Article

Integration of Repellents, Attractants, and Insecticides in a "Push-Pull" Strategy for Managing German Cockroach (Dictyoptera: Blattellidae) Populations

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ABSTRACT "Push-pull" is a behavior manipulation strategy in which behavior-modifying stimuli are integrated with a pest control agent. We evaluated the efficacy of an insecticide bait in combination with attractants ("pull"), repellents ("push"), or both ("push-pull") using a hydramethylnon-based bait, feces-contaminated surfaces as an attractant, and methyl neodecanamide-treated surfaces to repel cockroaches. Both adult males and first-instar German cockroaches, *Blattella germanica* (L.), chose shelters nearest the attractant-treated surfaces and farthest from the repellent-treated surfaces. Food consumption was highest from food nearest the preferred shelters, and mortality was highest when the insecticide bait was near the preferred shelter. These patterns were more apparent in first instars than in adults. Our results from large arena studies in the laboratory show that the push-pull strategy can be used to displace pests from resources or commodities that are to be protected, and simultaneously lure the pest to an attractant source coupled with a pest control agent. Concentrating cockroaches into a limited area should facilitate the precision-targeting of the pest population and promises to reduce insecticide use.

KEY WORDS *Blattella germanica*, German cockroach, repellent, attractant, methyl neoalkanamide

German Cockroach, *Blattella germanica* (L.), control has relied heavily on the use of broad-spectrum insecticides. Recent concerns with human and environmental safety, and widespread prevalence of resistance to insecticides (Cochran 1995) have prompted research on safer, reduced-risk, and environmentally compatible methods of insect control. However, the advent and intense promotion of integrated pest management (IPM) approaches have not reduced reliance on chemical insecticides as the preferred technology for cockroach control, in large part because the effectiveness of alternatives has been poor and inconsistent (Gold 1995). It is therefore important to research effective and safe alternative reduced-risk approaches and strategies.

"Push-pull" is a behavior manipulation strategy, in which behavior-modifying stimuli are integrated with a pest control agent. With the integrated use of attractants and repellents (or stimulants and deterrents), the pest is displaced from a resource that is to be protected, and simultaneously lured to an attractant that can be coupled with a pest control agent (i.e., "attract-and-kill"). The goal of the push-pull strategy is to concentrate the pest in a limited area, which would then be targeted with less insecticide or other pest control tools (Foster and Harris 1997). The efficacy of this concept has been demonstrated on several pests in agricultural and forest systems, including *Heliothis* sp. Ochsenheimer in cotton (Rice 1986, Pyke et al. 1987), *Licilia cuprina* (Weid.) (Rice 1986), the onion maggot (*Delia antiqua* Meigen) (Miller and Cowles 1990, Cowles and Miller 1992), the mountain pine beetle (*Dendroctonous ponderosae* Hopkins) (Borden and Lindgren 1988, Lindgren and Borden 1993, and Borden 1997) and *Chilo pertellus* (Swinhoe) and *Busseola fusca* Fuller (Khan et al. 1997).

This approach has not been researched on any structural arthropod pest. Nevertheless, physical modification of the indoor environment (e.g., improved sanitation) can enhance the efficacy of other tactics in cockroach control by reducing resources that support population growth and by facilitating movement, which increases contact of cockroaches with residual insecticides (Schal and Hamilton 1990). Repellents, which reduce the availability of limiting resources (water, food, and shelter) can serve a similar function. The responses of cockroaches to both chemical and environmental repellents have been examined in the laboratory (Steltenkamp et al. 1992, Brenner et al. 1998, Appel and Smith 1999).

Food attractants and pheromones have also been evaluated for use in cockroach pest management, primarily as lures in traps, or as attractants for admixing with baits and residual sprays. Whereas food odorants have contributed to the performance of insecticide bait formulations, aggregation and sex pheromones have not been used in practical cockroach population management, despite recent chemical characterization efforts (Charlton et al. 1993; Sakuma et al. 1997a, 1997b) and their demonstrated efficacy (Rust and Reierson 1977, Bell et al. 1984, Liang et al. 1998).

