Relative Significance of Direct Ingestion and Adult-Mediated Translocation of Bait to German Cockroach (Dictyoptera: Blattellidae) Nymphs

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ABSTRACT A novel experimental design that selectively excluded feeding of adults or nymphs on insecticidal baits was used to distinguish mortality caused by ingestion of bait from mortality caused by horizontal transfer of insecticide by foraging to nonforaging cockroaches. In large cage laboratory assays and in apartments, exposure of *Blattella germanica* (L.) to an insecticidal bait containing hydramethylnon resulted in high mortality in adult females and 1st instars. However, exclusion of adult females from feeding on the bait resulted in a significant decline in mortality among nymphs, suggesting that neonate mortality was caused primarily by adult-mediated horizontal toxicant transfer through feces. A reciprocal experiment provided support for this hypothesis: Adult females with access to bait transferred insecticide to neonates that were prevented from feeding on bait, resulting in high mortality in both groups. Conversely, mortality among 2nd instars was high and significantly less dependent on adult foraging, suggesting a shift to active foraging (i.e., direct ingestion of bait) during the 2nd stadium. We conclude that horizontal toxicant transfer is a key factor in suppression of cockroach pest populations. Small nymphs, especially 1st instars, which forage infrequently and are therefore least vulnerable to direct contact with insecticides, are most susceptible to this type of insecticide translocation. Horizontal toxicant transfer should be optimized to deliver insecticides and pathogens to nonforaging stages of *B. germanica*.

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

DESPITE INTENSIVE EFFORTS to eliminate the German cockroach, *Blattella germanica* (L.), from human dwellings, it remains the most prevalent and important indoor cockroach pest in the United States (Rust et al. 1996). Infestations may occur wherever human activity is concentrated, especially where food, water, and optimum environmental conditions are present. Although numerous tactics and technologies are available to effect suppression of indoor cockroach populations, heavy reliance on scheduled application of insecticides, especially as residual dust and spray formulations, still exists. However, heightened concern among consumers, pest control professionals, and regulatory authorities about indoor insecticide use patterns has recently prompted research on and implementation of reduced-risk strategies for cockroach control.

Bait formulations are generally integrated into programs designed to reduce insecticide use. Because baits are placed strategically only where cockroaches are likely to reside, less active ingredient can be used than with dust or spray applications. Moreover, a physiological requirement that each instar feed before molting to the next stage and an intimate association between food intake and reproduction in the German cockroach (Kunkel 1966; Schal et al. 1993, 1997) implies that baits should provide efficacious pest management, especially where food resources are limited. Yet, features of the ecology and reproductive physiology of the German cockroach appear to constrain bait deployment. For example, females spend most of their adult life in a gravid state during which they feed little and only intermittently (Cochran 1983, Hamilton and Schal 1988); therefore, baits might be less effective at targeting such females (Schal et al. 1997).

It has been suggested that during the 1st and 2nd instar, *B. germanica* nymphs are less efficient foragers than older nymphs and adults (Sommer 1975, Cloarec and Rivault 1991, DeMark et al. 1993). This too might reduce the efficacy of insecticidal baits, especially because early instars comprise a large fraction of cockroach populations. Therefore, young nymphs and reproductive females should be prime targets for pest control. Because certain life stages of the German cockroach exhibit limited foraging ranges, careful attention must be given to ensure that baits are placed near cockroach aggregations (Silverman 1986). Another approach is to employ foraging individuals to deliver insecticide or pathogens to nonforaging members of a population. Generally, this strategy would function best in gregarious or social insects and would require slow-

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acting insecticides so that foraging insects could return to their shelter before becoming imobilized by the insecticide.

