

METAPOPULATION CONCEPT and the PERSISTENCE of URBAN PESTS in BUILDINGS

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Abstract The dynamics of colonisation, persistence, and extinction of *Blattella germanica* and *Plodia interpunctella* populations was studied in a hospital kitchen and a food plant. Metapopulations of both pests persisted during the period of the study, despite the presence of regular monitoring and pest control. There was at least one extinction in each local population. Local pest populations did not intercorrelate in both aseasonal *B. germanica*, with 80% of the cases, or semi-seasonal *P. interpunctella*, with 83% of the cases. Density-dependent allocation of pesticide treatment created partial refuges for pests. Uneven distribution of pesticides and pests, and asynchrony of local populations apparently facilitated the survival of pest metapopulations. Results are consistent with the implication of metapopulation theory that contradicts the traditional urban IPM concept that pest eradication requires pesticide treatment to currently infested sites but also all suitable refuges that can be recolonized. As an alternative to the physiological hypothesis a metapopulation explanation of the historical success of blatticide baits is presented.

Key Words *Blattella germanica*, *Plodia interpunctella*, local populations asynchrony, human aggregative response, pesticides.

INTRODUCTION

Modern residual pesticides exhibit excellent toxicity to pests. Abd-Elghafar et al. (1990) found that only 0.5 µg of the pyrethroid cyfluthrin is sufficient to kill an individual of *Blattella germanica*. In spite of these materials, many urban pests persist. Increasing pesticide resistance is not the only cause of this failure, since low- or non-resistant pest populations can be observed to persist in buildings under a regular pesticide regime. Gould (1991), Hawkins et al. (1993), Ebert and Hall (1999), and others point out that the different spatial patterns of pests and pesticides, or bioagents, may influence pest control efficiency. Despite increasing evidence of the importance of spatial processes in applied ecology, there is continued effort to establish an IPM decision-making process based on single-number critical thresholds (Pinto, 2000).

Pesticides are evaluated according to their effects on the average parameters of pest populations. Current pest control philosophy is primarily based on the concept of one unit (location), one pest population, one reaction to treatment (OOO). This concept assumes that effects of intra-unit fragmentation of pest populations are negligible (Reid and Appel, 1994; Zeman, 1993; Larter and Chadwick, 1983). However, the urban environment is heterogenous and fragmented, and pest infested sites (patches) may not be accessible to pesticide treatment.

Human behaviour in pesticide application, particularly the ability to identify harborage, and the time allocated to pesticide spraying (Stejskal and Aulický, 2000), plays a role in the control of urban pests. This aspect should not be omitted from realistic models of urban pest control. According to the OOO concept, the pesticide affects all infested sites proportionally with the same intensity (Figure 1). The control then depends only on the efficiency of pesticide (Larter and Chadwick, 1983; Reid and Appel, 1994). After treatment the population will either disappear because the pesticide is 100% effective (Figure 1A), or slightly decrease because the pesticide is not 100% effective, or the pest is resistant to the pesticide (Figure 1B).

Population resurgence after its extinction (Figure 1A) is usually a result of pest immigration. Indeed, such situation frequently occurs in single-family dwellings. But a different situation can

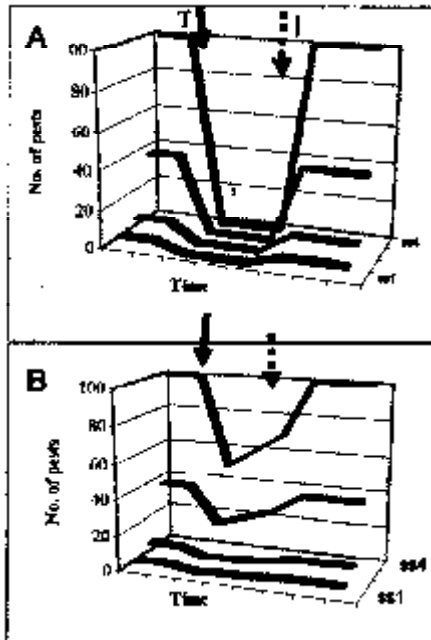


Figure 1. The “proportional control effect” of a pesticide (A –100% pesticide efficiency, B –50% pesticide efficiency) on a single population located at the 4 sites (SS_{1-4}) that differ in their suitability or capacity. (Black arrow - pesticide treatment; dashed arrow - immigration)

be found in complex buildings; here pest spatial patterns are often dynamic and do not match the OOO-concept. Spatially structured models are frequently employed by ecologists (Hassel, 2000; Helenius, 1999) and epidemiologists (Earn et al., 1997), but rarely by urban entomologists. This in spite of the potential of pest nuclei surviving after treatment, and forming the nuclei for future infestation (Schal, 1988; Robinson, 2002)

