Trivial Movements and Redistribution of Polyphagous Insect Herbivores in Heterogeneous Vegetation

Abstract

The aim of this thesis was to study the interplay between movement patterns of polyphagous insect herbivores and vegetation heterogeneity within agricultural fields. I examined if and how 1) host plant species, 2) host plant quality, 3) vegetation architecture, and 4) trap crop physical design influence movement patterns of individuals and spatial distribution of populations.

Foragers may aggregate in profitable areas by tactic movement, or by area-restricted search, i.e. by moving randomly but slowing down movement and increasing rate of turning after encountering a profitable patch. Movement patterns of polyphagous herbivores have a high potential for influencing their distribution among hosts differing in quality. However, information on the role random vs. non-random components in their movement behavior is scarce. The results of this thesis show that both host plant species and within species differences in host plant quality affect movement behavior of a polyphagous herbivore, the European tarnished plant bug nymphs. The host plant induced movement patterns also explained the distribution of nymphs in heterogeneous vegetation. Because redistribution was very fast, it appears that no tactic behavior is needed for the nymphs to locate preferred hosts in heterogeneous vegetation composed of small patches. Instead the nymphs may successfully locate superior hosts merely by random movement coupled with sensitivity to local host quality.

The physical structure of environment influences redistribution of populations at several spatial scales. At small scale the architecture of vegetation may influence redistribution of insects that move on the plant surface. At large scale e.g. trap crop physical design may affect redistribution of pests. In this thesis I derive a model for predicting the impact of vegetation architecture on the rate of displacement by insects moving on the plant surface. I also present and explore models of the interplay between pest movement and trap crop physical design. The trap crop models suggest that considerable reduction in pest density may be achieved using small trap crop cover with trap crops that the pest distinctly prefers over the crop. It supports also the idea that trap crop placement may have a dramatic impact on the efficiency of the trap crops.

Key words: *Lygus rugulipennis*, host plant, nitrogen, ecological diffusion, vegetation architecture, model, trap crop physical design

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Appendix

Papers I-IV

This thesis is based on the following papers, which are referred to by their roman numerals.

I.   Hannunen, S. & Ekbom, B. 2001. Host plant influence on movement patterns and subsequent distribution of the polyphagous bug *Lygus rugulipennis* (Heteroptera: Miridae). *Environmental Entomology 30*, 517-523.

II. Hannunen, S. & Ekbom, B. 2002. Within species variation in host plant quality and movement behavior of *Lygus rugulipennis* nymphs. *Entomologia Experimentalis et Applicata 104*, 95-101.

III. Hannunen, S. 2002. Vegetation architecture and redistribution of insects moving on the plant surface. *Ecological Modelling 155*, 149-157.

IV. Hannunen, S. 2002. Modeling the interplay between pest movement and the physical design of trap crop systems. *Manuscript*.

Introduction

The spatial dimension in population dynamics

The importance of the spatial dimension and organism movement for ecological dynamics is now widely recognized (Tilman & Kareiva, 1997; Bascompte & Sole, 1998; Turchin, 1998; Hanski, 1999; Turner, Gardner & O'Neill, 2001). Including the spatial dimension in population dynamics has provided new insights into several key population processes. For example, the role of space and especially spatial heterogeneity in the stability of consumer-resource dynamics (Hassell & May, 1974; May, 1978; Kareiva, 1987; Hassell *et al.*, 1991; Pacala & Hassell, 1991; Adler, 1993), and in the coexistence of competing species (Horn & MacArthur, 1972; Platt & Weis, 1977; Atkinson & Shorrocks, 1981; Ives & May, 1985; Nee & May, 1992; Tilman, 1994) are among the most visible developments of the spatial population dynamics.

The concept of metapopulation, *i.e.* a 'population' consisting of local populations connected by migration, and the related theory (see Hanski & Gilpin, 1997; Hanski, 1999; Hanski, 1998) have played a major role in the development of spatial ecology. The classical metapopulation models are spatially implicit, all the habitat patches are equally connected to the other patches, the number of patches is infinite, and all the patches are identical. Despite their simplicity the classical metapopulation models have already demonstrated some highly critical aspects of population dynamics in fragmented landscapes. For example, they have shown that currently unoccupied patches may be critical for long term persistence of the metapopulation. Since the classical models more realistic models have been developed where, for example, patch size and isolation and patch quality are considered (*e.g.* Pulliam, 1988; Hanski, 1994; Moilanen & Hanski, 1998).