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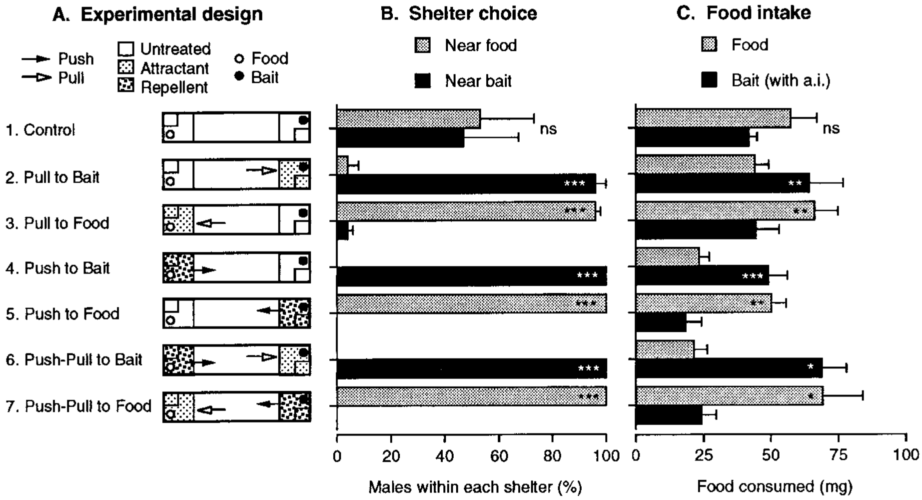

Fig. 1. Experimental design (A), shelter selection (B), and food consumption (C) of adult male German cockroaches in push-pull assays. The large square on either side of the arena in (A) represents a 30 by 30-cm vinyl floor tile. The small square represents a 10 by 10-cm vinyl tile shelter. N is five replications per experiment with 50 males each. In B and C, variation represents SEM; ns, not significant; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

No effort has been expended toward integrating repellents, attractants, and pest control agents into a single strategy for manipulating and controlling cockroach populations. In this article we report results of laboratory experiments designed to examine the effectiveness of integrating repellents, attractants, and insecticides in a push-pull strategy to manage German cockroach populations. Experiments were conducted to test the effect of an attractant or "pull" alone, repellent or "push" alone, and the combined effect of the "pull" and "push" components. We expected that integration of repellents and attractants would result in a predictable net displacement of the cockroach population. Because cockroaches tend to use local resources that are nearest to their shelters (Silverman 1986, Rivault and Cloarec 1991b, Kopanic and Schal 1999), we hypothesized that the integrated "herding" of cockroaches toward an insecticide bait would accelerate mortality and enhance bait efficacy compared with deployment of single tactics alone.

Materials and Methods

Insects. A laboratory colony of insecticide-susceptible German cockroaches (American Cyanamid strain, Princeton, NJ) was maintained at 27°C, ambient humidity, a photoperiod of 12:12 (L:D) h, and provided with water and Purina Rat Chow #5012 (Purina Mills, St. Louis, MO).

Experimental Design. Adult male German cockroaches 10–20 d and 1–3 d first instars were used in separate bioassays. All experiments were conducted at 27 ± 1°C and variable ambient humidity. The inner surface of Plexiglas arenas (120 by 30 cm) was coated with a thin layer of petroleum jelly to prevent escape of cockroaches. The floor of each arena consisted of Labmat (Green Bay Packaging, Green Bay, WI) and a 30 by 30-cm vinyl floor tile (Armstrong Industries, Lancaster, PA) at each end. A 10 by 10-cm section of vinyl tile, raised off the floor by a 1.25-cm metal nut, formed a shelter. Two shelters were placed at diagonally opposite corners of the arena.

The "push" component of this approach was generated by technical grade methyl neodecanamide, MNDA (Colgate-Palmolive, Piscataway, NJ) (Steltenkamp et al. 1992). MNDA in ethanol (9.3 mg/ml) was evenly spread on the base tile and the inner surface of one shelter to yield a deposit of 0.2 mg/cm^2. The treated tiles were allowed to dry in a fume hood before introducing them into the test arena. The "pull" component was generated by placing tile shelters in a German cockroach colony for 5–7 d so that cockroach feces, which contain aggregation pheromone (Ishii et al. 1967), would be deposited on them. In these experiments "bait" refers to a 1% (wt:wt) formulation of hydramethylnon (Clorox, Pleasanton, CA) incorporated in fine ground rat chow, whereas "food" refers to fine ground rat chow treated with acetone and dried. Both were provisioned in plastic holders (1.5 cm diameter, 1.5 cm high) and placed 2 cm from the shelter. A water vial plugged with cotton was placed adjacent to each food or bait.