Huffaker (1958) demonstrated that asynchronous spatial fluctuations of predator and prey populations enabled the persistence of both populations in a small microcosm. Spatial ecology has organized into a unified metapopulation theory by Hanski (1991, 1999). The basis of the metapopulation theory is that a set of small unstable populations can create one stable, large metapopulation, and local population asynchrony fuels a rescue effect (Brown and Kodric-Brown, 1977). The basic idea of metapopulation persistence in a stochastic balance between local extinctions and recolonisation of empty habitat patches is depicted by the Levins model (1969, 1970).

The rate of exchange in metapopulation size (P_t) is measured by the proportion of patches occupied at time t $dP/dt = cP(1-P) - eP$, where c is rate of colonisation and e is the rate of extinction. The equilibrium value (\hat{P}) for a metapopulation is $\hat{P} = 1 - e/c$. If the persistence / extinction threshold (e/c) is ≥ 1 , the metapopulation becomes extinct. Hanski (1991) explained that “in spite of simplicity and obvious limitations, this equation is fundamentally important in highlighting a key aspect of metapopulation dynamics: metapopulation persistence requires that, for a given extinction rate, the colonisation rate exceeds a threshold value, and that for a given colonisation rate the extinction rate is smaller than threshold value”.

Epidemiologists are interested in persistence/extinction thresholds from a different perspective than conservationists, since they wish to cause the extinction of a pest organism (Earn et al.,

1997). Because urban entomologists share the epidemiologists perspective, the establishment of analogous extinction thresholds for urban pests can be of practical importance. Hanski (1999) states that before the metapopulation model can be applied, four critical conditions should be satisfied: 1) local populations breed in relatively discrete patches; 2) no single population is large enough to ensure long-term persistence; 3) the patches are not too isolated to preclude recolonisation; and 4) local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely.

The objectives of the research presented here were to: 1) investigate whether local populations of the cockroach, *Blattella germanica* (L.) and the pyralid moth, *Plodia interpunctella* (Höbner), exhibit asynchronous dynamics in complex buildings; 2) review causes of local populations asynchrony and conduct an experiment documenting the aggregative response of human pesticide applicator to pests density at various patches; and 3) propose a metapopulation hypothesis alternative to the physiological hypothesis, the so-called domino effect, for explaining the historical role of cockroach baits in the recent worldwide decline of *B. germanica* (Robinson, 1999).

MATERIALS and METHODS

Environments

Spatio-temporal distribution of *B. germanica* and *P. interpunctella* was studied in two urban environments: kitchen with a floor area approximately 50 m², and used for food preparation; and a food factory, with a floor area approximately 10,000 m².

Monitoring

The long-term monitoring records were obtained from personnel of the kitchen and the food plant and analysed. The standard pest-monitoring procedures (SPMP) (Stejskal, 2001) differed in both buildings. Numbers of monitoring steps (MS) and sampling sites (SS) varied according to the specific demands of the personnel. MS signifies one visit to building with inspection of all traps/sampling sites, and SS signifies a site where samples are taken, using one trap.

The kitchen SPMP included 30 monitoring steps: MS₁₋₃₀ collected during the 9-month period of January-September with a frequency of 3 or 4 MS / month, and 6 sampling sites: SS₁₋₆ with an average density 1 trap / 8.3 m². The food plant SPMP included 48 monitoring steps: MS₁₋₄₈ collected during the 12-month period of January-December with a frequency of 4 MS / month, and 61 sampling sites: SS₁₋₆₁ with an average density of 1 trap / 164 m². *P. interpunctella* was monitored by Delta sticky traps lured by a ZETA sex-pheromone, and *B. germanica* by a sticky trap (Lo-Line) with a GP2 attractant.

