled and secondary mortality due to fecal and other residues (Fig. 2 B and D) clearly depended on the amount of insecticide deposited in the cage by foraging adults (Fig. 2 A and C). Thus, substantially lower mortality with the rat chow formulation can be attrib-

uted to its lower intake by adults and lower active ingredient in the feces. Less of the dry bait is ingested, probably because it is less attractive or palatable. It might also be retained longer within the alimentary tract, resulting in diminished excretion, particularly with the fast-acting insecticides.

A comparison of the commercial formulation of chlorpyrifos (0.528% [AI]) to ours (1.0% [AI]) further confirmed the role of the inert ingredients. Although the concentration of chlorpyrifos in Raid Max was only half its concentration in rat chow, Raid Max killed significantly more adults and nymphs (Mann-Whitney U test; $Z = 3.780$, $n = 10$ each, $P < 0.001$).

These data demonstrate that the bait formulation is responsible, in large part, for the level of secondary kill. Cockroaches generally prefer gel baits over dry baits (Appel and Benson 1995), and Maxforce gel was more toxic to the German cockroach than dryer paste formulations (Appel 1992). Cockroaches that ate gel baits also tended to defecate sooner and produced more feces than those ingesting the drier baits (G.B., unpublished data). We therefore conclude that, all else being equivalent, gel formulations are better suited to effect secondary kill because they are efficiently ingested and excreted by foragers, and remain attractive to nymphs.

Mechanisms of Secondary Kill: Fast- Versus Slow-Acting Insecticides. In equivalent gel formulations, with equal amounts of active ingredient, hydramethylnon residues killed more cockroaches than chlorpyrifos residues (adults: 27 ± 3.4% versus 0 ± 0%; nymphs: 89 ± 1.3% versus 24 ± 2.2%) (Fig. 2 B and D). The implication from this and a comparison of the small and large cage assays is that contact insecticides can exert high, but transient secondary kill when nymphs encounter dying insects or their excretions. Slow-acting insecticides, however, result in greater accumulation of translocated residues and therefore greater long-term secondary kill. Central to this comparison is the encounter rate between nymphs and translocated residues. Chadwick (1985) showed that the most important factor affecting residual insecticide performance is the length of time a cockroach contacts the treated substrate. In addition, location of insecticidal deposits within an arena significantly affects mortality in the exposed population (Le Patourel 1998). We therefore hypothesized that in the large arenas the distribution of dead insects and their feces would affect secondary kill.

Maxforce FC gel (fipronil) and Maxforce gel (hydramethylnon) resulted in dramatically different patterns. Only 27.5% of the males that ingested fipronil bait died within the shelter, compared with 84.2% of those that ingested hydramethylnon bait (Fig. 3A). The average distance between hydramethylnon-killed males and the shelter was 4.1 cm, while males that ingested fipronil died 53.7 cm from the shelter, significantly farther (Student's t-test, $t = 11.95$, $n = 120$, $P < 0.001$) (Fig. 3B). The hydramethylnon-killed males also defecated significantly more (Student's t-test, $t = 8.58$, $n = 4$, $P < 0.001$) (Fig. 3D), and their feces were concentrated within and near the shelter,

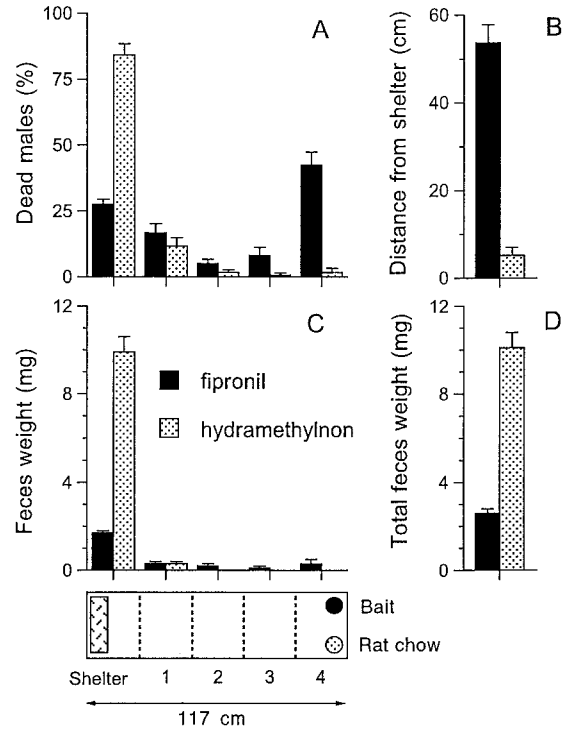

Fig. 3. Distribution of dead males (A, B) and the amount (D) and distribution (C) of their feces within a 117 by 15 cm cage. Four replicates of 30 males each.

