

5 Sustainable Cockroach Management Using Insecticidal Baits: Formulations, Behavioural Responses and Issues

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Introduction

Cockroaches are an important group of insect pests in the urban environment. Their adaptability has made them a universal pest associated with humans. The use of insecticides remains the most common method of control, among which use of insecticide baits is the most popular method. Baits are precise, use less toxicant and carry lower risks when applied. For example, a survey conducted in Kentucky, USA, showed that two-thirds of the 598 respondents preferred insecticide baits to sprays (Potter and Bessin, 1998).

This chapter discusses the fundamentals of cockroach baiting, paying particular attention to the science of bait formulation with emphasis on cockroach behavioural responses such as feeding and foraging strategies.

History of cockroach bait

The first cockroach bait was available commercially in 1896, when phosphorous was added to a sweetened flour paste and marketed to kill cockroaches in the USA and UK (Cornwell, 1976). Prior to that, do-it-

yourself cockroach bait was made by mixing 1 part plaster of Paris with 3–4 parts flour, and this mixture functioned as a stomach poison (Cornwell, 1976). Chronological analysis show that active ingredients from different classes of insecticides have been used in cockroach bait, including boric acid (inorganic compounds), chlordecone (organophosphate), chlorpyrifos (carbamate), hydramethylnon (amidinohydrazone), sulfluramid (fluorinated sulfonamide), abamectin (avermectin), imidacloprid (neonicotinoid), fipronil (phenylpyrazole) and indoxacarb (oxadiazine) (Fig. 5.1) (Cornwell, 1976; Reiersen, 1995; Benson and Zungoli, 1997). Today, only a limited number of compounds are available as toxicants in cockroach baits, such as abamectin, dinotefuran, fipronil, hydramethylnon, imidacloprid and indoxacarb.

Benefits of baiting

Baits are popular and highly acceptable because they have a number of benefits. Baits are ready to use without the need for dilution. They can be used on any type of treatment surface, and they are available in various formulations such as gel, paste, dry

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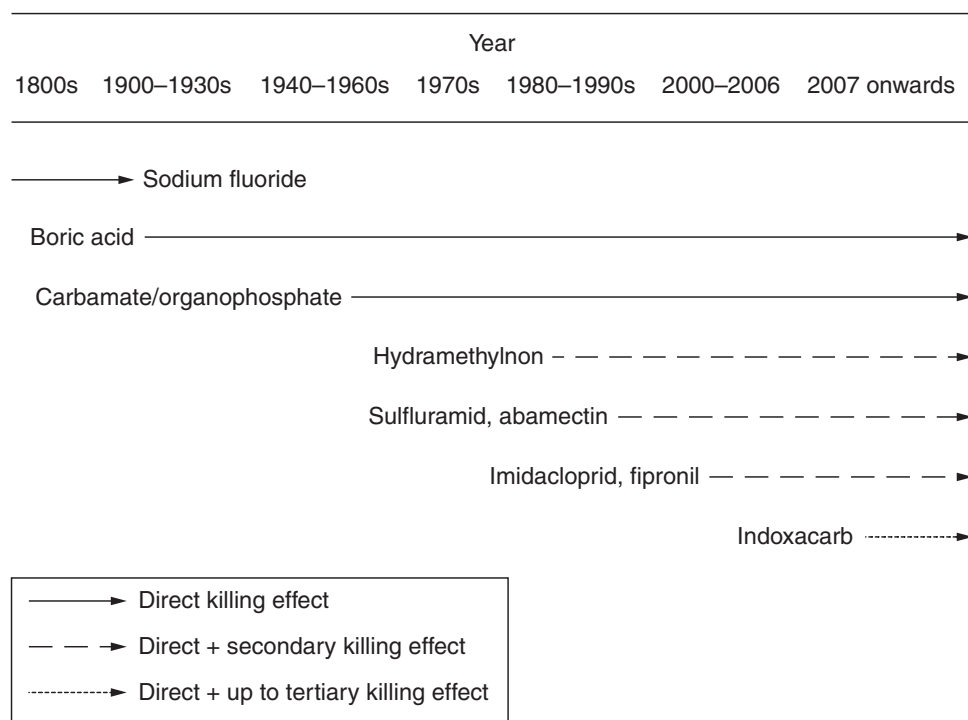


Fig. 5.1. Chronological development of active ingredients of insecticides used in cockroach baits.

powder and contained inside a bait station, optimized for use in different situations (Benson and Zungoli, 1997). Compared to residual spray formulations, baits are relatively less toxic, odourless and applied in minute amounts in areas identified as cockroach harbourage sites or where cockroach activity has been seen (Silverman and Bieman, 1996; Sever *et al.*, 2007). They are also useful in sensitive environments such as zoos, child-care facilities, computer rooms, and food preparation outlets, where residual spray is not permissible (Reierson, 1995; Lee and Ng, 2009). Thus baits easily integrate with other pest management programmes. In addition, baiting does not harm beneficial insects in the environment and it allows oothecal parasitoids of cockroaches to be conserved (Suiter, 1997) and incorporated into cockroach management programmes through biological control releases (Hagenbuch *et al.*, 1989; Bell *et al.*, 1998; Suiter *et al.*, 1998; Tee *et al.*, 2011).

Cockroach Baiting in Integrated Pest Management

In cockroach management efforts, emphasis has been placed on using the least amount of insecticide possible (Miller and Meek, 2004; Sever *et al.*, 2007). Baiting cockroaches is an important approach used in integrated pest management (IPM) programmes. Williams *et al.* (2005) reported that in schools with low *Blattella germanica* infestation, both IPM and residual spray treatments effectively managed cockroach populations. However, monitoring of the cockroach-infested areas using glue traps and visual inspection showed that residual spray treatment of many areas was unnecessary. In the IPM programme, cockroach population monitoring allowed precise placement of bait in infested areas only (Williams *et al.*, 2005). This led to a 275% decrease in active ingredients used and 99.9% fewer insecticide residues in the IPM-treated schools compared to schools

under conventional treatment (Williams *et al.*, 2005). In public housing heavily infested with *B. germanica*, an IPM programme that included vacuuming, monitoring and baiting successfully reduced the cockroach population better than monthly baseboard and crack-and-crevice treatment with insecticide sprays and dusts (Miller and Meek, 2004). In this field evaluation, the IPM strategy reduced the cockroach population by 75% after 3 months and consistently maintained about 80% reduction for up to a year. In comparison, the baseboard and crack-and-crevice treatments did not reduce cockroach infestation and a sharp increase (about 220%) in cockroach trap catch occurred during the peak population seasons. The IPM approach also used less insecticide (1.1–5.7 g per apartment unit per month) than the baseboard and crack-and-crevice treatments (96.0–294.1 g) (Miller and Meek, 2004). Control of *B. germanica* using the fundamental elements of IPM (inspection-guided baiting) significantly reduced cockroach populations compared with conventional residual spray treatment in multiple-unit public housing (Sever *et al.*, 2007) and food preparation establishments (Lee, 2002). Effective control of *B. germanica* also contributed to lower concentrations of indoor cockroach allergens in IPM-treated apartments compared with untreated and conventional treated houses (Sever *et al.*, 2007).