Each sapling site (SS) represents one local population. Metapopulation consists from pooled data from all SS for each MS. Extinction of SS is defined as a situation when no pests were found in particular trap (SS), and it was assumed that pests were eliminated from the active space of the trap. Cross-correlation analyses were made to evaluate population synchrony between various SS (local populations), using Statistica®.

Monitoring Assumption

Patchy And Discrete Pest Distribution. It is documented that the distribution of pests in stores (Arbogast et al., 1998), buildings (Reid and Appel, 1994) and food plants (Stejskal and Verner, 1996) is clumped since this environment is highly fragmented, or the urban and stored-product pests exhibit aggregative behaviour. Because of uneven distribution of suitable habitats, pest populations are frequently divided into distinct subpopulations. In food factories, pyralid moths develop in discrete patches of food residues inside machinery or wall and floor crevices; these are interconnected by occasional adult migration. *B. germanica* is aggregated at discrete shelters

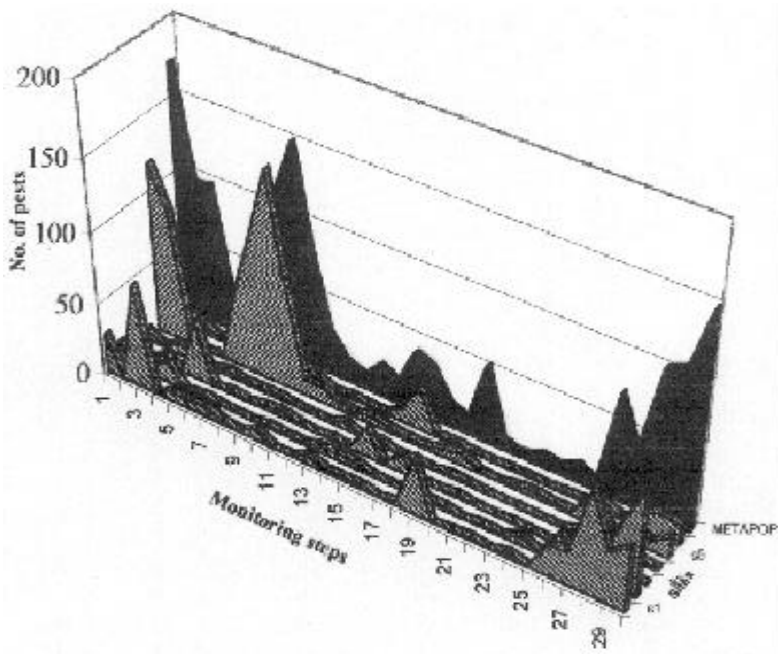


Figure 2. Spatiotemporal distribution of local populations (SS) of *Blattella germanica* in the kitchen (SS- sampling site, MS –monitoring step).

(Reid and Appel, 1994) and almost no exchange of individuals between aggregations was observed (Denzler et al., 1988).

Traps Indicate Patches Nearby. Food lures in traps are detected by cockroaches from a maximum distance of a few centimetres. Cockroach movement in food-rich environments may be limited since *B. germanica* tends to minimise the distance between food and shelter, and young larvae and gravid females seldom leave harborage (Rust et al., 1995). Mankin and Hagstrum (1995) and Mankin et al. (1999) reported that in enclosed environments the active space of pyralid moth pheromone traps ranged from 0.4-4 meters. They concluded that pheromone traps are less effective at sampling remote populations of insects in warehouse than in a field, but are helpful in locating nearby infestations.

Control Treatments

The staff of kitchen and food plant provided regular cleaning. Both environments received subcontracted monthly professional pest-control service, which included chemical treatment using non-residual pesticides (AquaPy, a.i. pyrethrum; Aqua-reslin, a.i. permethrin) or residual pesticides (Actellic, a.i. pirimiphosmethyl; Empire 20, a.i. chlorpyrifos; Detmol-Mic, a.i. fenitrothion, K-ohrine, a.i. deltamethrin). The monitoring data on population distribution and size were available to pest-management professionals. The managements of both buildings required monitoring-based targeted pest control that included no spray instruction for pest-free sites. During the regular monthly treatments various SSs received non-equal pesticide load if any.