whereas the small amount of feces produced after ingesting fipronil was more uniformly distributed throughout the cage (Fig. 3C).

These data suggest that baits containing slow-acting hydramethylnon, which impairs oxidative phosphorylation, might benefit from several advantages. First, hydramethylnon appears to remain palatable to cockroaches even at relatively high concentrations (2.15% [AI]). Second, its delayed toxicity might allow foragers to make multiple visits to the bait during the scotophase and therefore increase its translocation to the shelter. Third, it might promote secondary kill because feces is deposited and insects die within and near the shelter. Feces distribution is a good indicator of cockroach aggregation and distribution patterns in harborages (Stejskal 1997). Small nymphs and gravid females tend to remain close to the shelter (Sommer 1975, Cloarec and Rivault 1991, DeMark et al. 1993, Kopanic and Schal 1999), and they are the most difficult to reach with insecticides (Bret and Ross 1985), yet they comprise a large fraction of the population (Sherron et al. 1982, Ross et al. 1984, Schal 1988). Hydramethylnon, therefore, would be expected to efficiently facilitate secondary kill.

Conversely, fast-acting insecticides appear to exert high, but transient secondary mortality, probably from contact with fresh insecticide residues. They were less effective at causing secondary mortality in large cages, probably because of a less intimate association of dying adults with nymphs. Fipronil, for example, over-

stimulates the insects' nerves and muscles, resulting in hyperactivity and erratic movements (Colliot et al. 1992, Cole et al. 1993, Moffat 1993); cockroaches are paralyzed within 3–5 h (Table 1). This might prevent adults from returning to their shelters by affecting their locomotor, and possibly sensory, functions. Neuroactive insecticides cause extensive involuntary movements, which also tend to move the intoxicated insects away from the aggregation. Dying cockroaches defecate less before they succumb to the insecticide and the small quantity of feces they produce is more evenly distributed outside the shelter. The quick onset of the paralytic symptoms associated with neuroactive active ingredients might also interfere with passage of the bait through the alimentary canal, and indeed, cockroaches fed radiolabeled fipronil produced small amounts of feces which contained little fipronil (Buczkowski and Schal 2001b). As a consequence, the relatively high secondary kill in nymphs with fipronil (Table 2) is unlikely to occur through coprophagy. Lastly, some fast-acting insecticides (e.g., chlorpiryfos) are more repellent (Ebeling et al. 1966, Appel 1990, Rauscher et al. 1985), suggesting that nymphs might avoid contact with such residues.

Nevertheless, nonrepellent neurotoxins which are deployed at low concentrations (e.g., fipronil) might exert relatively high secondary kill in a proper bait formulation. Maxforce FC, a solid bait containing fipronil, provided identical secondary kill to Maxforce station, containing hydramethylnon. Our recent results indicate that ingested fipronil stimulates cockroaches to regurgitate. These oral secretions, containing fipronil, are highly attractive and are imbibed by first instars (Buczkowski and Schal 2001b). However, as these excretions age, their effectiveness diminishes (Buczkowski and Schal 2001a). Therefore, if intoxicated cockroaches die near the shelter, their fipronil-laden excretions can affect the local cockroach population. If, however, cockroaches succumb far away from the shelter, as shown in the large cages, they are much less likely to transmit fipronil to other cockroaches.

Because cockroaches die soon after ingesting fipronil, large amounts of active ingredient are retained within the dead insects. If cannibalism contributes significantly to secondary kill, as suggested by Gahlhoff et al. (1999), then fast-acting active ingredients, such as fipronil, might benefit by remaining concentrated within the cockroach rather than dispersed in its feces. It remains to be determined what role, if any, secondary kill plays in field populations of cockroaches.

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