The cost of IPM programmes is higher than that of conventional treatment during the initial stage of implementation. Once the IPM programme is established, however, its cost is similar to that of conventional treatments. For example, during the initial stage of cockroach control in public housing, Miller and Meek (2004) reported that IPM with vacuuming, monitoring traps and baiting cost more (US\$5.16–14.60 per apartment unit monthly) compared with conventional treatment (< \$2.75). This higher cost was due in part to the additional labour required for vacuuming and placement of traps and the higher product cost. After a while, however, the cost of the maintenance phase with IPM was reduced

to \$0.87–2.97, which was similar to the cost for conventional treatment (\$1.18–1.52). The reduction in IPM cost was due to lower quantities of insecticide and the fewer treatment trips needed after cockroach populations were suppressed.

For IPM programmes that consist only of monitoring-guided baiting, the cost is comparable to that of conventional residual treatment. Lee (2002) reported that the cost of cockroach IPM in Malaysia was \$0.08–0.30 per m², which was similar to that of residual treatment (\$0.17–0.30 per m²). In another study conducted in schools, the cost per service for IPM was \$8.57, which was comparable to the cost of residual treatment (\$7.49). Also, the timing of IPM-related tasks was flexible (Lee, 2002; Williams *et al.*, 2005). In contrast, residual treatment tasks could only be conducted after operation hours when businesses were closed (Lee, 2002) or at specific times when rooms in schools were vacant (Williams *et al.*, 2005). Re-treatment cost because of insecticide resistance could also result in additional costs (Lee, 2002), whereas baiting would overcome insecticide-resistant populations (Lee, 1998).

Cockroach Feeding Behaviour

For bait to be competitive when placed in the cockroach environment, it must contain nutrients that are limited and novel in the cockroach environment (Reiersen, 1995; Durier and Rivault, 2001) because food nutrition affects development and reproduction in cockroaches (Hamilton *et al.*, 1990; Cooper and Schal, 1992). Cockroaches are known to self-select nutrients to fill nutrient deficiencies when they are subjected to an imbalanced food source. For example, *Supella longipalpa* nymphs self-selected a 15.5:84.5 protein:carbohydrate diet when they were reared with two imbalanced diet cubes, one lacking protein and the other lacking carbohydrate. When they were given diets composed of 20:80 protein:carbohydrate, however, most of the nymphs did not grow into the adult stage

(Cohen *et al.*, 1987). The same study found the carbohydrate was taken mainly during the first week and then less was taken in each subsequent stadium, whereas protein was constantly ingested in a lower proportion throughout each life stage. If they were able to self-select nutrients, they grew normally by acquiring the nutrients needed at each nymphal development stage. In another study, Raubenheimer and Jones (2006) reported that, when subjected to nutrient deficiencies, *B. germanica* preferred to self-select an imbalanced food that compensated for the nutrient they were lacking to a balanced food. The ability to distinguish food of different nutritional value may be due to specific nutrient learning in cockroaches (Raubenheimer and Jones, 2006). Associative learning has been reported in *Periplaneta americana*, whereby they were able to associate food odours with proteins (Gadd and Raubenheimer, 2000). Therefore, several food types, mainly containing three macronutrients (carbohydrate, lipid and protein), are used in the matrices of cockroach baits.

In studies of the feeding patterns of pest cockroaches, Tsuji (1965, 1966) showed that several constituents from rice bran, some carbohydrates, and several substances from fatty acids and their related compounds were attractive and acted as a feeding stimulant to *P. americana*, *Periplaneta fuliginosa* and *B. germanica*. Sugars, including glucose, galactose, fructose, sucrose, maltose and L-arabinose, can stimulate feeding in cockroaches (Tsuji, 1965; Tsuji and Ono, 1969) and are used in cockroach baits (Gore and Schal, 2004; Bayer *et al.*, 2012). Peanut butter as an attractant is also used as a food base in most commercial baits (Appel, 1990; Nalyanya and Schal, 2001; Wang and Bennett, 2006). Recently, Karimifar *et al.* (2011) identified a volatile compound, 1-hexanol, from peanut butter that acts as a semiochemical that attracts *B. germanica*. Protein sources derived from poultry liver, silkworm pupae, and hydrogenated soy protein have been used in bait mixtures as feeding stimulants (Wolfe *et al.*, 1997). Other additives are

added to bait mixtures to prolong their lifespan. For example, p-nitrophenol inhibits the growth of mould on bait (Rust *et al.*, 1991) and polyols, such as sorbitol, mannitol and glycerol, act as humectants to stabilize and retain moisture content in the bait (Schal and Hamilton, 1990).

Cockroach baits are available in various formulation types. Gel and paste baits are the most common formulations with high moisture content; gels have a higher water content (39–80%) than pastes (14–30%) (Appel, 1992; Appel and Benson, 1995; Appel and Tanley, 2000; Appel, 2003). Gel and paste baits can be applied directly in cockroach-infested sites such as cracks, crevices and voids using a syringe or bait gun (Reiersen, 1995). Dry flowable powder baits also are formulated for use in cracks and crevices to reach deep spaces where the application of gel and paste is restricted (Dhang, 2011). Granular baits are designed for use outdoors against peridomestic pest cockroaches. They can be scattered into outdoor cockroach harbourage sites such as tree holes, firewood piles, heavy ground cover, landscape timbers and landscape mulch (Benson and Zungoli, 1997). Baits are also available in ready-to-use containerized stations (Reiersen, 1995).

