CHAPTER 11

Landscape-Scale Effects of Toxic Events for Ecological Risk Assessment

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INTRODUCTION

The effect of spatial heterogeneity on response of organisms has rarely been considered in ecological risk assessment or in ecotoxicological studies (Emlen 1989, Jorgensen 1990). Barnthouse (1992) cites examples of regional or "landscape" models of the distribution of ecosystems or land-use types to quantify ecological effects of regionally distributed stresses such as acid deposition, ozone, and climate change. In addition, Barnthouse (1992) recognizes the application of agricultural pesticides as a potentially important regional problem. Increased and widespread use of agricultural pesticides has been linked with population declines of plant, invertebrate, and vertebrate species (Grue et al. 1986, O'Connor and Shrubb 1986, Streibig 1988, Sheehan et al. 1987, Fox et al. 1989, Fuller et al. 1991, Sotherton 1991, Tew et al. 1992, Freemark and Boutin, in press).

In this chapter we argue that ecological risk assessments for toxicants must go beyond the current practice of only assessing effects at the spatial and temporal scales of direct impact (Cairns 1984). Our objectives are (1) to extend results of the effects of landscape pattern and variability on population survival to landscape-scale effects of toxic events, (2) to develop a conceptual model of landscape-scale effects of toxic events on species, and (3) to propose a practical approach for predicting when landscape-scale effects of toxic events are likely to occur. To date there has been little if any research on the interacting effects of landscape pattern and toxic events for ecological risk assessment. Therefore, we rely primarily on studies from the general ecological literature, particularly those on the dynamics of stochastic, spatially structured populations. We do so

by viewing a toxic event as just another type of ecological disturbance, thus enabling us to argue by extension from the existing literature (e.g., Fahrig 1990).

LANDSCAPE-SCALE PROPAGATION OF LOCAL EXTINCTIONS

Many, if not all, natural populations are comprised of many local populations. At the local scale, naturally occurring extinctions are frequent. Factors that cause population reductions such as disease, predation, and inclement weather can reduce a population to low levels, making local extinction likely (Paine 1988, Berger 1990). In many cases, "demographic stochasticity" results in the final extirpation (Hanski 1986). Demographic stochasticity includes factors such as skewed sex ratios or age ratios, which occur by chance. For example, if all five individuals surviving a disease happen to be male or past reproductive age, the population will die out.

High rates of natural (i.e., not caused by a toxic event) local extinctions have been documented. Addicott (1978) showed that local populations of aphids on fireweeds became extinct and colonizations occurred throughout the summer. In 23 wooded patches of 1 to 24 ha, Merriam and Wegner (1992) found between 8.7 and 15.2% of patches per year suffered local extinctions of white-footed mouse (*Peromyscus leucopus*). In a 5-year study of ambush bugs (*Phymata americana*) living in goldenrod (*Solidago*) patches, Mason (1977) found annual local extinction rates of 0 to 10% of 10 to 23 local populations. Van der Meijden et al. (1985) found that between 9 and 64% of local populations of nine species of biennial dune plants suffered local extinctions due to severe drought. Paine (1988) estimated the local extinction rate of sea palms to be between 0 and 64% per year. Finally, a number of studies have reported significant extinction rates even in highly vagile birds (Freemark 1989, Villard et al. 1992, Verboom et al. 1991).

Although local extinctions are common, the population at the larger regional or landscape scale (i.e., the metapopulation) can be stable. For example, populations of white-footed mice (*Peromyscus leucopus*) in small woodlots are highly variable, but, when integrated over several woodlots, the metapopulaton is more stable (Merriam and Wegner 1992). Ehrlich et al. (1975) and Thomas (1991) showed that population sizes of the Bay checkerspot butterfly (*Euphydryas editha bayensis*) and the silver-studded blue butterfly (*Plebejus argus*), respectively, are less variable at a large spatial scale than at a small scale. Villard et al. (1992) observed year-to-year dynamics in habitat patch occupancy at the landscape scale for three species of migratory birds breeding in temperate forests. The overall picture is of unstable population dynamics at the local scale but persistence of the metapopulations at the landscape scale because local extinctions are balanced by recolonizations.