The following assays were conducted to determine the effectiveness of the push-pull approach at accelerating hydramethylnon-caused mortality in first-instar and adult male cockroaches (Figs. 1A and 2A). *Assay 1.* Control: No push nor pull. The bait (with hydramethylnon) placed near one shelter and the food (without hydramethylnon) placed next to the other shelter. *Assay 2.* Pull to bait: The bait near the attractive feces-treated shelter and the food near an untreated shelter. *Assay 3.* Pull to food: The food near

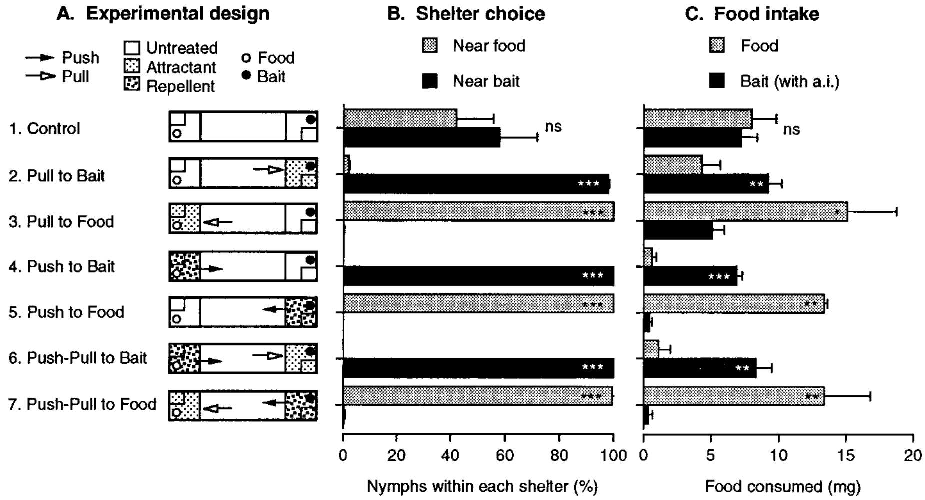

Fig. 2. Experimental design (A), shelter selection (B), and food consumption (C) of first-instar German cockroaches in push-pull assays. The large square on either side of the arena in (A) represents a 30 by 30-cm vinyl floor tile. The small square represents a 10 by 10-cm vinyl tile shelter. N is five replications per experiment with 50 nymphs each. In B and C, variation represents SEM; ns, not significant; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

the feces-treated shelter and the bait near the untreated shelter. *Assay 4.* Push away from food, toward bait: The bait near the untreated shelter and the food near the repellent shelter. *Assay 5.* Push away from bait, toward food: The food near the untreated shelter and the bait near the repellent shelter. *Assay 6.* Push-pull to bait: Integration of push and pull with the bait near the feces treated shelter (pull to bait) and the food near repellent shelter (push away from food). *Assay 7.* Push-pull to food: Integration of push and pull, with the food near the feces-treated shelter (pull to food) and the bait near repellent shelter (push away from bait)

Cockroaches of two stages were used: adult males represent active foragers that are relatively difficult to repel (Steltenkamp et al. 1992), whereas first instars represent a more sedentary stage. Fifty adult males or first instars that had acclimated to laboratory conditions for 24-36 h were released into each test arena. The mass of food consumed in each arena was determined gravimetrically after 24 h, shelter choice and the spatial distribution of cockroaches were recorded, and mortality was recorded daily in midphotophase until the entire cockroach population died. Mortality was defined as the inability of the insect to right itself within 30 s of being turned on its dorsal side. Dead insects were removed daily from the arena and food and water were replenished as needed. Each assay was replicated five times.

Data Analysis. Although some of the assays lasted for >60 d, the peak mortality was observed on day 2 of the experiment. Therefore, we used two parameters to measure mortality. Mean cumulative percent mortality on day 2 was computed, arcsine transformed and subjected to analysis of variance (ANOVA) (PROC GLM, SAS Institute 1997). Single degree contrasts were used to compare treatments, using the day 2 cumulative mortality. The second parameter was the time it takes to kill 50 and 90% of the test population. They were estimated assuming a Weibull survival distribution using PROC LIFEREG (SAS Institute 1997). Estimates of survival time were analyzed for first instars and adults separately, and pooled for both stages. The differences in the estimates of survival time from different treatments were determined by ANOVA. Paired *t*-tests were used to determine differences in food consumption and the *G*-test was used to determine differences in shelter choice. In the *G*-test, we assumed a 1:1 distribution of cockroaches in the two shelters.

Results

Distribution and Shelter Selection. The cockroaches were approximately evenly distributed in the two shelters in the control experiments (experiment 1) with no significant difference in the shelter choice observed for adult male cockroaches (Fig. 1B; Table 1) and in the nymphs (Fig. 2B; Table 2). Significantly more adult males and first instars (Tables 1 and 2) selected the feces-conditioned shelters in experiments 2, 3, 6, and 7, and avoided the repellent-treated shelters in experiments 4, 5, 6, and 7. In experiments where the repellent alone was used to push cockroaches away from either the food or bait, all the cockroaches selected the neutral untreated shelters and avoided the repellent-treated shelters. These responses were observed for both adult males and nymphs, and for both stages the repellent (push) appeared to be more effective than the attractant (pull), as some cockroaches sheltered on the untreated tile when an attractive feces-treated tile was in the same cage.