Spraying Time Allocation by PMP

The time required for three pest management professionals (PMPs) to treat infested sites that vary in pest population density of *B. germanica* was recorded. The PMPs made regular pesticide treatments in the kitchen. The goal was to determine whether PMSs exhibited the density-dependent aggregative response described by Hassel (2000). Ten sticky traps containing various density of adult *B. germanica* were placed in the open and visible in 10 separated sites, here considered as pest patches and spaced 1-2m² apart in the kitchen. PMPs were instructed to treat these sites properly using a compressed-air sprayer within the limit of 60 min. The treatment time was measured by stopwatch for each site and PMP.

RESULTS

The spatio-temporal distribution of populations of *B. germanica* (Figure 2) and *P. interpunctella* (Figure 3) in two types of urban environment was different. Most changes in the size of particular populations were asynchronous: the local populations (SS) did not intercorrelate in an aseasonal metapopulations of *B. germanica* (80% cases) or a semi-seasonal metapopulations of *P. interpunctella* (83% cases). Several extinctions were observed in each SS, but never at all at the same time.

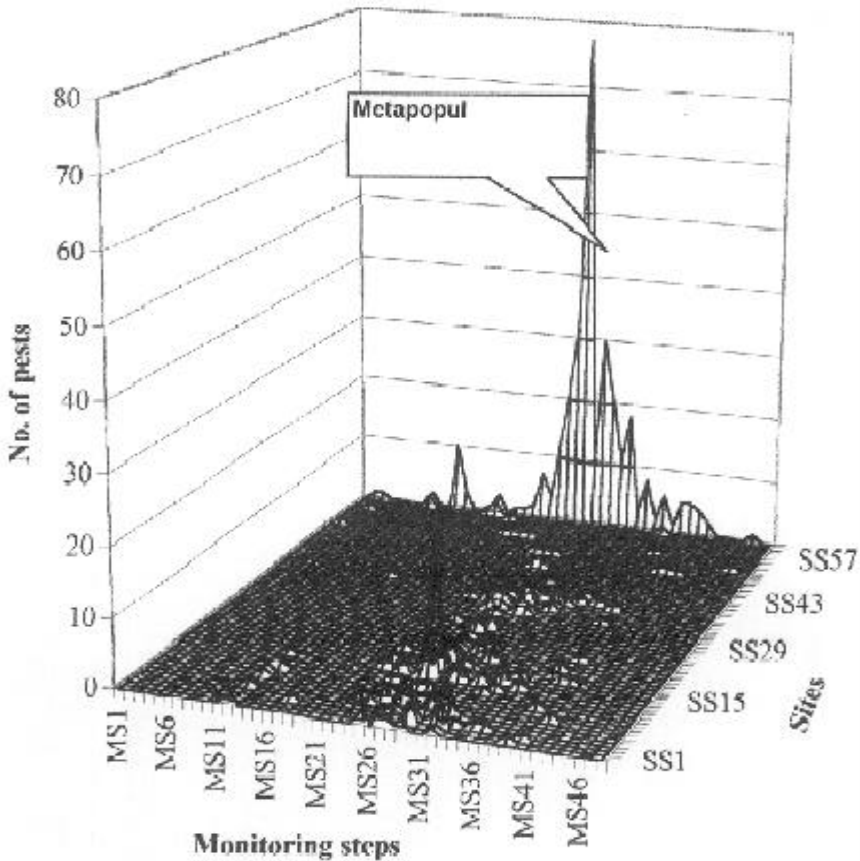


Figure 3. Spatiotemporal distribution of local populations (SS) of *Plodia interpunctella* in the food plant (SS- sampling site, MS –monitoring step).

For *B. germanica*, the overall ratio of colonization (c) to extinction rate (e) of local populations (SS) was close to 1 ($c/e = 0.94$). The metapopulation size of *B. germanica* positively correlated with the number of colonized SS (Figure 4). Figure 5 presents the influence of targeted pest control on the spatio-temporal dynamics of extinctions, and relative population maxima for *B. germanica*. The recolonization of vacant sites was enabled by degradation of residual insecticides within 1-3 weeks (Koehler and Patterson, 1991). The population maxima were confined to SS1, SS2, SS5, where the physical conditions for development of *B. germanica* were optimal. However, the relative population maxima were found at all SS.