This scenario of natural spatiotemporal fluctuations has implications for the impact of toxic events on population survival. If a toxic event wipes out a local population that is a critical source of colonists for other local populations (that may have experienced local extinctions unrelated to the toxic event), these other areas will not be recolonized. Other local areas that depend on these for colonists will also not be colonized, and so on. In this way the population reduction from a single local toxic event can be propagated through the landscape. In extreme cases, instability in metapopulation dynamics can result, causing regional extinction. Therefore, the effect of a toxic event can extend beyond the area of direct impact and can last much longer than the duration of effectiveness of the substance. In the remainder of this chapter we refer to this phenomenon as "landscape-scale propagation" of toxic event(s).

THE CONSTRAINT OF LANDSCAPE STRUCTURE

The landscape-scale outcome of a toxic event can range from no detectable effect, to a temporary reduction in landscape population size, to the extreme of regional extinction. The actual effect depends on (1) the spatiotemporal configuration of the population in the landscape, including between-area differences in population variability and habitat size, quality, and accessibility (Kareiva 1990) and (2) the spatiotemporal distribution of toxic event(s) in the same landscape (Fahrig 1990). In most cases, the spatial distribution of the population in the landscape is better defined by its "potential" spatial distribution since, at any time, some areas that could serve as habitat are empty due to local extinctions. The spatial distribution is therefore best described by the spatial distribution of habitat rather than the population itself. There are two general kinds of habitat distributions: patchy and continuous. The patchy population is subdivided into discrete local populations in suitable "habitat patches" surrounded by a "matrix" of unsuitable habitat, while the habitat of the continuous population is interconnected.

Populations that are continuous (habitat is interconnected at the landscape scale) are resistant to local extinctions (Fahrig 1991). This is because dispersal to the locally extinct area is not restricted by the spatial configuration of the habitat. Recolonization of the area occurs quickly from the neighboring habitat. However, many, if not most, populations are patchily distributed. In this case the large-scale implications of a local extinction depend on the spatial relationships between the affected area and other patches of habitat. To predict the effect, it is necessary to know whether the area in which the local extinction occurred is critical to metapopulation survival. The area is critical to metapopulation survival if it provides immigrants to other areas that would otherwise not sustain local populations (Pulliam 1988, Howe et al. 1991) and/or it provides a "stepping stone" (Kareiva 1990) between pairs of patches, thus allowing movement between them for recolonizations of local extinctions. The

status of the affected area (critical or not) depends on the spatial structure of the landscape (Fahrig and Merriam, 1994).

Landscape structure is defined as the extent and composition of habitat elements and their spatial arrangement (Dunning et al. 1992). Habitat elements are defined by the way in which they are used by a particular species. Examples are patches of breeding habitat or feeding habitat, areas of inhospitable habitat, and areas that can be used as dispersal corridors. Important characteristics of landscape structure include the following:

1. **Size, shape, and quality of patches** — the size of a patch has been shown to influence local population persistence. Verboom et al. (1991) and Villard et al. (1992) found a positive relationship between habitat patch size and persistence of local populations of forest birds. Also, positive relationships between patch size and local population size (e.g., Lynch and Whigham 1984) and between local population size and population persistence (e.g., Paine 1988, Berger 1990) imply a positive relationship between patch size and population persistence.

   Patch shape can influence population survival if the population dynamics change in relation to the distance from the edge of the patch. For example, Gates and Gysel (1978) found that the number of passerine birds increased at the field-forest edge. Ambuel and Temple (1983) suggest that forest-edge and farmland bird species exclude certain forest-dwelling species and that this exclusion has a greater impact than changes in patch area or isolation. Best et al. (1990) found that bird species abundance decreased as the size of crop fields increased because of a reduced edge effect. They predicted that narrower and/or more irregularly shaped fields would support more birds because they have proportionately more edge. Thus, two patches of the same area but having different amounts of edge may have different population dynamics.