Silverman et al. (1991) proposed that German cockroaches redistribute ingested insecticides within aggregations and concluded from laboratory translocation assays that coprophagy plays a major role in this process. Although this mechanism has been demonstrated in small arena laboratory assays (Silverman et al. 1991), it remains unknown whether various life stages are equally susceptible to this approach and what role, if any, coprophagy serves in suppressing field populations of cockroaches. The aim of our study was to compare susceptibility of 1st- and 2nd-instar German cockroaches to toxic residues delivered to shelters by foraging adults. Using assays that excluded nymphs or adults from feeding on toxic baits, we have quantified the relative contributions of direct (ingestion of bait) and indirect (ingestion of insecticide-laden feces) routes of insecticide entry in laboratory and field populations. We conclude that high mortality of 1st instars can be attributed almost entirely to insecticides delivered to shelters by foraging adults. By contrast, 2nd instars forage actively and are as likely to ingest bait as they are to ingest insecticide-laden feces.

Materials and Methods

Insects. Cockroaches were obtained from an insecticide-susceptible laboratory strain that originated from an American Cyanamid (Princeton, NJ) stock. Insects were reared at 27°C, variable ambient 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. Adult females were used to vector insecticide to nymphs because such females feed and defecate more than most other stages. Insects were selected early in each developmental stage to capture the peak feeding period of adult females (days 0–4; Cochran 1983, Hamilton and Schal 1988) and nymphs (days 1–3; Valles et al. 1996). For all assays, females were collected from synchronous cultures within 24 h of eclosion, and 1st and 2nd instars were collected within 24 h of hatch or ecdysis, respectively.

Insecticide Bait. We used MAXFORCE Roach Killer bait gel (Clorox, Pleasanton, CA) purchased from a local pesticide distributor. MAXFORCE contains 2.15% hydramethylnon, an amidinohydrazone insecticide known to have delayed toxicant activity (Silverman et al. 1991).

Insect Exclusion Assays. To compare the relative importance of direct (through bait ingestion) and indirect (through coprophagy) uptake of hydramethylnon in nymphs, we monitored mortality in laboratory and seeded field populations (see below) of known composition. By excluding either adult females or nymphs from the bait, we were able to uncouple direct from indirect effects of toxic baits. Exclusion was effected by securing a

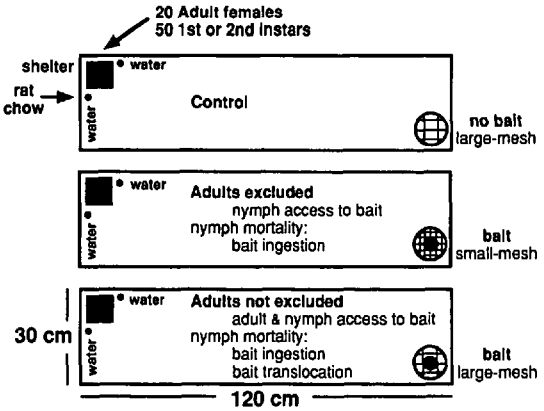

Fig. 1. Large-cage exclusion assay showing placement of shelter, water, food, and bait.

stainless steel screen to the opening of a petri dish bait "station" (60 by 15 mm) containing 250 mg of bait (Fig. 1). Screens were of 2 mesh sizes. A large-mesh screen (6 mm) served as a control; it did not exclude any insects from feeding on the bait. Thus, results observed in this treatment represented the combined effects of direct and indirect routes of bait entry into nymphs. A small-mesh screen (2 mm) excluded adults but allowed nymphs access to the bait. Any mortality of nymphs in this treatment would represent primary mortality as a result of ingestion of bait. Untreated control cages were run simultaneously with other treatments. They included an identical design, but no bait was used. Our design defined secondary mortality in nymphs as the difference between mortality in nymphs when adults fed on bait and when adults were excluded from the bait. Therefore, the assay afforded only an indirect measure of the importance of coprophagy.

To obtain a direct measure of mortality caused by horizontal transfer of bait from adults to nymphs, a 2nd exclusion design was tested. This design excluded nymphs rather than adults from the bait. Plastic scintillation vials (10 and 20 ml) were cut with a razor to make cups 1.5 cm in height. The smaller-diameter cup, which contained the bait, was centered and fastened with plasticine to the bottom of the larger cup. The space between the 2 cups was filled with mineral oil to create a moat; adult females easily traversed the moat to gain access to the bait, but 1st instars were excluded from the bait. The smaller cup could be fitted with a screen to further exclude adults as well.