Although optimal environmental conditions predicted sites with absolute population maxima, the relative maxima were unpredictable. The pattern shown by Figure 5 resembles the pattern of the Huffaker (1958) metapopulation showing predator and prey dynamics. Both patterns could originate from a common mechanism. Pesticide applicators delivered pesticide in a density-dependent manner (Figure 6).

DISCUSSION

Theory predicts that stability is not a necessary condition to population persistence if local populations are discrete and semi-independent (Murdoch et al., 1985). In this work data show the importance of spatio-temporal dynamics of local pests populations for their survival in unstable conditions, such as under insecticide pressure. Local pest populations asynchronously switched on by colonising, and switched off by becoming extinct, on various sites in space (SS) and time (MS). The concurrent extinction at all SS and the consequent total metapopulations was not observed. The number of traps used by hygienic personnel in both environments could not detect all infested sites (Reid and Appel, 1994). The unmonitored and uncontrolled sites could have contributed to metapopulation persistence. It is notable that even selected and a limited number of SSs was sufficient to provide the stability and persistence of *B. germanica* metapopulation. Semi-seasonal *P. interpunctella* adult metapopulation persisted during the spring-autumn season.

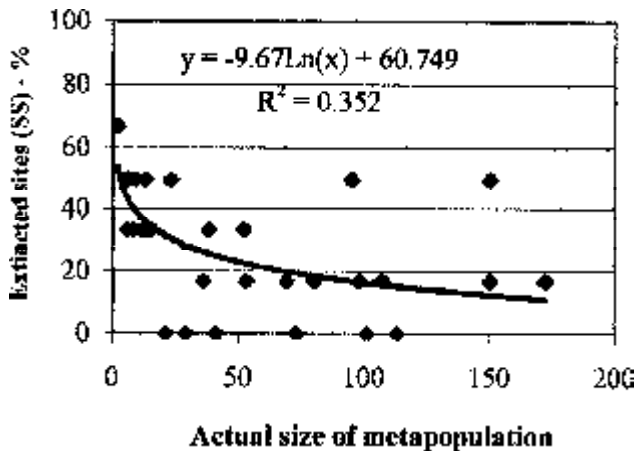


Figure 4. Metapopulation size of *B. germanica* was negatively correlated with No. of extincted sites.