Table 1. Shelter choice of adult male German cockroaches in push-pull experiments

Experiment	Adult males in shelter[a]		df	G^b	P
	Near food	Near bait			
1. Control	139	149	1	0.8	>0.05
2. Pull to bait	10	233	1	299.3	<0.001
3. Pull to food	183	8	1	198.3	<0.001
4. Push to bait	0	237	1	328.5	<0.001
5. Push to food	228	0	1	316.1	<0.001
6. Push-Pull to bait	0	223	1	323.0	<0.001
7. Push-Pull to food	231	0	1	320.2	<0.001

[a] The number of cockroaches in each shelter is pooled from all five replicates of each treatment with 50 insects per replicate (The control experiment had seven replicates). Some males were elsewhere in the arena.
[b] *G*-test values obtained assuming a 1:1 ratio of all the cockroaches that selected a shelter.

Food Intake. The patterns of food consumption on day 1 generally mirrored the distribution of cockroaches within shelters (Figs. 1C and 2C). There was no significant difference between the amount of bait (with active ingredient) and food (without active ingredient) that was eaten in the control experiments by adult males (t-test $t = 1.4$, df = 5, $P > 0.05$) and by nymphs ($t = 0.7$, df = 6, $P > 0.05$). Cockroaches consumed significantly more of the food item to which they were directed (Figs. 1C and 2C). Again, the repellent effect appeared to be more effective than the attractant. Adult males consumed 1.5-times more bait than food when they were attracted (pulled) to the bait, and twice as much bait as food when they were repelled (pushed away) from the food. When the attractant and repellent were combined to direct cockroaches to the bait, the adult males ate threefold more bait than food. The opposite was true when the cockroaches were pushed and pulled toward the food source (Fig. 1C).

The pattern of food and bait intake of first instars was even more related to their choice of shelter. When nymphs were lured to the bait, they ate twice as much bait as food (Fig. 2C). Twelve times more bait than food was eaten when first instars were repelled from the food and attracted to the bait. In converse experiments where cockroaches were directed away from the bait, up to 44 times more food than bait was eaten. First instars consumed a very small fraction of the food that was distant from the shelter compared with the food that was proximal to the shelter.

Mortality. There were significant treatment effects in day 2 cumulative mortality of adult males ($F = 11.7$; df = 6, 28; $P < 0.001$) and first instars ($F = 34.7$; df = 6, 28; $P < 0.001$). However, the stage of development of the cockroach did not exert a significant effect on the mortality caused by each respective treatment ($F = 0.6$; df = 1, 48; $P > 0.05$) suggesting that these treatments performed equally well against adult and first-instar cockroaches. When cockroaches were directed toward the bait, significantly more adult males ($F = 4.9$; df = 1, 28; $P < 0.05$) and first instars ($F = 54.1$; df = 1, 28; $P < 0.001$) died than in the control trials. In adult male cockroaches, the integrated push-pull toward the bait yielded the greatest and significantly higher day 2 mortality ($F = 5.4$; df = 1, 28; $P < 0.05$) than when either the attractant (pull) or repellent (push) was used alone (Fig. 3).

A similar trend was seen in first instars, where again, the greatest mortality occurred by the combined push-pull, followed by push and then pull to the bait (Fig. 4). But in this case, mortality from push-pull to the bait was not significantly different from pull or push alone ($F = 0.24$; df = 1, 28; $P > 0.05$). When first instars were directed away from the hydramethylnon bait, mortality was significantly lower than in the respective controls ($F = 8.2$; df = 1, 28; $P < 0.05$).

A second measure of the effectiveness of the seven treatments was the time taken to achieve 50 and 90% mortality of the cockroaches, estimated from Weibull survival distributions. The time taken to kill 50% of the test population was significantly affected by stage ($F = 90.9$; df = 1, 48: $P < 0.001$) and treatment ($F = 32.6$; df = 6, 48; $P < 0.001$). Similarly, time required to achieve 90% mortality was significantly affected by stage ($F = 67.1$; df = 1, 48; $P < 0.001$) and treatment ($F = 21.1$; df = 6, 48; $P < 0.001$). A significant interaction between stage and treatment affected 50% ($F = 18.0$; df = 6, 48; $P < 0.001$) and 90% ($F = 9.7$; df = 6, 48; $P < 0.001$) mortality. Directing cockroaches to the bait produced faster mortality than in the respective control treatments in first instars ($F = 6.1$; df = 1, 24; $P < 0.05$) but not in adult males ($F = 2.1$; df = 1, 24; $P > 0.05$). When they were directed in the opposite direction (away from the bait) mortality was significantly slower than in the control in first instars ($F = 33.5$; df = 1, 24; $P < 0.001$) and adult males ($F = 13.1$; df = 1,24; $P < 0.05$). The push-pull to the bait treatment yielded the fastest adult mortality, with 100% dead after 4 d compared with 5 and 6 d needed with push to the bait and pull to the bait, respectively; nonetheless, there were no significant differences among these three treatments ($F = 0.8$; df = 1, 24; $P > 0.05$). Conversely, repelling males away from the bait yielded the slowest mortality with 100% dying in 28 d.