Bait was previously considered to be ineffective in attracting cockroaches over distance (Reiersen, 1995). Laboratory olfactometer experiments have, however, demonstrated that baits were able to induce upwind movement of cockroaches. Traps baited with commercial baits placed 25–30 cm away from corners and edges of walls successfully caught cockroaches in field evaluations (Silverman and Bieman, 1996; Nalyanya *et al.*, 2001). Attractiveness alone, however, is not sufficient to prove whether bait is intrinsically effective. A substance can act as both an attractant and a feeding stimulant but a substance that is attractive may not necessarily stimulate feeding and vice versa (Tsuji, 1965). An attractant functions by attracting cockroaches toward bait, whereas a feeding stimulant induces and promotes increased consumption of the bait (Durier and Rivault, 2000a). The amount of bait consumed is an important

criterion for bait with secondary kill effects because it determines whether a lethal dose is being ingested and it influences the amount of toxicant available for horizontal transfer. Consumption of more bait means that poisoned individuals will defecate or regurgitate more materials containing toxicant and contain more toxicant within the cadaver (Silverman *et al.*, 1991; le Patourel, 2000; Buczkowski and Schal, 2001a). In a laboratory study, Durier and Rivault (2000a) documented that German cockroaches often chose Goliath gel bait (0.05% fipronil) in preference to Avert (0.05% abamectin), Maxforce (2.15% hydraethylnon), and Drax (33.3% boric acid) gels. Nevertheless, Maxforce and Avert gels stimulated more feeding than Goliath because they induced longer feeding duration on the bait.

Furthermore, certain attractants and feeding stimulants are species specific and mixtures of these substances may have synergistic effects (Tsuji, 1965, 1966; Wada-Katsumata *et al.*, 2013). Previously, Tsuji (1966) demonstrated that several fatty acids and related compounds were both attractive and a feeding stimulant to *P. americana*, *P. fuliginosa* and *B. germanica*, whereas certain compounds acted as species-specific attractants or feeding stimulants. In a study (Wada-Katsumata *et al.*, 2013), a mixture of glucose and fructose stimulated a higher feeding rate and a greater response of sugar-gustatory receptor neurons in wild-type *B. germanica* than either fructose or glucose alone.

The nature of bait formulation also affects cockroach mortality. Studies have shown that indoxacarb and abamectin gel baits resulted in faster mortality (lower LT_{50}) of German cockroaches than powder formulations with a similar concentration of the active ingredient (Buczkowski *et al.*, 2001; Appel, 2003). Buczkowski *et al.* (2001) attributed this difference to the secondary kill effect of the bait. They found that hydramethylnon gel bait caused significantly more secondary mortality in adult German cockroaches than the solid block of hydramethylnon in a bait station. In general, gel baits are superior to solid ones for secondary transfer of toxicant

because gels are efficiently consumed and excreted from the insect body and therefore more readily available for horizontal transmission (Buczkowski *et al.*, 2001). Durier and Rivault (2002a) reported that the efficacy of bait could also be attributed to the design of the bait station. They demonstrated that German cockroaches were attracted by a novel object introduced into their foraging home range. When the complexity of the introduced object increased, such as a bait station with several entrances, German cockroaches spent more time exploring the exterior and inner parts and were even more attracted to it if it contained food. The attractiveness of the bait station enhanced its efficacy and was especially important for bait containing toxicant with contact toxicity because it retained the cockroaches for a longer period of time, allowing more toxicant to be picked up (Durier and Rivault, 2002a).

Cockroach Foraging Behaviour

An urban environment composed of complex manmade structures and resources invites cockroaches to find harbourages and establish an infestation. At nightfall, cockroaches begin to leave their daytime harbourage sites to forage for resources and seek mates, and their activities normally peak approximately 2–4 h after sunset (Mellanby, 1940; Appel and Rust, 1986).

Importance of path integration

Studies of the foraging strategies of cockroaches using *B. germanica* as a model revealed that cockroaches are aware of the spatial distribution of resources in their environment, and they exhibit efficient foraging trips between resources and harbourage sites (Demark *et al.*, 1993; Durier and Rivault, 2001, 2003a). Although cockroaches live in an aggregate, they forage in their environment individually based on their own knowledge of their surrounding environment; they do this by using path integration and previously experienced

odours and learned visual cues from past excursions (Dabouineau and Rivault, 1995; Durier and Rivault, 1999, 2000b, 2001; Rivault and Durier, 2004). Path integration is a navigation system that a cockroach actively updates with information on the direction and distance of a new-found location from the harbourage site (Durier and Rivault, 1999; Collett and Graham, 2004). The memory of a rewarding food source in a specific location can be enhanced by olfactory and visual cues, such as odours emitted from the food and visual landmarks located around the food source (Durier and Rivault, 2000b, 2001, 2002b).

In a familiar environment, when stimuli from food odours and learned visual cues are absent, German cockroaches explore in a random pattern that covers all accessible surfaces in the surrounding environment (Durier and Rivault, 2003a). Upon finding a rewarding food source, they memorize its position (direction and distance) and the landmarks (visual cues) associated with the location in relation to the harbourage. In subsequent foraging trips, cockroaches orient themselves in a more or less direct path toward the learned location. This strategy improves foraging efficiency and guides cockroaches nearer to the location where the opportunity of finding food is high (Durier and Rivault, 2003a).

Depending on the goal of the foraging activity, cockroaches change the order of importance of the environmental information (e.g. olfactory and visual cues) retrieved during the foraging trip (Durier and Rivault, 2000b; Rivault and Durier, 2004). In a laboratory test arena equipped with landmarks associated with a food source, German cockroaches oriented towards the landmarks by relying on visual cues when food was not present (Durier and Rivault, 2000b, 2001). When a visual cue was placed at one end of the test arena and a food source placed at the opposite end, however, cockroaches gave more weight to olfactory cues and moved towards the food source (Durier and Rivault, 2000b). Decision making on the basis of the reliability of the information may be involved, such as the presence of a food

odour indicating the presence of food source on the food foraging trip (Durier and Rivault, 2000b). In contrast, visual cues overrode olfactory cues (aggregation pheromone) in a study of German cockroaches returning to the harbourage. In this situation, visual cues were perceived from a distance and acted as reliable information that helped cockroaches reach their harbourage (Rivault and Durier, 2004).