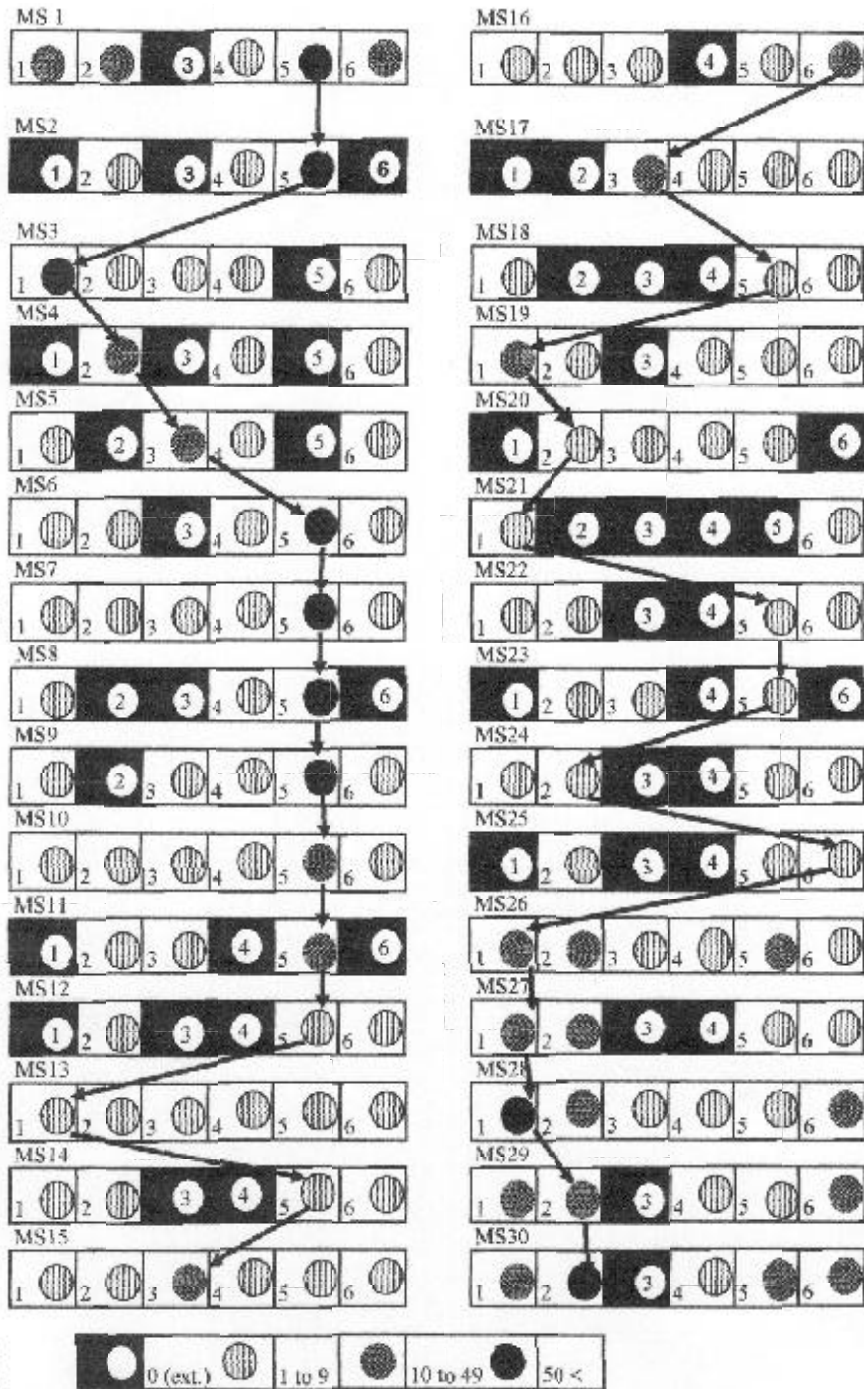


Figure 5. Human and pest playing “hide and seek”: Spatiotemporal dynamics of extinctions and relative population maxima (indicated by arrows) of *B. germanica* in the kitchen.”

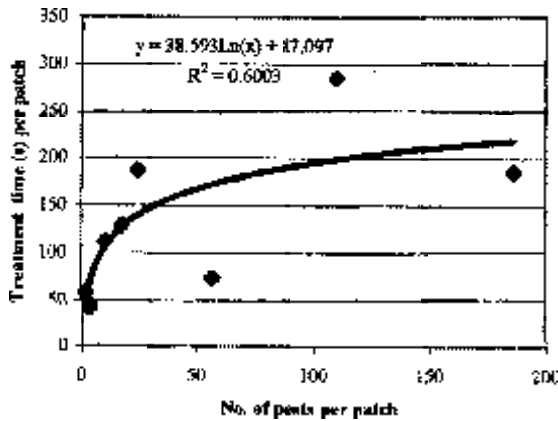


Figure 6. "Aggregative response" of human pesticide applicator: The pesticide treatment-time positively correlates with a pest density at 10 different sites in the kitchen.

Human behaviour plays an important role in the survival of pests in the urban environment. I observed the density-dependent allocation of pesticide treatment time (Figure 6) among SS with different pest population sizes. This could provide partial refuges to pests.

Causes of Population Fluctuations

Urban environment seems to be stable in terms of the stable temperature, humidity, and food supply that should ensure stable populations. However, the rate of increase of local populations may be affected by the temperature conditions of specific microhabitats that may differ from the average conditions. Human behaviour, such as cleaning to remove pest food patches, and pesticide treatment, may cause strong fluctuations in both local populations and in the whole metapopulation (Figure 2, 3). Godfray (1987) reported that the predatory pressures may explain population cycles in climatically stable environments, and Briggs et al. (2000) reported that solely intrinsic population factors may be responsible for strong fluctuations in stored product pests, such as half generation cycles in *P. interpunctella*, even in the absence of predators and competitors.