Similarly, push-pull to the bait took 4 d to kill 100% of the first-instar population, and 5 and 6 d when the

Table 2. Distribution and shelter choice of first-instar German cockroaches in push-pull experiments

Experiment	First-instars in shelter[a]		df	G^b	P
	Near food	Near bait			
1. Control	56	78	1	3.5	>0.05
2. Pull to bait	2	238	1	274.3	<0.001
3. Pull to food	239	2	1	310.1	<0.001
4. Push to bait	0	95	1	65.8	<0.001
5. Push to food	200	0	1	276.6	<0.001
6. Push-Pull to bait	0	234	1	324.4	<0.001
7. Push-Pull to food	205	1	1	172.7	<0.001

[a] The number of cockroaches in each shelter is pooled from all five replicates of each treatment with 50 insects per replicate. Some nymphs were elsewhere in the arena.
[b] *G*-test values obtained assuming a 1:1 ratio of all the cockroaches that selected a shelter.

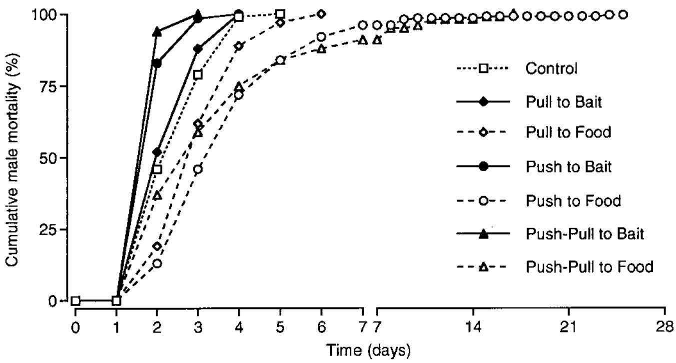

Fig. 3. Cumulative percentage mortality of adult male German cockroaches in push-pull assays. N is five replications per experiment with 50 males each.

insects were pulled to the bait and pushed to the bait, respectively and the rates were not significantly different ($F = 0$; df = 1, 24; $P > 0.05$). However, when first instars were directed away from the bait, 100% mortality was often not reached for >60 d. The significant stage by treatment interaction resulted from the slow mortality displayed by first instars compared with males when directed away from the bait. Rates of mortality of first instars and adult males were not significantly different in treatments that vectored insects toward the bait but they were significantly different in treatments directing insects away from the bait.

Discussion

The push-pull strategy aims to behaviorally manipulate pest populations using various stimuli (e.g., chemical, visual, acoustic, mechanical) to displace the pest from an area, a resource, or commodity to be protected, and luring it to an attractant source. Because semiochemicals, when employed alone, may have limited efficacy, a pest control agent can be incorporated into the strategy (Rice et al. 1986, Pyke et al. 1987, Miller and Cowles 1990, Foster and Harris 1997). Our study took advantage of an effective repellent that directed German cockroaches away from treated areas. Attractants and arrestants, presumably components of the aggregation pheromone (Sakuma et al. 1997b) lured cockroaches toward specific areas. The combined push-and-pull effect vectored the cockroaches to predictable areas of the arena. Placement of an insecticide-containing bait strategically at one end of the arena, combined with push-pull in the same direction, caused increased feeding and accelerated mortality. Indeed, the distribution of resting cockroaches, their food intake, and mortality were interdependent (Figs. 1–4).

Shelter selection was greatly influenced by the presence of the repellent and attractant. Cockroaches chose feces-contaminated or neutral untreated shelters and avoided methyl neodecanamide-treated shelters. Steltenkamp et al. (1992) similarly reported that adult male cockroaches were repelled from MNDA-treated surfaces for >10 d. Furthermore, established aggregations of cockroaches in laboratory arenas were disrupted and deterred from reestablishing in the same shelters once the shelters were treated with the MNDA repellent (Brenner et al. 1998).