Large Cage Assays: Indirect Measures of Horizontal Transfer. Plexiglas sections were assembled into rectangular cages (120 by 30 by 15 cm high). The inside lower 10 cm of each wall was coated with a thin layer of petroleum jelly to prevent cockroaches from escaping. The floor of each cage was composed of the absorbent side of disposable

Labmat (Scienceware, Bel-Art Products, Pequannock, NJ). A section of cardboard egg carton was placed in one corner of each cage and served as a shelter. To ensure that introduced cockroaches would remain in this shelter rather than aggregating elsewhere in the cage, we preconditioned the egg carton for 7 d in a cockroach colony; this procedure results in the deposition of aggregation pheromone on the egg carton (Ishii 1970). Fecal particles were removed before the shelter was used in assays. Two stainless steel planchetes packed with finely ground rat chow were placed 2 cm from the shelter, 1 near each wall. A cotton-stoppered water vial was placed next to each planchete. Insecticide bait was placed in the diagonal corner of the cage opposite the shelter, a linear distance of 124 cm from the shelter. Placement of food and water near and on either side of the shelter and positioning of the bait as far as possible from the shelter were meant to minimize long forays by cockroaches, and thus maximize our ability to detect secondary mortality caused by horizontal toxicant transfer.

Each assay cage contained 20 adult females and 50 first or second instars. During midphotophase, cockroaches were placed for 2 h in a small staging cage that contained the preconditioned (aggregation pheromone-laden) shelter. Shelters with clinging insects were then gently moved into the large assay cages. After 48 h, baits were removed and adult and nymphal mortality were recorded 24 h later. All experiments were conducted under controlled environmental conditions identical to the rearing regime. A treatment block consisted of 3 laboratory assays that included a bait covered with large-mesh screen (no exclusion—results in primary and secondary mortality of nymphs), a bait covered with small-mesh screen (adults excluded—results in primary mortality of nymphs), and a control covered with large-mesh screen without any bait. This block was replicated 3 times.

Large Cage Assays: Direct Measures of Horizontal Transfer. Using the moat-screen combinations, each treatment block consisted of the following 3 designs: (1) no mineral oil and small-mesh screen over the bait (all nymphal mortality caused by ingestion of bait—primary mortality); (2) mineral oil in moat and no screen over the bait (all nymphal mortality due to horizontal transfer of bait—secondary mortality); and (3) mineral oil in moat and small-mesh screen over the bait (an untreated control, which would be expected to result in no mortality of either adults or nymphs). All other procedures of this design were identical to those described in the previous section.

Field Exclusion Assays. Bait-exclusion assays also were conducted in vacant public-housing apartments (Raleigh Housing Authority, Raleigh, NC) that were devoid of *B. germanica* because the apartments were unheated and without water during the previous winter. Only bedrooms 2.4 by 3.6 m were used in this study. Before use, the floor of each room was cleared of debris and mopped with a mild detergent. The general design and procedures used for large cage assays were applied in the field study. An egg carton shelter was placed in one corner of a room. As with large cages, rat chow and water were placed 2 cm in either direction of the shelter adjacent to each wall, and 2 screened bait stations, containing 250 mg of MAXFORCE gel each, were placed 150 cm from the shelter, adjacent to walls. Treatments were blocked in groups of 3 and replicated 5 times. As in large cage assays, mortality was recorded 3 d after the start of the experiment. However, in field assays all cockroaches were collected. Dead cockroaches were removed from shelters and the floor, recorded, and discarded at 72 h; whereas, live cockroaches were carefully transferred to petri dishes 9 by 1.5 cm, provisioned with rat chow and water, and held for 7 d in the laboratory. Because none of the collected insects died in the laboratory, mortality in field assays was defined as the number of dead insects recorded in the field.