   Pulliam (1988) simplified the issue of patch quality by referring to two qualitatively different kinds of patches: sources and sinks. Source patches are those that, on average, produce more offspring than they are able to maintain. The excess emigrate and are potential colonists of other patches. In sink patches, the habitat quality is low, so the productivity rate is below that needed to sustain a population over the long term. Sink patches are therefore dependent on source patches for their persistence. Best (1986) argues that croplands can act as sink habitats for many bird species because reproduction and survival are reduced by frequent and untimely agricultural disturbances including pesticide applications. Although sink populations are not self-sustaining, Howe et al. (1991) have demonstrated that they can make a significant contribution to the size and longevity of the metapopulation. In addition to creating sink habitats, pesticides, and presumably other toxicants, can also lower the carrying capacity

of habitats (Sheehan et al. 1987, Sotherton 1991, Fuller et al. 1991, Rogers and Freemark 1991). This results in smaller populations at the local and landscape scales, which increases the probability of local extinction from stochastic processes and decreases rates of recolonization from reductions in numbers of dispersing individuals. This outcome is particularly likely when the toxic event is not of short duration but is chronic (e.g., acid deposition).

2. **The presence of dispersal routes through the landscape** — Fahrig and Merriam (1985) showed that fencerows, which function as dispersal routes for white-footed mice (*Peromyscus leucopus*) in a landscape of woodlots and farmland, are important for regional population abundance. Dmowski and Kozakiewicz (1990) found that a shrub strip between a forest and a littoral zone acted as a corridor enhancing movements of birds. Bennett (1990) showed that survival of regional populations of small mammals in a fragmented landscape in Australia was facilitated by movements between remnant forest patches along vegetated corridors (but see Simberloff et al. 1992). Verboom and van Apeldoorn (1990) found that the amount of hedgerow surrounding wooded fragments was positively related to the presence of red squirrel (*Sciuris vulgaris*) in the fragment. Clearly, habitat patches themselves can also act as dispersal routes within the landscape.
3. **The quality of dispersal routes** — quality can affect the likelihood of dispersers using the route and/or the probability that dispersers using the route will survive. Henein and Merriam (1990) showed in a simulation study that the quality of dispersal routes can be important for the abundance of the regional population. Availability of corridors with qualities permitting both breeding and movement between patches is also important to population survival (Bennett 1987). Extreme low quality is equivalent to a barrier effect. For example, Duelli (1990) showed that edges of agricultural fields can be barriers to movement through the landscape by some farmland arthropods. Mader et al. (1990) showed that minor roads blocked the dispersal of some forest arthropods.
4. **Spatial configuration of habitat elements** — Lefkovitch and Fahrig (1985) showed in a simulation study that, for population survival and abundance, the total number of dispersal corridors in the landscape may be less important than their configuration relative to the habitat patches. In particular, they found that it is the overall shape and size of the geometric figure formed by interconnected patches that is most important; large, closed figures produce the highest probability of regional persistence. Seno (1988) modeled a one-dimensional patchy population, in which one patch was different from the others in terms of population demography and/or dispersal. The model showed that the spatial location of this patch affected the regional population

dynamics; the more central the patch, the greater its impact. Herben et al. (1991) showed in a model of moss population dynamics that degree of clumping of substrate patches affects population persistence. The importance of clumping for increasing persistence has also been demonstrated in modeling studies (Adler and Nürnberger 1994).

Many field studies have demonstrated the importance of spatial configuration of the landscape, particularly the importance of patch isolation on local population abundance and persistence. Lawton and Woodroffe (1991) showed that breeding water voles were less likely to be present in isolated sites. Dingle (1991) found that the large milkweed bug was less likely to be found in host patches that were far from major rivers. He hypothesized that this was due to the fact that the bugs follow water courses during migration. Potter (1990) found that degree of isolation of forest remnants affected the probability of use by the brown kiwi in New Zealand. If large remnants are interspersed with small ones, the kiwis can move between the large remnants by using the small ones as "stepping stones". Burel (1989) reported similar use of stepping stones by forest carabid beetles in Brittany farmland. Freemark and Collins (1992) have shown that the variety and abundance of forest birds in small forest patches are positively related to the amount of forest nearby and proximity to larger forests.

IMPORTANCE OF DISPERSAL AND HABITAT-SPECIFIC DEMOGRAPHICS

Dispersal acts to increase population stability by decreasing the effects of disturbances (or toxic events) (Reddingius and den Boer 1970, Roff 1974a, Vance 1980), except for the rare situations when dispersal rate is highest at low population densities (Vance 1984). Our use of "dispersal" refers to a change in location of organisms, accompanied by reproduction. Reproduction can occur after the move to the new area, or the organisms may reproduce in the original area, and their offspring disperse to a new one (Lidicker 1975). The effect of landscape spatial structure on movement and recolonization depends on the dispersal characteristics of the organism.