While metapopulation theory considers populations in distinct patches embedded in a matrix of unsuitable featureless environment, landscape ecology concentrates on population dynamics in continuous environments composed of two or more habitat types (Turner, Gardner & O'Neill, 2001). The impact of landscape patterns on population processes, including organism movement, is among the major interests of landscape ecology (Turner, 1989; Gardner *et al.*, 1989; Gustafson & Gardner, 1996; Schumaker, 1996; With, Gardner & Turner, 1997; With & King, 1999). One important idea that has emerged from this research is that habitats suitable for an organism are either connected or disconnected, and the change between these two states occurs at a threshold of habitat abundance (Turner, Gardner & O'Neill, 2001). The threshold habitat abundance depends on the spatial arrangement of the habitat, the biology of the considered species, and the nature of the non-habitat matrix between the habitat patches (With & Crist, 1995; With, 1997).

Including the spatial dimension in population dynamics has emphasized the role of mathematical modeling in ecology (see *e.g.* Tilman & Kareiva, 1997; Bascompte & Sole, 1998; Turchin, 1998). Predicting the outcome of nonlinear non-spatial dynamics, brought about for example by inter- or intraspecific

interactions, is often practically impossible without mathematical models. Apparently, adding the spatial dimension in the dynamics further complicates the task. The need for mathematical models is additionally stressed by the advantages of quantitative compared to qualitative predictions. While a qualitative prediction defines only the expected direction of change, a quantitative prediction also defines the expected quantity of change. Thus a quantitative prediction provides a stronger test of a hypothesis than a qualitative prediction. In spatial ecology quantitative predictions are especially valuable because empirical studies are often extremely laborious and costly.

Population redistribution in heterogeneous environments

According to the ideal free distribution model (Fretwell & Lucas, 1970) foragers should distribute themselves so that each obtains the same food intake. The amount of food obtained in a site depends on the density of food and on the interference produced by other foragers. Thus, if the ideal free distribution model is obeyed the foragers should distribute themselves so that the influences of food abundance and interference balance out. The ideal free distribution model assumes the consumers to be 'ideal' in their judgement of profitability, and to move 'freely' from patch to patch. Ideal free distribution models describe an optimal equilibrium distribution of animals. However, the success of foragers in achieving the optimal distribution is clearly constrained by limits of their sensory perception, memory, and locomotion. Optimality models, such as the ideal free distribution model, do not determine if and how foragers attain the optimal distribution. Neither do optimality models explain which forager distributions are attainable from specific types of foraging behaviors.

The searching behaviors of foragers can be divided in two categories, those that involve the location of the resource patch and those that represent the response of the consumer once it is within the patch (see *e.g.* Bell, 1990). The first type of behavior involves tactic movement governed by, for example, visual or chemical cues. The later strategy involves changes in the consumer movement behavior only after encountering a profitable patch. In particular, animals engaged in so called area-restricted search slow down their movement and increase the rate of turning after encountering profitable patch.

Both the tactic and area-restricted search strategies, and combinations of the two can be modeled as biased random walk using simulations or the equivalent diffusion equations (Okubo, 1980). A biased random walk is a process in which the forager's movement decisions are stochastic but have biases that make some outcomes more likely than others. For example when simulating movement during area-restricted search the movement parameters are randomized from probability distributions that are biased according to the habitat types. Random walk models have made an important contribution to our thinking by highlighting the role of randomness as a fundamental element of animal movement. However, the actual degree of randomness in animal choices is generally unknown (Morris & Kareiva, 1991; Fransworth & Beecham, 1999).

The efficiency of different searching behaviors, and the role of random movement in the strategies, has been studied by modeling different movement behaviors in heterogeneous environments (Kareiva, 1982; Cain, 1985; Kareiva & Odell, 1987; Morris & Kareiva, 1991; Grünbaum, 1998; Fransworth & Beecham, 1999). Kareiva & Odell (1987) demonstrated that area-restricted search, which has been observed in numerous insect taxa (Chandler, 1969; Evans, 1976; Jones, 1977; Bond, 1980; Carter & Dixon, 1982; White, Tobin & Bell, 1984; Nakamuta, 1985; Kareiva & Odell, 1987) concentrates foragers in areas of high resource density. Morris & Kareiva (1991), in turn, demonstrated that the effectiveness of area-restricted search depends on an interplay between mean plant quality and the sensitivity of movement to changes in plant quality. When the mean plant quality is low herbivores that have long residence times on most host types and short residence times only on the poorest host types (non-choosy herbivores) do best. On the other hand, when the mean host quality is high herbivores that have short residence times on most hosts and long residence times only on the best host plants (choosy herbivores) are the most successful.