Cockroaches fed more on the food that was nearest to their aggregation (Silverman 1986, Rivault and Cloarec 1991a,b, Kopanic and Schal 1997, 1999). Be-

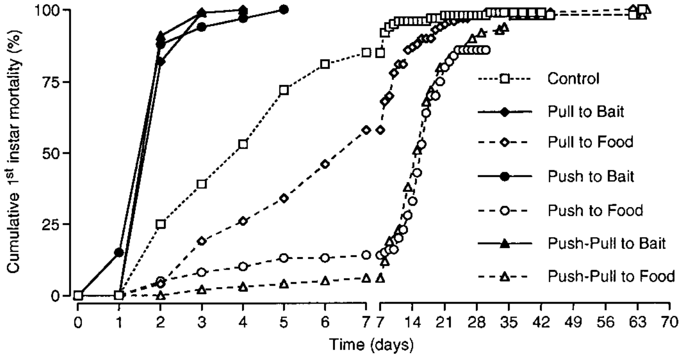

Fig. 4. Cumulative percentage mortality of first-instar German cockroaches in push-pull assays. N is five replications per experiment with 50 nymphs each.

cause cockroaches rested on the feces-contaminated surface and avoided the MNDA-treated surface, the position of the insecticide bait markedly influenced the survivorship of the population. In the push-pull assays, the cockroaches fed significantly more on whichever food was nearest to their shelter. The combination of a repellent and attractant probably limited foraging and feeding to a fraction of the arena, exerting a "corralling" effect (Steltenkamp et al. 1992) on the cockroaches and directing them to the food nearest the favored shelter. This feeding pattern was evident in both the adult males and nymphs, but was more pronounced in the nymphs. First-instars forage over a short range (Rivault and Cloarec 1991a, Kopanic and Schal 1997, 1999) and therefore tend to remain within an adequate shelter and feed nearby, as clearly shown when the insects were directed away from the insecticide bait; few died in the first 5 d because they remained near the untreated shelter and avoided the insecticide bait. Subsequently there was a steady increase in mortality as the nymphs became second instars, which are more mobile (Kopanic and Schal 1999) and more readily forage 120 cm to the bait. Conversely, when the cockroaches were directed toward the insecticide bait, mortality was rapid because the first instars fed almost exclusively on the nearby bait.

Our results are consistent with those of other workers who have used the push-pull strategy in insect pest management. Miller and Cowles (1990) reported a greater reduction in eggs laid by the onion maggot when an oviposition deterrent and attractant were deployed together, than when each was used separately. Likewise, there was a greater reduction in eggs oviposited on cotton plants by *Heliothis* sp. when a trap crop and a repellent were used, than when either was used alone (Pyke et al. 1987). Shea and Neustein (1995) heroically saved a stand of rare pines from destruction by *Ips paraconfusus* Lanier using a push-pull strategy, and recently the push-pull strategy was shown to be more effective than attractants or repellents alone in the control of *Chilo pertellus* and *Busseolla fusca* in Africa (Khan et al. 1997).

Constraints of Push-Pull in German Cockroach Control. Successful deployment of the push-pull strategy requires in depth knowledge of the basic biology (especially sensory biology), behavior, and ecology of the pest. Furthermore, use of this strategy requires the following: (1) a clearly defined resource or object to be protected from the pest, (2) well identified cues and signals used by pests to locate resources, and (3) knowledge of the destructive behaviors that the pest displays while on the host, behaviors that can be manipulated to control the pest (e.g., oviposition behavior, feeding behavior). Many phytophagous and hematophagous pests meet these criteria, but less so the German cockroach. The commodity to be protected from cockroaches and the damage are often not clearly defined. Likewise, the sensory cues that cockroaches use to locate food are poorly understood and, being a generalist feeder, the German cockroach does not seem to have specific behaviors or habits that are amenable to manipulation, hence use of the push-pull strategy to target this pest could be challenging. Nevertheless, preference of the German cockroach for certain microhabitats and its use of semiochemicals for aggregation and mate-location can be targeted by repellents and attractants, respectively, as in our current study.

Powerful attractants for luring cockroaches to insecticide treated surfaces, traps, and baits are sorely needed. Research efforts have concentrated on chemical characterization of food attractants, sex pheromones, and aggregation pheromones for the German cockroach (Sakuma and Fukami 1990; Schal and Smith 1990; Sakuma et al. 1997a, 1997b). There is also a need for more potent but safe repellents that can effectively displace and push cockroaches from commodities toward the attractants.

Methyl neodecanamide, the repellent we used in this study, appears to be highly effective (Steltenkamp et al. 1992, Brenner et al. 1998) but other more effective repellents might improve the efficacy of the push-pull strategy.