Influence of age and developmental stages

Cockroaches at different life stages and ages exhibit different foraging efficiencies. In a laboratory test, foraging efficiency of second instar nymphs did not improve over the entire nymphal period. However, fifth instar nymphs showed improved foraging efficiency by commuting over shorter and more direct paths between resources (Demark *et al.*, 1993). In a field study conducted in a swimming pool facility infested by German cockroaches, Cloarec and Rivault (1991) found that large nymphs and adults were the first to arrive at a food source, and they wasted no time seeking other foods once the first food source was depleted. Small nymphs arrived late at the food sources and were late to leave it. Upon hatching, nymphs have the ability to use path integration but experience and learning gained from previous excursions and developmental changes (e.g. maturation of organs, body size increase) between stadia contribute to the temporal improvement of foraging ability in cockroaches (Dabouineau and Rivault, 1995).

Behavioural implications for bait placement

Cockroaches establish complex networks connecting food, water and harbourage based on their knowledge of the spatial distribution of resources. How bait as a novel food is perceived by cockroaches in their environment has been studied in terms of novelty, position, distance from the

harbourage and competition with other food items.

Durier and Rivault (2001, 2002b) reported cockroaches foraging preferentially on a gel bait over a familiar food source when it was placed in a new location and also when the familiar food source was presented at the same distance (60 cm) away from the harbourage at a landmark cockroaches used to associate with the familiar food. The novelty of the gel bait became less preferable to cockroaches, however, when: (i) the placement of the two food types were interchanged, i.e. gel bait was placed in the known feeding area and the familiar food source was placed at the new location; and (ii) the familiar food source was located nearer to the harbourage than the gel bait (30 cm versus 60 cm). These experiments showed that cockroaches differentially evaluate the food presented in their home in relation to its spatial distribution. Compensation for nutrient deficiencies and maintenance of a balanced diet are some of the reasons why cockroaches foraged preferentially for novel food in situations in which they were given a common food for a period of time (Durier and Rivault, 2001). However, the benefit of the novel food became less obvious to cockroaches when it was situated further away from the harbourage than the familiar food source. In a field study at a swimming pool facility, food sources nearest to the harbourage of German cockroaches were first consumed (Rivault and Cloarec, 1991). Nevertheless, the presence of a novel food in a known feeding site in which cockroaches used to find their familiar food resulted in a discrepancy between stored information and the ongoing situation. Cockroaches were initially attracted to the novel food odour placed in a known feeding site but the visual cues they perceived upon approaching the familiar landmark contradicted their previous feeding experience. They identified this local modification as a potential threat and changed their behaviour to explore and forage for the safer and familiar food source that matched their stored information (Durier and Rivault, 2001, 2002b). From these experiments,

Durier and Rivault (2002b) suggested that bait, as a novel food for cockroaches, should be placed in areas nearer to the harbourage sites.

Studies have also indicated that bait applied in many small drops or as thin smears at multiple locations provided greater control efficacy than use of a few large drops in fewer locations (Milio *et al.*, 1986; Appel and Benson, 1995; Durier and Rivault, 2003b). This could be because aggression behaviour among cockroaches interrupts feeding and reduces the number of cockroaches that can access the bait (Durier and Rivault, 2003b). The efficacy of bait also is greater if it is applied at cockroach harbourage sites identified through placement of traps or visual inspection rather than at predefined locations because infestation areas vary from house to house (Silverman and Bieman, 1996). In addition, a laboratory study (Durier and Rivault, 2003a) indicated that cockroaches were not always edge followers in their familiar environment. Baits placed near edges as well as in the centre of an arena were equally located and preferred by cockroaches. Silverman and Bieman (1996) reported a similar finding in their field study because baits placed at corners and 25 cm away from corners were equally fed upon by cockroaches.

Horizontal Transfer of Bait Toxicant

Traditionally, horizontal transfer of insecticides among cockroaches was not considered to be a trait of cockroach baits because baits have been constrained by insecticide resistance (both physiological and behavioural resistance) and lack of non-repellent active ingredients (Buczowski *et al.*, 2001). However, with advancements in bait technology and a better understanding of cockroach biology (especially their social interactions) (Rust *et al.*, 1995; Lihoreau *et al.*, 2012), horizontal transfer of bait toxicant is well documented and now it is one of the benefits of using bait to manage cockroaches (Kopanic and Schal, 1999; Buczowski *et al.*, 2001).

Horizontal transfer of toxicants relies on intoxicated cockroaches contaminating their aggregation site and the surrounding environment with their bait-contaminated appendages, excretion (vomitus and faeces) and dead bodies (Fig. 5.2). Additional healthy individuals are affected through consumption of, or lethal contact with, these contaminated materials (Durier and Rivault, 2000c; Buczkowski *et al.*, 2001). Some of the secondary effects may also help transfer of toxicant to sedentary life stages (young nymphs and gravid females) that do not venture far for their resources. The feasibility of horizontal transmission of bait toxicants under field conditions was documented in an apartment infested with *B. germanica* using bait containing hydramethylnon (Silverman and Bieman, 1996). Secondary killing property of baits is therefore considered an important criterion for the evaluation of baits (Jordan *et al.*, 2013).

Several mechanisms of horizontal transfer of toxicant have been documented and they are classified on the basis of the route of entry of the toxicant into healthy cockroaches as described below.

Coprophagy

In cockroaches, coprophagy occurs to transfer hindgut symbionts, nutrients, and

microbes and their byproducts from donors to recipients via ingestion of excreted faecal materials (Bell *et al.*, 2007). Coprophagy occurs in all life stages but is most prominent in early instar nymphs (Silverman *et al.*, 1991; Kopanic *et al.*, 2001). Kopanic *et al.* (2001) found that 90% of newly hatched German cockroach nymphs could survive for up to 10 days and maintain more than 70% survivorship for more than 14 days by consuming adult faeces when food sources were not available. In comparison, nymphs without adult faeces available died 60-fold faster than those given adult faeces. Interestingly, 54.5% of first instar nymphs were able to successfully moult into second instars when female faeces were provided as a food source, whereas only 8% could do so when fed with male faeces. In contrast, second instar nymphs provided with adult faeces survived only slightly longer than those without access to faeces. These findings suggest that coprophagy is stage specific and adaptive. Cockroaches are known to defecate on their harbourage site (Stejskal, 1997), which acts as an aggregation pheromone and provides odour cues for cockroaches during their homing trip (Rivault and Durier, 2004). For newly hatched nymphs, coprophagy reduces the risk of long-range food searching when food is not available in the immediate surroundings of the harbourage. At the same time,