Data Analysis. Nonparametric, single-factor analysis of variance was performed on mortality and cockroach recovery data in field assays by using the Kruskal–Wallis test to identify differences by rank (Zar 1996). For a posteriori separation of treatments, we used the Nemenyi test of multiple comparisons. Differences between 2 samples were compared using the Mann–Whitney *U* test (Zar 1996). Data are presented as means ± SEM.

Results

Large Cage Assays: Indirect Measures of Horizontal Transfer. Mortality of adult females and nymphs is shown in Fig. 2. No mortality was observed over the 3-d assay period in control cages that received no insecticide. In assays that excluded neither adults nor 1st instars (i.e., large-mesh screens), both stages experienced high mortality (95.8 ± 4.2 and 92.5 ± 1.3% in adults and 1st instars, respectively) (Fig. 2A). For 1st instars, this represented a combined measure of primary mortality caused by ingestion of bait and secondary mortality caused by transfer of hydramethylnon from adults to nymphs.

Exclusion of adults from baits (i.e., small-mesh screen) dramatically reduced mortality in both adults and nymphs. Only 3.3 ± 3.3% of adults and 1.4 ± 0.7% of 1st instars died in 3 replications of this assay (Fig. 2A). Differences in adult and nymphal mortality between large-mesh screen and small-mesh screen treatments were significant (Mann–Whitney *U* test, $P = 0.043$, $Z = 2.023$; $P = 0.0369$, $Z = 2.087$, in adults and 1st instars, respectively). These data suggest a coupling of nymphal and adult mortality: 1st instars experienced mortality in these assays only when adults were permitted to ingest the bait. Conversely, nymphal mortality was minimal when adults were excluded from the bait. This suggests that adults play an important role in nymphal mortality. Some mortality of adults in

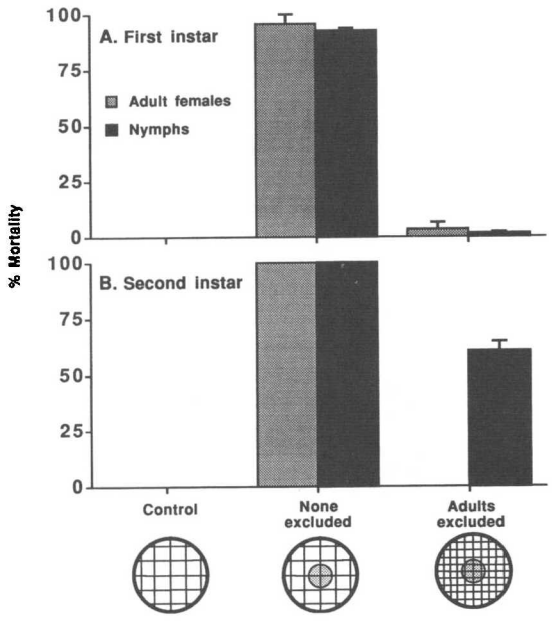

Fig. 2. Percent mortality of *B. germanica* adult females and nymphs in large-cage exclusion assays designed to obtain indirect measures of horizontal transmission of insecticide (A) adult females and 1st instars. (B) adult females and 2nd instars. Schematics below x-axis depict bait station design for each treatment. Error bars represent ±SEM.

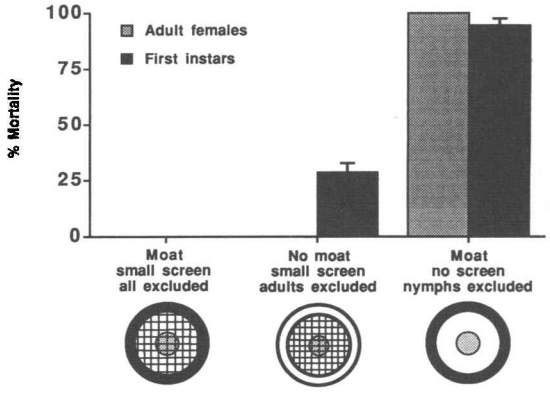

Fig. 3. Percent mortality of *B. germanica* adult females and 1st instars in large-cage exclusion assays as a direct measure of horizontal transmission of insecticides. Schematics below x-axis depict bait station design for each treatment as described in the materials and methods. Error bars represent ±SEM.

small screen assays could be caused either by antennal contact with the bait followed by ingestion during antennal grooming, or possibly, though unlikely, by a reversal of the horizontal transfer pathway whereby adults contacted insecticide that was delivered to them by nymphs.