The components of dispersal that are important for population response to the constraint of landscape structure are as follows (Fahrig and Paloheimo 1988a, Fahrig 1991):

1. Dispersal probability, or the probability of individuals leaving a patch per unit time.
2. Dispersal distance, or the probability of individuals successfully reaching a range of distances or landscape components. If the dispersers do not travel far enough to move among habitat patches, they will not be able to recolonize local extinctions.

3. Temporal pattern of dispersal. For example, dispersal may be seasonal. If local extinctions (or toxic events) are more likely to occur at some times of the year than others, the timing of movement that results in recolonization will affect its demographic impact.
4. Dispersal behavior that improves the probability of dispersers finding habitat patches and/or decreases the risk of disperser mortality. For example, some herbivorous insects including bark beetles (McMullen and Atkins 1962), desert locusts (Wallace 1958), and cabbage root fly (Prokopy et al. 1983) locate and orient toward host plant patches from a distance.

Fahrig and Paloheimo (1988a) conducted a simulation experiment in which they examined the relative importance of various components of demography and dispersal on regional abundance in patchy environments. In general, dispersal was shown to be more important than demography (e.g., birth rate) in determining regional population abundance. This result is supported in a study of small rodent populations in which immigration was found to be more important than local demographics in affecting local population persistence (Blaustein 1981). Fahrig and Paloheimo (1988a) also found that the most important determinant of regional population abundance was the probability that dispersers successfully locate new patches. The exact spatial pattern of habitat patches was found to be most important when dispersal distances are small relative to the distance between patches. For highly mobile species such as birds, habitat-specific demographic factors such as survival and fecundity have a strong impact on metapopulation size and persistence (Urban and Shugart 1986, Lande 1988, Temple and Cary 1988, Noon and Biles 1990). Toxic events can have a direct effect on reproduction and survival of local populations, which, in turn, can propagate to the landscape scale (Pulliam 1994).

SCENARIOS FOR LANDSCAPE-SCALE PROPAGATION OF TOXIC EVENTS

In this section, we discuss toxic events in the following three types of exposure scenarios: (1) single local toxic event, (2) several local toxic events, and (3) large-scale toxic event. For each of these we consider effects on both continuous and patchy populations.

SINGLE LOCAL TOXIC EVENT

We first take the case of a single, unusual local toxic event such as a localized toxic spill. We would like to predict the landscape-scale effects of this event on the survival of a particular species. In other words, will the effects of the event remain local and short-term, or will they propagate through time over the landscape to destabilize the regional population?

As for the general case of local extinctions discussed above, we do not expect the effect of a local toxic event in a continuous population to propagate through the landscape. This is because dispersal to the area is not restricted by the spatial configuration of the habitat. Recolonization is expected to occur quickly from the neighboring areas. Even if the toxic event is chronic, its effects will remain local.

However, if the population is patchy, the large-scale effect of the toxic event depends on the predisturbance relationship of the population in that area to the dynamics of the regional population. In particular, it depends on whether that population was critical to regional survival. This in turn depends, as described above, on the spatial structure of the landscape, and the dispersal characteristics of the organism. In general, the larger the landscape and the more local populations, the more resistant it is to the effects of a single local toxic event (Agur and Deneubourg 1985, Roff 1974b). The longer-lasting or more chronic the local effects of the toxic event (e.g., a toxic dump site), the more likely it is to propagate to the landscape.

MANY LOCAL TOXIC EVENTS

Many toxic substances in the environment are distributed not in single rare events but as multiple, frequent events. For example, agricultural habitats experience disturbances (including applications of pesticides and other agrochemicals) that are usually frequent, synchronous, and large scale (O'Connor and Shrubb 1986). In a continuous population in which the frequency of the toxic event is low, the above generalization for single toxic events holds: the effects of the toxic events are not expected to propagate but will remain local. However, if the frequency of toxic events is high, this generalization does not hold. In this case the toxic events themselves can restructure the population so that it is no longer continuous. The ability of organisms to recolonize affected areas may be constrained by the imposed spatial structure. Fahrig (1991) showed in simulation analyses of disturbances on a landscape, that when the frequency of disturbance (here, toxic event) is low, the dispersal distance of the organism does not affect regional population size; affected areas are recolonized even if the organism's dispersal range is small. However, if the disturbance frequency is high, there is a positive relationship between population size and dispersal distance, indicating the importance of the spatial pattern of the population in relation to the spatial pattern of the toxic events.