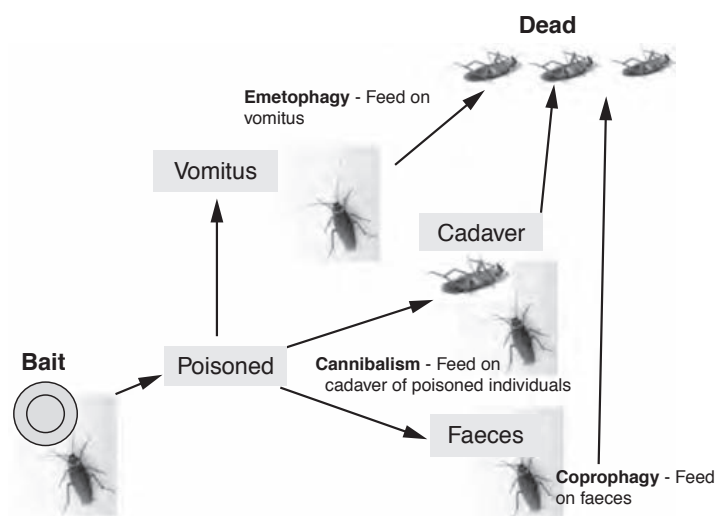


Fig. 5.2. Mechanisms of horizontal transmission (coprophagy, emetophagy and cannibalism) of insecticide baits in cockroaches (from Lee and Ng, 2009).

this behaviour allows them to gain nutrients needed for growth into second instar nymphs (Kopanic *et al.*, 2001).

For a toxicant to be transferred horizontally among cockroaches through coprophagy, it must be stable during passage through the digestive tract and slow acting enough to allow its excretion before insect death (Kopanic and Schal, 1999). By tracing dyed rat chow within the digestive tract of German cockroaches, Kopanic and Schal (1999) determined that at least 12 h was required for insecticide baits to be defecated; however, this time interval could be shorter for more liquid formulations such as gel and paste baits. Among the active ingredients used in cockroach baits, hydramethylnon has been shown to transfer horizontally via coprophagy in several cockroach species, including *B. germanica*, *P. americana* and *P. fuliginosa* (Silverman *et al.*, 1991; Shimamura *et al.*, 1994; Kopanic and Schal, 1999). Silverman *et al.* (1991) confirmed that faecal materials obtained from the abdomen of hydramethylnon-fed German cockroaches were responsible for the horizontal transfer, whereas residues secreted from the head were not toxic and contact with hydramethylnon bait or faeces was not lethal. Based on the amount of radiolabelled hydramethylnon bait ingested, Silverman *et al.* (1991) found that 22.3–44.7% of the ingested hydramethylnon was excreted in faeces for all life stages of the German cockroach and 51% of this was the unmetabolized parent compound of hydramethylnon.

Kopanic and Schal (1997, 1999) demonstrated that adult cockroaches were responsible for the translocation of insecticide bait via coprophagy to the sedentary early nymphs. In their experiment, when food was located near the harbourage and hydramethylnon (2.15%) bait was placed 124–150 cm away from the harbourage, nymphs had low mortality rates when adult cockroaches were excluded from access to the bait. When adults had access to the bait and nymphs did not, however, high nymphal mortality was recorded after 3 days.

The magnitude of coprophagy in young nymphs is influenced by the availability of

food and its distance from the harbourage (Kopanic and Schal, 1997, 1999) because German cockroach nymphs were shown to engage in more coprophagous behaviour when food was placed farther away from the harbourage. Because the first instar nymphs were less efficient foragers and tended to stay close to the harbourage, their intake of adult faeces was consistent between experiments conducted in a laboratory test arena (120 × 30 cm) and in a vacant apartment room (240 × 360 cm). However, second instar nymphs were found to be more efficient foragers than the first instars (Dabouineau and Rivault, 1995). The difference in coprophagous behaviour between first and second instar nymphs may be due to their different foraging abilities and body reserves. During a 24-h starvation period, first instar nymphs ate three times more faeces by mass than regular food. In contrast, second instar nymphs with two times more body mass and three times greater food consumption ingested lower amounts of faeces than first instar nymphs (Kopanic and Schal, 1999). As the starvation period increased from 24 to 48 h, second instar nymphs resorted to coprophagy and ate as many faeces as the first instar nymphs (Kopanic and Schal, 1999). These findings show that coprophagy is an adaptive behaviour. Although faeces provide minimal nutrients for newly hatched nymphs, they are poor foragers and faeces consumption allows them to sustain themselves prior to moulting into second instar nymphs when food is not within the vicinity of their harbourage site. As they grow into second instar nymphs, improved foraging ability allows them to find a more balanced diet to sustain development.

For horizontal transfer of insecticide to have an impact on the population of cockroaches, cockroaches that ingest toxic baits must return to their harbourage to distribute their toxic-laden faeces to other healthy conspecifics. By analysing the distribution of carcasses and faeces in a test arena (117 × 15 × 15 cm) after cockroaches were baited with hydramethylnon, Buczkowski *et al.* (2001) reported that 84.2% of poisoned carcasses were scattered

within the harbourage and faeces were concentrated within and around the harbourage. This distribution pattern of poisoned carcasses and faeces close to harbourage shows that the insecticide was transferred to other conspecifics.

Emetophagy

Buczowski and Schal (2001a) first described emetophagy, or the ingestion of vomitus, as a possible mechanism for the horizontal transfer of fipronil bait in cockroaches. Fipronil is a fast-acting neurotoxic insecticide that contains chemicals that induce vomiting. Emetophagy may also occur when other fast-acting neurotoxic insecticides that are emetogenic are used (Buczowski and Schal, 2001a).

Regurgitation in German cockroaches coincides with the onset of paralytic symptoms 4 h after ingestion of fipronil bait (Buczowski and Schal, 2001a, 2001b). Buczowski and Schal (2001a, 2001b) recovered 4.5% of the ingested fipronil from the outer surface of adult cockroaches. Of this, > 74% was regurgitated from the oral region during the first 12 h. The remaining fipronil was excreted from the anal region for up to 48 h. Although only a low amount of ingested fipronil was regurgitated, the vomitus appeared to be very attractive and toxic. A fipronil-intoxicated female was as attractive as the standard laboratory diet (rat chow) when first instar German cockroach nymphs were given the choice. Most of the contact made by the nymphs with the fipronil-intoxicated females was with the mouth part (77%) and the remainder was with the anal region (23%). In this experiment, nymph mortality was < 58% within 12 h. When food was not available, the nymphs contacted the fipronil-intoxicated females 2.7 times more frequently and consequently > 88% mortality occurred within 12 h.