In large-screen assays, in which neither adults nor 2nd instars were excluded from the bait, all cockroaches died within 3 d (Fig. 2B). These results were similar to those obtained with 1st instars (Fig. 2A), suggesting that either horizontal transfer of hydramethylnon was operative or that older nymphs obtained the bait directly from the bait station. Results from small-mesh screen experiments with 2nd instars support the latter hypothesis. Primary mortality of 2nd instars in the absence of adult mortality was 60.2 ± 4.2%, significantly higher than the 1.4% mortality experienced by 1st instars in an identical treatment (Mann–Whitney *U* test, $P = 0.046$, $Z = 1.993$).

These results support the hypothesis that older nymphs actively forage and feed at the bait station and therefore are less dependent than are 1st instars on translocation of bait by adults. Studies of coprophagy (Silverman et al. 1991) and recent data demonstrating that 1st instars engage in coprophagy more than 2nd instars (R.J.K. and C.S., unpublished data) suggest that coprophagy mediates these interactions.

Large Cage Assays: Direct Measures of Horizontal Transfer. Although the adult exclusion assays quantified the relative magnitude of horizontal toxicant transfer, the results were derived from indirect measures of secondary mortality obtained by subtraction of primary mortality of nymphs in small-mesh screen assays from total nymphal mortality when adults could deliver bait to nymphs (i.e., large-mesh screens). To obtain direct results on adult-mediated secondary mortality in nymphs, we designed assays that excluded nymphs from the bait. Thus, nymph mortality could be attributed only to horizontal toxicant transfer. Results from this set of experiments did not differ from results obtained in adult-exclusion assays (Fig. 3). The control treatment, in which an oil moat excluded nymphs and a small-mesh screen excluded adults from feeding on the bait, successfully kept cockroaches from contacting the bait and resulted in no cockroach mortality in any of the replicates. Allowing 1st instars access to the bait while excluding adults (i.e., no moat but a small screen over the bait) resulted in a significant rise in mortality of 1st instars to 28.7 ± 4.1% (Mann–Whitney *U* test, $P = 0.0369$, $Z = 2.087$) but no concomitant mortality among adult females. However, this moderate increase in primary mortality caused by ingestion of bait was significantly lower than mortality of 1st instars when females were permitted access to the bait (Mann–Whitney *U* test, $P = 0.0495$, $Z = 1.964$). In direct assays of secondary mortality, wherein an oil moat excluded nymphs and adults had access to the bait, mortality of 1st instars was 94.7 ± 2.9% and 100% for adult females over 3 replicates. Thus, these results confirmed our earlier finding (Fig. 2A) that 1st-instar mortality was coupled to ingestion of bait by adult females.

Field Exclusion Assays. The adult exclusion assays also were conducted in the field. Our goals

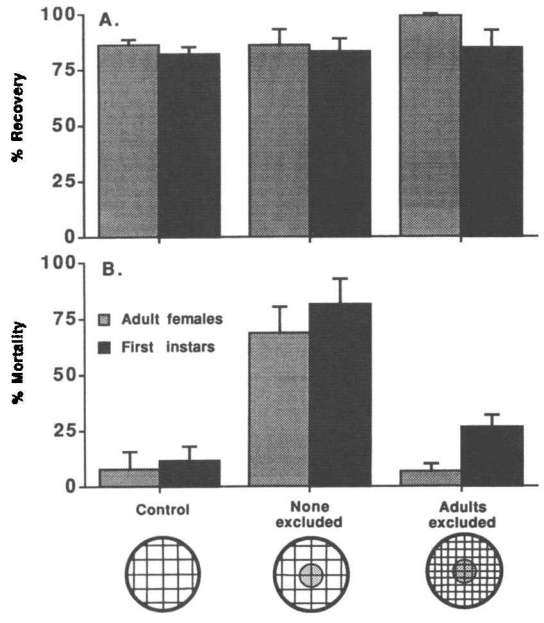

Fig. 4. Field exclusion assays with *B. germanica*. (A) Percent recovery of adult females and 1st instars. (B) Percent mortality of adult females and 1st instars. Schematics below x-axis depict bait station design for each treatment. Error bars represent ±SEM.