Grünbaum (1998) studied the process of population redistribution of foraging animals using advection-diffusion equations. Grünbaum (1998) introduced the term 'turning threshold', *i.e.* the prey density at which the predators' turning rate increases fastest, and demonstrated its importance for the efficiency of foraging. Like Morris & Kareiva (1991) the results in Grünbaum (1998) also show that when the overall abundance of resources is low being non-choosy is a good strategy, and when the overall abundance of resources is high being choosier is more profitable. Grünbaum (1998) suggests that foraging is most effective when the turning threshold is tuned to reflect the physiological or energetic requirements of the forager. If the turning threshold were at a much lower prey density than where the forager achieves the needed rate of payoff, the foragers would spend time in resource patches from which they cannot profit sufficiently. If on the other hand the threshold were at prey densities yielding much higher than the needed rate of payoff, the foragers would ignore perfectly good patches.

Both Morris & Kareiva (1991) and Grünbaum (1998) demonstrate that the effectiveness of a searcher depends on the balance between random and tactic movement. If the rate of random movement is high compared to tactic movement herbivores will tend to wander away from high quality hosts and never accumulate on the good patches. On the other hand without any random movement the foragers are likely to get caught in patches of locally good quality and thus miss nearby patches of even higher quality. The importance of random movement in avoiding settling within sub-optimal resource peaks (Morris & Kareiva, 1991; Grünbaum, 1998) is, however, a product of the assumption that searching individuals cannot respond to distant peaks in resource quality or quantity. Fransworth & Beecham (1999) who propose a mathematical framework for studying foraging with varying spatial ranges of forager perception, show that highly deterministic behavior coupled with a mild impact from far away resources results in a forager distribution that is closest to the optimal.

Although modeling can aid us in determining how a forager should behave to attain the optimal distributions in different environments, only empirical studies on

animal movement behavior can tell us how animals actually behave. Unfortunately, studies that could be used to interpret how animals search for resources in variable conditions are scarce (Morris & Kareiva, 1991; Grünbaum, 1998). For example, the existing studies on searching behavior of phytophagous insects are somewhat confusing. On one hand, laboratory experiments give the impression that phytophagous insects are highly effective in orienting toward stimuli indicating good host plants (Bernays & Chapman, 1994). Yet, on the other hand, field observations of insect behavior have shown that insects often miss seemingly good host plants (Cain, 1985; Cain, Eccleston & Kareiva, 1985; Dethier, 1989; Kareiva, 1982). The laboratory results lead us to believe that directed deterministic movement might be the mechanism herbivores use to locate host plants, yet the field observations do not really confirm this hypothesis. Consequently, it is not at all clear if herbivores locate superior host plants using highly tuned sensory abilities or by wide ranging motion combined with some sensitivity to local conditions (Morris & Kareiva, 1991).

Vegetation heterogeneity within agricultural fields

Trap cropping (Hokkanen, 1991; Javaid & Joshi, 1995) and intercropping (Risch, Andow & Altieri, 1983; Andow, 1991) are pest control strategies, where within field vegetational diversity is used to manipulate pest movement behavior in order to reduce the damage caused by the pest. In intercropping the crop plants are grown together with non-host plants, while in trap crop systems the crop plants are grown together with more preferred host plants. Although in both strategies the effect of non-crop plants on pest density is mediated through pest behavior, the impact of trap and intercrops on the pest behavior is very different. In intercropping the non-host plants disrupt the searching process of the pest, thus reducing the number of insects settling in the field. Trap crops, on the other hand, reduce the pest infestation on the principal crop by attracting the pests away from the crop plants. Intercrops are more likely to be effective when considering specialist insects, whereas trap crops have been suggested as a strategy to control generalist pests (Andow, 1991).

Apart from the fields where vegetational diversity is promoted in the form of trap or intercropping, agricultural fields are typically very homogeneous environments. Nevertheless, presence of weeds, heterogeneous application of fertilizers, variation in plant density, field margins, and buffer zones along watercourses may create some spatial heterogeneity in the field environment.

Outline of this thesis

The general aim of this thesis was to shed light on the interplay between vegetation heterogeneity found within agricultural fields and movement patterns of polyphagous insect herbivores. I was especially interested in if and how host plant species (I), host plant quality (II), vegetation architecture (III), and field composition and configuration (IV) influence the non-migratory (*i.e.* trivial) movements of insect individuals and the subsequent spatial distribution of populations. The first two papers of this thesis present empirical studies that

examine the host plant's impact on movement behavior (I, II) and the subsequent spatial distribution of a polyphagous herbivore, *Lygus rugulipennis* nymphs (I). The last two papers present and explore models for studying the impact of the physical structure of environment on redistribution of insects (III, IV).