The toxicity of the fipronil-laced vomitus excreted from intoxicated cockroaches declines with time (Buczowski and Schal, 2001b). The authors also found that excreted fipronil was most toxic when healthy

B. germanica were exposed continuously to adults that had just fed on fipronil bait and their freshly deposited residues. In this exposure condition, the mortalities of healthy adults (males and females) and nymphs (first and second instars) were 48–85% and 100%, respectively. The mortality of adults declined to 15–39% and < 19% when they were exposed to both the fipronil-intoxicated adults and their deposited residues that had been aged for 6 and 24 h, respectively. For nymphs, the mortality remained high (> 96%) after 6 h and declined to 60–89% after 24 h of ageing. When fipronil-intoxicated adults were removed, the mortality of healthy adults exposed to fipronil-containing residues that had been aged for 6–24 h was only < 1.7%, whereas nymphs still exhibited 33–45% mortality.

Hyperactivity and convulsion, which are typical symptoms of neurotoxic insecticides, impair the ability of intoxicated cockroaches to return to their harbourage after bait ingestion (Buczowski *et al.*, 2001). In a test arena used to examine the distribution of fipronil-intoxicated male German cockroaches, 27.5% were found dying inside the harbourage and the remaining specimens were scattered around the test arena at an average distance of 53.7 cm from the harbourage (Buczowski *et al.*, 2001). Earlier Ross (1993) reported a similar distribution pattern for German cockroaches fed on abamectin gel bait. This type of distribution of dying cockroaches contrasts with slow-acting insecticides, in which a more concentrated distribution of intoxicated cockroaches and faeces was found within the harbourage (Buczowski *et al.*, 2001). Buczowski and Schal (2001a) reported that fipronil-intoxicated cockroaches were as attractive as the common food sources and toxic to young nymphs. Also, Lihoreau and Rivault (2011) reported that odours emitted from recently fed cockroaches attracted other conspecifics over a short distance, presumably because they acted as short-range volatile cues to promote the formation of feeding aggregates. Therefore, although the number of fipronil-intoxicated cockroaches in the harbourage

is relatively low, their attractiveness may encourage the transfer of bait toxicants to other members resting within the harbourage.

Cannibalism

Cannibalism occurs in cockroaches during laboratory rearing and during experimental testing as observed by Gahlhoff *et al.* (1999), Durier and Rivault (2000c), le Patourel (2000), Tabaru and Watabe (2003) and Tabaru *et al.* (2003). The degree of cannibalism depends on the quantity and quality of food and also the population density of the cockroach (Bell *et al.*, 2007), and is most prominent when cockroaches are deprived of food (Appel *et al.*, 2008). It is often directed toward individuals that are newly hatched or moulted, injured or weak (Cornwell, 1968). Cannibalism may also be an adaptive behaviour because it allows adjustment of population density, concentrates the resources into groups that have higher potential of survivorship and acts as a sanitary practice that prevents the spreading of disease pathogens (Ross and Mullins, 1995; Bell *et al.*, 2007). A relatively large amount of ingested bait tends to remain within the dead body (Silverman *et al.*, 1991; Buczkowski and Schal, 2001b). Therefore, cannibalism in cockroaches is one mechanism by which bait toxicants are disseminated to healthy conspecifics and its effect is influenced by food availability, life stage of the bait-fed donor and type of insecticide used (Appel *et al.*, 2008; Wang *et al.*, 2008).

In the presence of food, Appel *et al.* (2008) reported that *B. germanica* males preferred dog food to cadavers of nymphs and adult males. Thus, no mortality of *B. germanica* males occurred in treatments containing cadavers of bait-fed conspecifics. Cannibalism was most prominent when males were denied access to food during a test period of 14 days. This indicates that cockroaches may rely on body reserves during periods of starvation and opt for cannibalism when food is not available. Tabaru and Watabe (2003) reported that

43% of adult *P. fuliginosa* were cannibalized when they were reared with only faeces and water.

Differences in the mode of action of active ingredients in various baits also explain the differences in translocation of baits through cannibalism. Durier and Rivault (2000c) found that cannibalism of cadavers intoxicated with fipronil bait by German cockroaches was low (3.55%), whereas it was higher (12.1%) in the hydramethylnon bait treatment. Nevertheless, the resultant mortality was higher in the fipronil (47.3%) treatment than in the hydramethylnon (29.7%) treatment. This suggests that fipronil, which functions through ingestion and contact, may work well even with a low cannibalism rate, whereas hydramethylnon is less efficient because it is less toxic by contact than by ingestion. In another study, le Patourel (2000) demonstrated that cadavers of *Blatta orientalis* intoxicated with 0.05% fipronil bait still managed to result in $\geq 64\%$ secondary mortality via cannibalism among adult females.

Factors Affecting Bait Performance in the Field

Sanitation of the treatment area

Cockroaches find suitable harbourage close to food and water (Ross *et al.*, 1984). Several studies reported that poor sanitation is positively correlated to cockroach infestation level (Wright, 1979; Schal, 1988), whereas a few others contradicted (Gold, 1995; Lee and Lee, 2000a). In a field evaluation, Lee and Lee (2000b) found that cockroach bait reduced the cockroach population faster in houses with good sanitation compared to those with poor sanitation. Moreover, the reduction in well-sanitized houses could be sustained for up to 12 weeks, whereas it was only 6 weeks for those with poor sanitation. In low-income houses and apartments, higher numbers of baits were also required to reduce the cockroach population compared to residences with good sanitation (Lee and

Yonker, 2003). Sanitation alone may not explain the complexity of cockroach infestation because many other factors and their interactions are involved, including the density of residents living inside the premises, building effects and role of outdoor reservoir populations (Rivault and Cloarec, 1995; Robinson, 2002). Nevertheless, the effects of food and water deprivation on cockroach biology support the importance of sanitation for cockroach management using toxic baits (Lee and Lee, 2000a).