Connectivity and Isolation of Local Populations

Both buildings may seem to be too small to support the existence of local populations with different dynamics. However, human beings perceive the environment at a different scale compared to arthropods. Huffaker (1958) observed complex spatial population dynamics in a small laboratory arena. The published data indicate that the dispersal of pests in urban environments is strongly dependent and variable (Rust et al., 1995). Local pest populations may be isolated or inter-connected from the human perspective. Stejskal (2001) reported that the cockroach perception of one linear meter could range from 1-80 meters, depending on body size and level of heterogeneity of the environment, which was measured by its fractal dimension. Arthropods not only move in different spatial scales but their dispersal is strongly affected by the context of the landscape (Wiens, 2001). Pesticide barriers may themselves be a cause of population isolation, even in a homogenous environment (Collins et al., 1988).

Metapopulation Theory, Critical Thresholds, and Pesticide Evaluation

Figures 2 and 3 show that local population dynamics does not necessarily correlate with the metapopulation dynamics. This implies that the single-number critical action or economic thresholds (Pinto, 2000) are not always suitable for the fragmented urban environment. Also the evaluation of the relative pesticide efficiency differs according to whether we take into account effects on metapopulation or on a particular population. While evaluating the influence of pesticides on spatially structured populations we should be able to discriminate the effect of immigration from natality or emigration from mortality. Little work has been conducted to evaluate the efficiency of pesticides under conditions of permanent pest immigration (Doud and Philips, 2000). Pulliam (1988) reported that small populations could persist in highly adverse conditions through a continuous immigration from source patches (sink-source model).

Metapopulation Theory and IPM-Monitoring Paradigm

Monitoring and target control measures are considered keystones of IPM. However, the above results support the important implication of metapopulation theory, which contradicts the traditional urban IPM precept that pest eradication requires the pesticide treatment not only of the currently infested sites, but also of all suitable refuges that can be (re)colonized. Pest control based on monitoring may enable pest persistence in heterogeneous environments due to the following factors: 1) impossible (technical, economical) to find the last pest in the infested heterogeneous unit (Reid and Apple, 1994); 2) existence of local semi-connected populations providing pest recolonization potential; 3) limited residual effect of pesticide and its density-dependent application; 4) time delay between monitoring and control action; and 5) non-instant action of some pesticides.

Emigration from diminishing pest groups is not only the effect of chance or pesticide repellency, but also the decreasing pest density itself, due to decreasing concentration of aggregation pheromone (Ross et al., 1984). The synchronous treatment (Helenius, 1999) of all suitable sites by non-residual pesticides is probably the best option for pest eradication but is difficult logistically. The serial treatment of all suitable habitats is more feasible, provided that the long-term residual effect of the pesticide, such as bait, is guaranteed.

Baits Prevent Recolonisation

Robinson (1999, 2002) stressed that the introduction and a global adoption of the new bait generation was the crucial factor that enabled the extremely efficient control of *B. germanica*. The most popular explanation of the historical success of bait use has been the physiological hypothesis, known as a domino effect (Silvermann et al., 1991). In brief, the domino effect claims that young nymphs feed upon toxic feces or carcasses of adults that consumed baits distant from their shelter. Although the domino effect may increase and speed up the suppressive effect of baits, many traditional residual pesticide sprays are able to eradicate local populations, but without comparative long-term success (Figure 2). Clearly, the key factor of the success must be different. Metapopulation theory and long-term residual effect of bait may provide an alternative explanation. In contrast to spray residual pesticides, the baits remain effective in treated cockroach infestation sites or refuges for several weeks or months. Repetitive visits of infested buildings enable gradual location and treatment of most of the suitable pest patches. Even the smallest aggregations will increase to the detection threshold and will be treated after some time. Most important is, however, that the long-lasting effect of baits prevents recolonization of patches already treated during the previous visits. These cycles lead to a step-by-step (patch-by-patch) treatment of most, if not all, suitable patches and to a complete breakdown of pest metapopulation dynamics.

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