Polyphagous herbivores often live in highly heterogeneous vegetation where several plants are suitable but not equally good hosts. Thus their movement patterns have a high potential for influencing their distribution among hosts differing in quality. The searching behavior of polyphagous herbivores is bound to be deterministic to some extent. In fact it has been suggested that all herbivores slow down movement in high quality host patches (Morris & Kareiva, 1991). However, a degree of randomness in movement behavior is also likely to be important for the foraging success of polyphagous herbivores. This is because the danger of staying too long in locations with sub-optimal resources (Morris & Kareiva, 1991; Grünbaum, 1998) is probably very real for them. However, for polyphagous herbivores information on movement behavior, and especially on the role of random vs. non-random components of movement is scarce. In this thesis I studied if host plant species (I), and within species differences in host plant quality (II) can affect movement behavior of *L. rugulipennis* nymphs. In the first paper I also studied if redistribution by *L. rugulipennis* nymphs could be described as area-restricted search, *i.e.* if the possible host plant induced movement patterns could explain the spatial distribution of nymphs in heterogeneous vegetation.

The physical structure of vegetation is likely to influence redistribution of insects, such as *L. rugulipennis* nymphs, that move mainly on the plant surface (Kareiva & Perry, 1989; Yang, 2001). Rate of redistribution, in turn, can profoundly affect, for example, the predator-prey interactions in the plant dwelling communities (Cuddington & Yodzis, 2001). Movement in complex environments has been studied intensively in physics and chemistry (Orbach, 1986; Weiss & Havlin, 1986; Havlin & Ben-Avraham, 1987) and in landscape ecology (Gardner *et al.*, 1989; Gustafson & Gardner, 1996; With & King, 1999). From these disciplines we know that the rate of displacement in complex environments, such as vegetation, can be predicted using fractal and fracton dimensions of the structure (Orbach, 1986), or by simulating movement in the environment in question, as is commonly done in landscape ecological studies (*e.g.* Johnson, Milne & Wiens, 1992, Johnson *et al.*, 1992). However, there are no easily accessible methods that could be used to quantify the impact of vegetation architecture on the rate of population spread by insects moving on the plant surface. To this end I derived and tested a simple analytical model for predicting the impact of vegetation architecture on rate of displacement by insects moving on the plant surface (III).

Trap cropping has been studied rather intensively (see Hokkanen, 1991; Javaid & Joshi, 1995 for reviews), and it has been suggested to have potential as a pest control strategy (Banks & Ekbom, 1999). Yet, attempts to quantify the interplay between the physical design of trap crop systems and the spatiotemporal pest dynamics are surprisingly scarce (but see Banks & Ekbom, 1999; Åsman 2001). Consequently, no general principles for the physical design of efficient trap crop systems have been suggested (Hokkanen, 1991). In paper IV I studied the interplay between pest movement and trap crop physical design. I modeled redistribution of

pests engaged in area-restricted search, and I asked (1) how does the proportion of trap crop area affect equilibrium distribution of pests among crop and trap crop, and (2) how does crop patch size and shape affect the maximum speed of pest redistribution from crop to trap crop.

Materials and Methods

The polyphagous bug, *Lygus rugulipennis*

The European tarnished plant bug, *Lygus rugulipennis* Poppius (Heteroptera: Miridae) is an extremely polyphagous herbivore. It has been reported from 437 plant species belonging to 57 families (Holopainen & Varis, 1991). Nitrogen content of the host plant has been suggested as a key factor in host plant selection by *L. rugulipennis*, partly because most of its preferred host plants, such as *Artemisia vulgaris* and *Tripleurospermum inodorum*, are nitrophilous (Holopainen & Varis, 1991). The importance of host plant nitrogen to the bugs is also supported by the fact that *L. rugulipennis* feeds mainly on the nitrogen rich plant parts, *i.e.* meristematic tissues and developing reproductive organs (Varis, 1972).

   L. rugulipennis is spread throughout the Palaearctic region. In Finland it is univoltine (Varis, 1972), while in southern Europe it may have up to four generations per year (Rancati, Tavella & Arzone, 1996). *L. rugulipennis* hibernates as an adult, usually in coniferous forests in the forest litter or in the lower branches of spruce trees (Varis, 1972). In Finland the bugs appear in the fields in mid or late May. The nymphs go through five nymphal stages, and in total the development from egg to adult takes about ten weeks. New adults emerge in late July or August, and movement to overwintering sites starts at the end of August (Varis, 1972).