were to increase the area available to foraging cockroaches and to determine what effect starvation would have on foraging patterns. In all treatments, total recovery of live and dead cockroaches was ≥80% (Fig. 4A), suggesting that mortality data are a reasonable reflection of treatment effects.

Mortality of released insects after 3 d in the field is shown in Fig. 4B. Unlike large cage assays in the laboratory, adult mortality occurred in treatments where adults did not have access to bait (7.81 ± 7.81% in controls without bait, and 6.7 ± 3.4% in small-mesh screen assays that excluded adults). Likewise, some 1st instars died (11.50 ± 6.5% in controls without bait, and 26.5 ± 13.4% in small-mesh screen assays that excluded adults) despite the fact that they foraged little in laboratory assays. These results are attributable in part to observed predation by spiders, particularly on nymphs. Nevertheless, as in laboratory assays, when adults fed on toxic bait (large-mesh screen), high mortality was observed in both adults (68.7 ± 17.2%) and 1st instars (81.3 ± 9.6%). In small-mesh screen assays, which excluded adult females from the bait, mortality of nymphs declined significantly by almost 3-fold (Fig. 4B), as in laboratory assays. These results corroborate our large-cage observations in an open experimental field design, and they strongly support the hypothesis that adult-mediated delivery of insecticide to the shelter plays a major role in bait efficacy, especially with respect to 1st instars.

Discussion

Our experiments were designed to discriminate between mortality caused by ingestion of bait and mortality caused by horizontal transmission of insecticide. Our design furthermore quantified the relative magnitudes of each to the first 2 instars of *B. germanica*. Results from field and large-cage assays clearly demonstrated that foraging adults fed upon and translocated insecticidal baits to the shelter where other cockroaches were aggregated. First and 2nd instars were readily killed by these residues, but horizontal transmission was much more significant with 1st instars, presumably because of their inherent tendency to remain near the shelter and feed on feces.

Although our initial intent was to quantify the relative significance of horizontal transmission under more realistic conditions (large cages, field), several observations prompted us to contrast 1st and 2nd instars. First, several references allude to or document differential foraging during the 1st stadium. Although 1st instars presumably constitute a major demographic class in *B. germanica* populations, as they do in laboratory colonies, few are usually captured or sighted in monitoring and pest control programs (Bret and Ross 1983, Ross et al. 1984; R.J.K., unpublished data), suggesting that they have limited foraging ranges. In addition, available observations suggest that nymphs range farther from the shelter as they grow older. Cloarec and Rivault (1991) demonstrated in a field study that young nymphs foraged less frequently and with "less efficiency" than older nymphs, and DeMark et al. (1993) confirmed a similar developmental shift in a comparison of 2nd and 5th instars in the laboratory. Thus, translocation of bait to the shelter might affect early instars more than other developmental stages. Second, 1st instars appear to exhibit greater "fidelity" to their shelters (Ross et al. 1984, R.J.K. and C.S., unpublished data), and they exhibit strong arrestant responses to aggregation pheromone (Ishii 1970, Sakuma and Fukami 1985), suggesting that they might seldom encounter insecticide baits in large arenas or in the field. Third, we have demonstrated an adaptive significance to coprophagy in 1st instars. Starved 1st instars readily ingest adult feces, which can increase their survivorship in the absence of other food sources. In contrast, feces fails to significantly extend longevity of starved older nymphs (R.J.K. and C.S., unpublished data). It thus appears that 1st instars possess several characteristics that constrain their foraging and intensify their interaction with feces thereby promoting ingestion of translocated insecticide more than in older nymphs.