Proper sanitation alone is not sufficient to reduce cockroach population size because many pest cockroaches are able to withstand food and water deprivation for a period of time (Willis and Lewis, 1957). However, Lee and Heng (2000) reported that cockroaches are more susceptible to insecticide treatment under starvation stress. Removal of food and water sources directly reduces competition between bait and other food sources, induces stress among cockroaches for resource foraging (Ballard *et al.*, 1984; Barcay and Bennett, 1991) and has a greater impact on cockroach populations when toxic bait is applied (Lee and Soo, 2002a). Durier and Rivault (2001) demonstrated that the attractiveness of cockroach bait is reduced if there are other food sources present nearer to their harbourage. In the field, Rivault and Cloarec (1991) found that German cockroaches ate the food sources they first encountered and foraged further away once the food source was depleted. Consequently, cockroaches that are fully fed and satiated may not respond well to bait. Cockroaches react to food and water deprivation by increasing their time spent in movement, foraging distance and speed (Barcay and Bennett, 1991). This is useful for baiting of cockroaches because it eventually leads to a higher chance of bait being encountered and consumed in a larger amount. Under food and water deprivation, cockroaches readily eat more bait as their body reserves start to decrease (Smith and Appel, 1996). A moisture source is important for the survival of cockroaches (Appel *et al.*, 1983; Appel, 1995). This characteristic is particularly favourable for baits with a high moisture content and may explain why

gel formulations are more preferable and have faster killing effects than other formulations in laboratory and field studies (Appel and Benson, 1995; Appel and Tanley, 2000; Buczkowski *et al.*, 2001; Appel, 2003).

Ageing and contamination of bait

When baits are applied, they are subjected to interaction with the ambient environmental conditions. The efficacy of baits depends on the ability to prolong their attractiveness over time. Feeding activity of cockroaches varies at each interval of their developmental stage. For example, *B. germanica* and *P. americana* nymphs ingest more food during the initial stage of each stadium and gradually reduce their intake to a low level until next moulting (Richter and Barwolf, 1994; Valles *et al.*, 1996) and females feed little for a few days before ovulation and only resume feeding after oothecae are dropped (Bell *et al.*, 2007).

After application, moist baits are susceptible to desiccation, and the rate of desiccation depends on the formulation itself and on conditions such as temperature, humidity, air currents and the amount of surface area exposed to desiccation (Appel and Benson, 1995). The amount of water loss for gel baits was reported to be around 80% after 3–4 days of desiccation (Appel, 1992; Appel and Tanley, 2000; Appel, 2003). Appel and Benson (1995) found that the final texture of dried bait is more important than the amount of water loss in determining its attractiveness and palatability. They demonstrated that dried baits, which were hard and not palatable to German cockroaches, resulted in faster mortality after they were ground and filtered into fine particles similar in size to a powder bait formulation. Although most moist baits eventually become solid, hard, and unpalatable to cockroaches, there are formulations that can remain soft, sticky and palatable to cockroaches (Appel and Benson, 1995; Appel and Tanley, 2000; Appel, 2003). Studies of *B. germanica* showed that the attractiveness and palatability of 2.15% hydramethylnon gel bait and 0.25%

indoxacarb gel bait after 7 days of ageing under room conditions remained comparable to those of freshly deposited baits, whereas this was not true for aged 0.05% abamectin powder bait (Appel, 2003; Nalyanya *et al.*, 2001). Interestingly, toxicants from cockroach bait can remain within a cadaver for a long time. Cadavers of oriental cockroaches that had fed on 0.05% fipronil gel bait remained toxic after storage at 33–76% relative humidity and 28°C for a maximum duration of 7 weeks. Exposure of healthy adult conspecifics to these fipronil-poisoned cadavers resulted in 64–100% mortality (le Patourel, 2000).

Besides interaction with the ambient environment, repellent substances may contaminate cockroach baits or the areas where baits are to be applied. Appel (2004) found that placement of baits of all formulation types (gel, dust, dry and bait station) on a surface contaminated with compounds such as repellent insecticides, cleaning agents, cooking oils and solvents reduced the consumption of bait by German cockroaches and increased the kill time. In addition, the surface of dry bait contaminated with repellents had lower bait consumption and toxicity, whereas direct contamination did not affect gel baits (and in some cases even increased gel bait toxicity). Appel (2004) suggested that contaminants may have been absorbed by the gel bait and only a negligible amount was available at the surface of the bait. Exposure of cockroaches to repellents and sublethal doses of insecticides disrupts activities such as induced dispersion, feeding inhibition and avoidance behaviour (Bret and Ross, 1985; Haynes, 1988; Barcay *et al.*, 1990), which eventually reduces their ability to forage efficiently.

Resistance to insecticide baits

Resistance to insecticides is a major concern in the management of *B. germanica*. Since the introduction of newer insecticides used in cockroach bait, low to moderate levels of physiological resistance of *B. germanica* to some of these insecticides has been detected

(Table 5.1). However, many of the evaluations of physiological resistance among field-collected *B. germanica* were conducted before new insecticide groups were used in the field (Holbrook *et al.*, 2003; Chai and Lee, 2010). Therefore, there is a possibility that the selection pressure from previously used insecticides could have conferred cross-resistance toward the newer insecticides used in cockroach baits (Holbrook *et al.*, 2003; Kristensen *et al.*, 2005; Gondhalekar and Scharf, 2012). For example, based on a topical LC₅₀ bioassay, a field strain (Cr-Al) from North Carolina that had no history of fipronil treatment showed 17-fold greater resistance to fipronil compared with that of a laboratory susceptible strain (Holbrook *et al.*, 2003). At present, there are no reports of control failure of bait products containing these active ingredients against *B. germanica* due to physiological insecticide resistance. Bait formulated as palatable food mixture is one reason why physiological insecticide resistance does not lead to control failure among these newer insecticides. When cockroaches feed on a highly palatable bait, the toxicant is normally ingested at higher doses than that required to cause a lethal response (Holbrook *et al.*, 2003; Gondhalekar *et al.*, 2011; Gondhalekar and Scharf, 2012). It was noted that *B. germanica* consumed 150 to > 1300 times and 218–441 times the LD₅₀ of fipronil and indoxacarb, respectively, after 24 h of exposure to the gel baits (Bayer *et al.*, 2012). In another study, a field strain of *B. germanica* was 36-fold more resistant to fipronil compared to a laboratory susceptible strain when the insecticide was applied topically; two- to three-fold more resistance was achieved when they were fed 0.01% fipronil bait (Gondhalekar *et al.*, 2011). Consumption of active ingredients in such a great amount eventually kills all of the cockroaches and development of resistance may not occur, or may be delayed in cockroach populations (Holbrook *et al.*, 2003; Gondhalekar and Scharf, 2012).