Advantages of the Push-Pull Strategy. The push-pull approach of controlling cockroach populations is compatible with currently available pest control technology, and so it can be integrated with other tactics to enhance their performance. For example, chemical insecticides and biological control agents can be incorporated into a push-pull strategy. Our results, showing higher mortality with the combined effects of an attractant and repellent, suggest that the integrated push-pull approach may be more effective in controlling pests than either the repellent or attractant alone. Repellents alone effect a multidirectional dispersal of the pest population. The net displacement of cockroaches would move them away from the insecticide-treated surfaces when repellents and insecticides are combined (see Schal and Hamilton 1990, Steltenkamp et al. 1992). Incorporation of an attractant into the system should redirect repelled insects, thus providing a way to concentrate the cockroach population in a defined area, and to target them with reduced-risk pest control agents. As a result of this concentration and precision targeting, the area to be treated with a selective pesticide can be reduced, and the amount of insecticide can also be reduced. Because each component of the push-pull approach is relatively less effective when used alone than in concert with the others, it is expected that resistance would not develop quickly to the components of the push-pull strategy. In addition, this approach can be implemented at different scales. For example, the operational unit for a push-pull strategy can be a whole room or a single item within the room. Such a strategy can be exceedingly useful in situations where insecticide use is restricted, for example in hospital rooms, zoos, animal rearing facilities, sensitive electronic equipment, and food-handling facilities.

With increasing human awareness and concern about the harmful effects of insecticides and stringent regulations of pesticides, there is a need for safer pest management strategies. The push-pull strategy of sensory manipulation could potentially become a highly effective behavioral management strategy that could be used to safely control cockroaches and other pests of agricultural, medical, and veterinary importance. Our research has shown that push-pull manipulates pest distribution and shelter choice, prolongs exposure of cockroaches to a toxic bait and consequently results in greater dose transfer and faster mortality. Push-pull resulted in more predictable and consistent mortality compared with the other treatments that directed cockroaches to the bait. However, research is needed to generate more potent attractants and repellents.

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References Cited

Appel, A. G., and L. M. Smith. 1999. Perception and repellency of moving air by American and smokybrown cockroaches (Dictyoptera:Blattidae). J. Econ. Entomol. 92: 70–75.

Bell, W. J., J. Fromm, A. R. Quisumbing, and A. K. Kydonieus. 1984. Attraction of American cockroaches (Orthoptera: Blattidae) to traps containing periplanone B and to insecticide-periplanone mixtures. Environ. Entomol. 13: 448–450.

Borden, J. H. 1997. Disruption of semiochemial mediated aggregation in bark beetles, pp. 421–438. *In* R. T. Cardé and A. K. Minks [eds.], Insect pheromone research: new directions. Chapman & Hall, New York.

Borden, J. H., and B. S. Lindgren. 1988. The role of semiochemicals in IPM of mountain pine beetle, pp. 247–255. *In* T. L. Payne and H. Saarenmaa [eds.], Integrated control of Scolytid bark beetles. Virginia Polytechnic Institute and State University, Blacksburg, VA.

Brenner, J. R, D. E. Milne, K. M. Kinscherf, and T. F. Connors. 1998. Measuring spartial displacement of *Blattella germanica* (Blattaria: Blattellidae) populations by repellent treated harborages. Environ Entomol. 27: 10–21.

Charlton, R. E., F. X. Webster, A. Zhang, C. Schal, D. Liang, I. Sreng, and W. L. Roelofs. 1993. Sex pheromone for the brownbanded cockroach is an unusual dialkyl-substituted α-pyrone. Proc. Natl. Acad. Sci. U.S.A. 90: 10202–10205.

Cochran, D. 1995. Insecticide resistance, pp. 171–192. *In* M. K. Rust, J. M. Owens, and D. A. Reierson [eds.], Understanding and controlling the German cockroach. Oxford University Press, New York.

Cowles, R. S., and J. R. Miller. 1992. Diverting *Delia antiqua* (Diptera: Anthomyiidae) oviposition with cull onions: field studies on planting depth and a greenhouse test of stimulo-deterent concept. Environ. Entomol. 21: 453–640.

Foster, S. P., and M. O. Harris. 1997. Behavioral manipulation methods for insect pest management. Annu. Rev. Entomol. 42: 123–146.

Gold, R. E. 1995. Alternate control strategies, pp. 325–344. *In* M. K. Rust, J. M. Owens, and D. A. Reierson [eds.], Understanding and controlling the German cockroach. Oxford University Press, New York.

Ishii, S., and Y. Kuwahara. 1967. An aggregation pheromone of the German cockroach, *Blattella germanica* (L.) 2. Site of pheromone production. Appl. Entomol. Zool. 2: 203–217.