The reciprocal exclusion design, whereby either adults or 1st instars are prevented from ingesting insecticide bait, leaves little doubt that we were either deducing or directly measuring horizontal transfer of insecticide to nymphs. An alternative hypothesis might, however, account for the linkage

between nymphal mortality and bait ingestion by adults. Foraging adults may stimulate nymphs to forage by delivering novel odors or flavors from the bait to the shelter, thereby stimulating locomotor activity in nymphs. We are currently testing this idea by offering cockroaches identical baits 2 and 125 cm from the shelter, with only the latter containing insecticide. Preliminary data confirm our conclusion that the link between adult foraging and nymphal mortality is unrelated to differential foraging by nymphs under different experimental conditions. A more direct means of resolving whether nymphs foraged more when adults feed on toxic bait is through video recording. We have monitored frequency of visits to the bait by using this procedure. Preliminary data indicate that 1st instars infrequently visit baits 125 cm from their shelter and activity of 1st and 2nd instars appears to be independent of whether adults have access to the bait. Again, these results lend support to the hypothesis that, at least when food is nearby, 1st instars forage only short distances away from the shelter. However, 2nd instars, which are only 7 d older, are significantly more active than 1st instars (R.J.K. and C.S., unpublished data). These preliminary observations thus corroborate the conclusion that intrinsic differences in foraging ranges, and possibly shelter-fidelity, between 1st and 2nd instars influence their relative susceptibility to bait as well as to horizontal transmission of bait ingredients.

We hypothesize that coprophagy mediated the horizontal transfer of insecticide from adults to nymphs in our laboratory and field studies. Although other mechanisms of insecticide translocation are possible, including by contact, several lines of evidence support the coprophagy hypothesis. Silverman et al. (1991) demonstrated coprophagy in *B. germanica* in small cages, wherein young nymphs fed upon fecal residues contaminated with hydramethylnon. They demonstrated experimentally that radio-labeled hydramethylnon in adult feces was ingested by all stages of *B. germanica* but that relative mortality of 1st through 3rd stadium nymphs was significantly increased when adults were present in the assay. We recently confirmed these observations in petri dish assays. Using a tracking dye, we conclusively showed that adult feces was ingested by 1st instars even in the presence of alternative food sources (R.J.K. and C.S., unpublished data). Moreover, hydramethylnon residues are much less active against cockroaches by contact than by ingestion, suggesting that translocated bait is ingested by nymphs. We have shown directly that 1st instars feed on conspecific feces; insecticide-laden feces therefore effectively target 1st instars.

In conclusion, mortality of 1st instars in our experimental design is largely dependent on adult-mediated translocation of insecticide to the shelter. In contrast, causes of mortality of 2nd instars are approximately equally divided between direct ingestion of bait and horizontal transmission. Adults are a key determinant of mortality in 1st instars because adults effect horizontal transfer of toxic bait to nymphs. Exclusion of adult females from the bait significantly reduces mortality in 1st instars (by 91% in Fig. 2A and by 66% in Fig. 3, respectively), whereas exclusion of 1st instars from the bait does not decrease relative mortality so long as they interact with foraging adults. Conversely, older nymphs appear to visit remote baits more frequently than 1st instars, suggesting that horizontal transfer of insecticides to 2nd instars contributes less to overall mortality than it does in 1st instars. Discrimination between key mortality factors is possible only in large cages and with experimental exclusion of adults or nymphs. Clearly, small cages fail to resolve these effects because the cage is explored exhaustively by all life stages. Conversely, field studies are difficult because 1st instars reside in hidden shelters. By seeding field populations of cockroaches, we have successfully demonstrated in the field that horizontal transfer of bait, most likely through coprophagy, plays a major role in effecting mortality in nymphs. In future experiments we will delineate the mechanisms of bait translocation, examine demographically complex field populations of cockroaches, and explore factors that enhance or diminish cockroach-mediated translocation of insecticides.

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