Nevertheless, the frequency of a resistance gene within a *B. germanica* population may increase if a portion of the cockroach population survives and breeds under

Table 5.1. Insecticide resistance profiles of field-collected strains of *B. germanica* against several insecticides commonly used in cockroach baits based on LD₅₀ values obtained from topical bioassays.

Active ingredient (class of insecticide)	Resistance ratio based on LD ₅₀	Location	Reference
Abamectin (avermectin)	2.5	Ohio, USA	Wang <i>et al.</i> , 2004
	6.8	Indiana, USA	Wang <i>et al.</i> , 2004
Imidacloprid (neonicotinoid)	10	Alabama, USA	Wei <i>et al.</i> , 2001
	1.8–3.8	Singapore	Chai and Lee, 2010
	7.6	Florida, USA	Gondhalekar <i>et al.</i> , 2011
Indoxacarb (oxadiazine)	1.9–5.3	Singapore	Chai and Lee, 2010
	5.9	Florida, USA	Gondhalekar <i>et al.</i> , 2011
	2.3	Alabama, USA	Wei <i>et al.</i> , 2001
Fipronil (phenylpyrazole)	8.7	Ohio, USA	Wang <i>et al.</i> , 2004
	9.3	Indiana, USA	Wang <i>et al.</i> , 2004
	2.0–15.0	Denmark	Kristensen <i>et al.</i> , 2005
	2.0–10.0	Singapore	Chai and Lee, 2010
	37.9	Florida, USA	Gondhalekar <i>et al.</i> , 2011
	2.1–44.8	Indonesia	Rahayu <i>et al.</i> , 2012

continuous sublethal exposure to the insecticides used in baits. Holbrook *et al.* (2003) described conditions in which sublethal exposure may occur, such as through ingestion of lower doses of insecticide deposited within oral and anal excretions produced by bait-fed cockroaches and exposure to lower doses of insecticides used in ant and termite management programmes. In addition, *B. germanica* may ingest sublethal doses of an active ingredient in bait when feeding is interrupted because of aggressive behaviour among individuals within a feeding aggregate (Durier and Rivault, 2003b) or when they are partially satiated after feeding on alternative food sources before consumption of bait (Reiersen, 1995). In a laboratory study, field-collected *B. germanica* strains subjected to bait selection (0.05% fipronil and 0.6% indoxacarb baits) for five generations exhibited a steady increase of physiological resistance levels (Ang *et al.*, 2013). Due to palatability of baits, these F₅ generation cockroaches with increased physiological resistance exhibited only low levels of resistance to gel baits and 100% mortality was achieved by bait treatment within 14 days. This study demonstrated that resistance level can be enhanced under baiting conditions, but whether the selection pressure will result in control failure in the field remains to be seen. If increasingly

higher doses of toxicant are required for toxic baits to be effective, high-dose management strategies may only provide short-term solutions (Gondhalekar and Scharf, 2012). Alternatively, rotation of toxic baits with active ingredients with different modes of action could be a feasible way to reduce the potential risk of insecticide resistance development (Gondhalekar *et al.*, 2013).

Bait aversion behaviour

Another major challenge to overcome in cockroach baiting is the phenomenon of glucose and bait aversion in German cockroaches. Silverman and Bieman (1993) reported control failure for hydramethylnon bait containing glucose in a study conducted in Florida. They found that avoidance of the glucose used in the bait formulation was responsible for this phenomenon. Glucose aversion is an inherited trait rather than a learned trait (Silverman and Bieman, 1993; Wang *et al.*, 2006). Subsequently, glucose aversion was found among field strains of *B. germanica* from other locations in the USA and South Korea (Silverman and Ross, 1994). In Malaysia, screening of the 41 strains of *B. germanica* collected from the field revealed that 12% of the strains exhibited a negative response to glucose

(Lee and Soo, 2002b). However, substitution of glucose with fructose increased bait efficacy against glucose-averse *B. germanica* (Silverman and Bieman, 1993; Silverman and Ross, 1994). There are associative costs in glucose-averse *B. germanica*, in that they have smaller and fewer numbers of eggs in oothecae and, if fed diets supplemented with glucose, they have lower population growth rates than non-averse cockroaches. This fitness cost gives them an advantage, however, in environments implemented with cockroach baiting (Silverman, 1995; Wang *et al.*, 2004).

Wada-Katsumata *et al.* (2013) described the chemosensory mechanism responsible for glucose aversion in *B. germanica*. The authors reported that glucose stimulated responses on sugar-gustatory receptor neurons in both averse and non-averse cockroaches. However, glucose also induced responses on bitter-gustatory neurons in glucose-averse cockroaches, and this overrode the responses stimulated by sugar-gustatory neurons. They hypothesized that one or more mutations may have resulted in changes in the structure of gustatory receptors on bitter-gustatory neurons to accept glucose.

A decade later, Wang *et al.* (2004) reported that German cockroaches exhibited aversion to multiple sugar compounds (glucose, fructose, sucrose and maltose) in some field cockroach populations. This discovery, however, was disputed by Silverman (2005) on the basis that it is unlikely that independent mutations for each sugar could all occur at the same time. Lee (2007) speculated that bait aversion in the German cockroach may not be due to aversion to the sugar compound but instead

to aversion to one (or more) components used in the bait formulation. Bait manufacturers have since produced gel bait formulations that can overcome bait-averse German cockroaches.

Conclusion

Improvements in bait technology and the availability of novel toxicants suitable for incorporation into baits have contributed to the efficacy of cockroach baits, which in turn has led to the popularity and great acceptance of cockroach baiting. Nevertheless, the potential of baits can only be maximized when information about the biology and behaviour of pest cockroaches is used in the baiting programme. Foraging strategies of cockroaches greatly influence where bait should be placed in the cockroach environment. Placement of bait that disrupts the familiar environment of cockroaches may result in lower acceptance of bait. In addition, the nutritional requirements and foraging efficiency of each life stage require that bait be long lasting and placed as close as possible to all the identified harbourage sites. The importance of sanitation cannot be neglected because it can create an environment that promotes cockroach exploratory behaviour, which increases the likelihood of the cockroaches coming in contact with the bait and enhances the effects of horizontal transmission. Lastly, the strong adaptive behaviour of cockroaches, as demonstrated by the incidence of bait aversion, and the proliferative nature of *B. germanica* will continue to make cockroach management using toxic bait challenging.

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