If either the population is patchy or the frequency of toxic events is high, the spatiotemporal pattern of the toxic events can have a large impact on the long-term survival of the population. The most important aspect of this pattern is the degree to which the toxic events in different locations are synchronous. In general, the more synchronous the events, the lower the survival probability for the regional population (Levins 1969, Harrison and Quinn 1989, Gilpin 1990, Hanski 1991).

As in the case of a single toxic event, the long-term effects of multiple events on a patchy population depend on the distribution of the events in relation to the landscape-scale dynamic of the group of local populations. To use a simple example, if all the affected areas function as source populations (Pulliam 1988, Howe et al. 1991), the stability of remaining unaffected sink areas will be decreased due to a decrease in immigration rate. If the affected areas remain uncolonized for a significant length of time, the regional population size can enter a self-perpetuated decline, which can propagate to extinction at the landscape scale. To predict the long-term effects of the toxic events it is therefore necessary to consider the interaction of these events with the extinction-recolonization dynamic on the landscape.

LARGE-SCALE TOXIC EVENT

Some toxic events, such as acid rain or ozone, occur over an area that is as large as or larger than the scale of the metapopulation. Events such as these represent the most serious threat to species survival. The immediate effect is reduction in numbers across all local populations. Some of these reductions, in combination with other stochastic factors, are likely to lead to local extinctions. Since the regional population is reduced, the probability of reestablishment of such local extinctions is reduced. If the habitat is continuous, the limiting factor is the reproductive rate of the species. If there has been a severe reduction in numbers, there will be an initial period in which chance events on the small populations may result in large-scale extinction. However, if several local populations recover to high levels, dispersal to other areas will be rapid in the continuous habitat, and the effect of the toxic event will not propagate. In a patchy population however, the regional effect of the large-scale toxic event depends on the dispersal rate, disperser survival rate, and dispersal distance of the organism affected (Fahrig and Paloheimo 1988a, Fahrig 1991) as well as the spatial structure of the landscape. In both cases, the longer lasting (more chronic) the event, the higher the probability of regional extinction.

PRACTICAL APPROACH FOR ASSESSING LANDSCAPE-SCALE EFFECTS OF TOXIC EVENTS

In the above discussion, we indicate that the landscape-scale effect of toxic event(s) on population survival depends on the landscape structure, the spatiotemporal distribution of the toxic event(s), and the dispersal characteristics and habitat-specific demographics of the organism. In other words, it depends on the interaction between the "natural" spatiotemporal functioning of the population (the extinction-recolonization dynamic) and the spatiotemporal dynamic of the toxic event(s). To make a prediction for a particular case, it will in general be necessary to develop a model that incorporates these spatiotemporal dynamics.

Since model development always has an intuitive component, it is not possible to present a perfectly standardized methodology. The choices that are made about the structure of the model ultimately depend on the question(s) the model will be used to explore (Fahrig 1991). The methodology we propose includes field studies to validate and refine the ecological realism of the simulation models for subsequent use in risk assessment. The methodology steps are as follows:

1. Build a computer model that simulates the spatial distribution of habitats and toxic events and the associated population dynamics in the landscape. This can generally be done if there is some information on the dispersal and life history characteristics of the organism.
2. Conduct sensitivity analyses to identify parameters that determine whether local toxic events propagate to regional extinction.
3. Use the model to make predictions of short-term population dynamics (e.g., 1 year) for different values of the critical parameters.
4. Test the short-term predictions with field studies.
5. Conduct long-term simulation experiments to identify circumstances in which toxic events are likely to propagate to long-term, landscape-scale impacts.