Khan, Z. R., P. Chiliswas, K. Ampong-Nyarko, L. E. Smart, A. Polaszek, J. Wandera, and M. A. Mulaa. 1997. Utilization of wild graminaceous plants for management of cereal stemborers in Africa. Insect Sci. Applic. 17: 143–150.

Kopanic, R. J., and C. Schal. 1997. Relative significance of direct ingestion and adult-mediated translocation of bait to German cockroach (Dictyoptera: Blattellidae) nymphs. J. Econ. Entomol. 90: 1073–1079.

Kopanic, R. J., and C. Schal. 1999. Coprophagy facilitates horizontal transmission of bait among cockroaches (Dictyoptera: Blattellidae). Environ. Entomol. 28: 431–438.

Liang D., A. Zhang, R. J. Kopanic Jr., W. Roelofs, and C. Schal. 1998. Field and laboratory evaluation of female sex pheromone for detection, monitoring, and management of brownbanded cockroaches (Dictyoptera: Blattellidae). J. Econ. Entomol. 91: 480–485.

Lindgren, B. S., and J. H. Borden. 1993. Displacement and aggregation of mountain pine beetles, *Dendroctonous ponderosae* (Coleoptera: Scolytidae) in response to their antiaggregation and aggregation pheromones. Can. J. For. Res. 23: 286–290.

Miller, J. R., and R. S. Cowles. 1990. Stimulo-deterent diversion: A concept and its possible application to onion maggot control. J. Chem. Ecol. 16: 3197–3212.

Pyke, B., M. Rice, G. Sabine, and M. Zaluki. 1987. The Push-pull strategy—behavioral control of *Heliothis.* Australian Cotton Grower, May–July: pp. 7–9.

Rice, M. 1986. Semiochemicals and sensory manipulation strategies for behavioral management of *Heliothis* species Ochsenheimer (Lepidoptera: Noctuidae), pp. 27–45. *In* M. P. Zaluki and P. H. Twine [eds.], Proceedings: *Heliothis* Ecology Workshop, 1985. Queensland Department of Primary Industries, Brisbane, Australia.

Rivault, C., and A. Cloarec. 1991a. Exploitation of food resources by the cockroach *Blattella germanica* in an urban habitat. Entomol. Exp. Appl. 61: 149–158.

Rivault, C., and A. Cloarec. 1991b. Age-related changes in foraging in the German cockroach (Dictyoptera: Blattellidae). J. Insect Behav. 4: 661–673.

Rust, M. K., and D. A. Reierson. 1977. Increasing blatticidal efficacy with aggregation pheromone. J. Econ. Entomol. 70: 693–696.

Sakuma, M., and H. Fukami. 1990. The aggregation pheromone of the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): isolation of the attractant components of the pheromone. Appl. Entomol. Zool. 25: 355–368.

Sakuma, M. H., H. Fukami, and Y. Kuwahara. 1997a. Aggregation pheromone of the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae): Controlled release of attractant amines by salt formation. Appl. Entomol. Zool. 32: 143–152.

Sakuma, M. H., H. Fukami, and Y. Kuwahara. 1997b. Attractiveness of alkyl amines and aminoalcohols related to the aggregation attractant pheromone of the German cockroach, *Blattella germanica* (L.) (Dictyoptera: Blattellidae). Appl. Entomol. Zool. 32: 197– 205.

SAS Institute. 1997. SAS/STAT user's guide, version 6.12, 4th ed., vol. 2. SAS Institute, Cary, NC.

Schal, C., and R. L. Hamilton. 1990. Integrated suppression of synanthropic cockroaches. Annu. Rev. Entomol. 35: 521–551.

Schal, C., and A. Smith. 1990. Neuroendocrine regulation of pheromone synthesis and release in cockroaches, p. 179–200. *In* I. Huber, E. P. Masler, and B. R. Rao [eds.], Cockroaches as models for neurobiology: applications in biomedical research vol. II. CRC, Boca Raton, FL.

Shea, P. J., and M. Neustein. 1995. Protection of a rare stand of Torrey pine from *Ips paraconfusus. In* S. M. Salom and K. R. Hobson [eds.], Proceedings of the symposium on application of semiochemicals for management of bark beetle infestations. U.S. Dep. Agric. For. Serv. Gen. Tech. Rep. INT-GTR–318.

Silverman, J. 1986. Adult cockroach (Orthoptera: Blattellidae) feeding and drinking behavior as a function of density and harborage-to-resource distance. Environ. Entomol. 15: 198–204.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. Freeman, New York.

Steltenkamp, R. J., R. L. Hamilton, R. A. Cooper, and C. Schal. 1992. Alkyl and aryl neoalkanamides: highly effective insect repellents. J. Med. Entomol. 29: 141–149.

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