Although the following examples are not of toxic events, they contain the basic elements of this methodology. Fahrig and Merriam (1985) developed a model of white-footed mice (*Peromyscus leucopus*) in patches of wooded habitat (woodlots) using literature values for parameters. They tested the short-term prediction of the model, that population size within a season depends on habitat interconnections. Lefkovitch and Fahrig (1985) then used the model to make predictions about the long-term survival of mice in different spatial configurations of woodlots. Fahrig and Paloheimo (1987) studied the dispersal behavior of cabbage butterflies (*Pieris rapae*). They incorporated the results into a model of population dynamics and tested the short-term (1 year) predictions (Fahrig and Paloheimo 1988b). The model was then used to study the general relationships between dispersal behavior and population survival (Fahrig 1988, Fahrig and Paloheimo 1988a).

This methodology is similar to methods used in Population Viability Analysis (PVA), in which one attempts to determine the survival prospects of a population. An example of this approach is a PVA of a patchy population of an endangered plant, Furbish's lousewort (*Pedicularis furbishiae*) (Menges 1990). Menges built a stochastic simulation model of the population, which included empirically observed variation in demographic parameters and estimated rates of natural catastrophes. He used the model to predict the long-term fate of the population.

A drawback of this method is that it is limited to single species analyses. Even though the extrapolation to the landscape scale is an improvement over current approaches, one would like to be able to make statements concerning the multispecies-level effects of a toxic event (Cairns 1984). Propagation to the landscape scale depends on a wide variety of factors for which we have very

little empirical data. Extrapolations and/or generalizations among species is difficult because inter- and intra-family, genus, and species variations in response to chemical intoxication are large. Given the state of existing data, any predictions of potential effects on untested species will have to be tempered by many qualifiers. In addition, propagation of toxic effects to the landscape scale depends on dispersal characteristics and habitat-specific demographics of the organism. These traits are, in general, poorly known and vary substantially among species. Multispecies predictions will therefore be difficult at best (even ignoring the complications posed by species interactions). Some researchers have begun to explore the utility of comparing life history traits of species among different geographic regions to predict faunal response to changes in landscape structure (e.g., Hansen et al. 1992, Hansen and Urban, 1992). At present it appears that the most promising approach is to conduct our proposed analysis for the species that, due to high exposure, low fecundity and/or limited dispersal abilities, are most likely to experience landscape-scale propagation.

Apart from a few exceptions, there are no general rules for predicting whether the effects of toxic event(s) will propagate across the landscape to larger scales and longer time periods than the impact of the initial event(s). We suggest that the above method is a practical approach for determining whether such propagation is likely in a particular case. However, some speculation can be made without this detailed analysis. From our arguments above, we propose the following ranking, under the assumption that the toxic events are equal in their direct and chronic effects. This ranking does not take into account details such as the organism's dispersal behavior but is intended as a starting point only. The ranking is from lowest to highest probability of propagation:

1. single local toxic event in a continuous population,
2. multiple local toxic events at a low frequency and/or low synchrony in a continuous population,
3. single local toxic event in a patchy population,
4. multiple local toxic events at a high frequency and/or high synchrony in a continuous population,
5. single large-scale toxic event in a continuous population,
6. multiple local toxic events in a patchy population,
7. single large-scale toxic event in a patchy population.

SUMMARY

In this chapter, we argue that ecological risk assessments for toxicants must go beyond the current practice of only assessing effects at the spatial and temporal scales of direct impact. Propagation of the effects of toxic event(s) beyond these scales occurs because of the interaction of the toxic event(s) with the normal landscape-scale dynamic of extinctions and recolonizations of local populations. Landscape-scale propagation of a toxic event can occur if the event wipes out or greatly reduces a local population that is a critical source of

colonists for other local populations (that may have experienced local extinctions unrelated to the toxic event). These other areas will then not be recolonized, and other local areas that depend on these for colonists will not be recolonized, and so on. Whether landscape-scale propagation of toxic events occurs depends on the landscape structure, the spatiotemporal distribution of the toxic event(s), and the dispersal characteristics and habitat-specific demographics of the organism. In other words, it depends on the interaction between the "natural" spatiotemporal functioning of the population (the extinction-recolonization dynamic) and the spatiotemporal dynamic of the toxic event(s). In general, landscape-scale propagation is more likely to occur the more patchily distributed the population, the more widespread and/or chronic the toxic event, and the more synchronous the occurrence of separate toxic events over the landscape. We propose a method for predicting in particular cases whether landscape-scale propagation of toxic events will occur.

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