   L. rugulipennis is a pest particularly in northern and central Europe. The damaged plants include, for example, alfalfa, clover, potato, cereals, sugar beet, and pine seedlings (Holopainen & Varis, 1991). In most cases the serious damage is caused in early summer when the overwintered adults feed on the plants that are beginning their development. Feeding by the bugs may cause small seedlings to wilt, or if the plant's growth point is destroyed lateral shoots may develop (Varis, 1972). Later in the summer high numbers of bugs may cause damage, for example, to strawberry (Easterbrook & Tooley, 1999) and lettuce (Rämert *et al.*, 2001).

Ecological diffusion

Redistribution of populations is frequently treated as a diffusion process, with movements of individuals treated as random walk (Okubo, 1980; Kareiva, 1983; Corbett & Plant, 1993; Turchin, 1991). When an organism moves according to simple random walk its subsequent moves are independent of each other, and its movement behavior is influenced only by the habitat where it is at the time of the move. Treating animal movement as such a simple process is often possible even if the organism's movement patterns were not random at the scale of an individual's short-term behavior. This is because the resulting movements may appear random over broader spatial and longer temporal scales.

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The equation for ecological diffusion that models movement of animals by simple random walk is (Patlak, 1953)

$$\frac{\partial u}{\partial t} = \nabla^2 \mu u$$

where u = density, t = time, μ = motility, and ∇^2 is the Laplacian operator, equal to the sum of the second partial derivatives of μu with respect to each of the spatial coordinates. Motility is a term that defines the rate of population spread and it is defined as (Turchin, 1991; Turchin, 1998)

$$\mu = \frac{m_2}{2nt}$$

where m_2 = mean square displacement of individuals, and n = number of dimensions in the studied space. When motility varies in space ($\mu = \mu(x,y)$), for example in response to variation in the quality of the environment, the resulting random walk is biased. Ecological diffusion with spatially variable motility can be used to model movement of individuals engaged in area-restricted search.

The equilibrium distribution of animals moving according to random walk with spatially variable motility can be predicted using a concept that is based on the equilibrium solution of the ecological diffusion equation, the residence index (Turchin, 1991). The residence index is a relative measure of the time that an organism spends between entering and leaving a unit area. The ratio of residence indices in different patches equals the ratio of densities in the patches (Turchin, 1991).

Studying movement

To study the impact of host plant species on movement patterns of *L. rugulipennis* nymphs I observed behavior of nymphs on two different host plant species, wheat (*Triticum aestivum*) and a common weed *T. inodorum* (I). Both wheat and *T. inodorum* are known to be suitable host plants for all life stages of *L. rugulipennis* (Holopainen & Varis, 1991). Yet, *T. inodorum* is favored clearly over wheat for both food and oviposition (Varis, 1972).

To study the impact of within species variation in host plant quality on movement behavior I observed behavior of *L. rugulipennis* nymphs on wheat cultivated using three different levels of nitrogen fertilization (II). I chose to use the availability of nitrogen to host plant as the means of manipulating host plant quality, because elements of behavior and performance of *L. rugulipennis* have previously been related to nitrogen concentration in host plants (Holopainen & Varis, 1991; Holopainen *et al.*, 1995).

I observed movement behavior of individual *L. rugulipennis* nymphs in the laboratory. To study if the host plant in itself, without the impact of previous experiences from better or poorer hosts, could affect movement behavior of the bugs I used nymphs that had been reared on the same host type as on which their behavior was observed.

Observations of behavior were short term only twenty or forty minutes per nymph. To measure the activity of each nymph I recorded, and summed up all the times the nymph spent moving during the observation (I, II). To obtain parameters that could be used for modeling redistribution of populations I measured the nymphs' net displacements after ten minutes, and the turning angles between two consecutive ten-minute net displacements (I).

Predicting and observing redistribution

I modeled redistribution of individuals as uncorrelated random walk, *i.e.* simple ecological diffusion with spatially variable motility (equation 1). I studied autocorrelations of subsequent moves to test whether the observed movement of *L. rugulipennis* nymphs could be described as random walk in paper I. In papers III and IV I merely assumed movement to be by random walk. I modeled random walk using an individual based simulation of random walk (I), by solving the equation for ecological diffusion numerically (I, III), and analytically (IV), and by employing the residence index (I, IV).

I observed redistribution of *L. rugulipennis* nymphs in small laboratory arenas where two different environment types were contrasted (I, III). In paper I the contrasted environment types were different plant species, wheat and *T. inodorum*. In paper III they were artificial vegetation types differing in architecture.

I predicted the distribution of individuals in the arenas in paper I by modeling ecological diffusion that was parameterized using movement patterns of nymphs observed on the two plant species. In the third paper I first used the derived model of the impact of vegetation architecture on motility through vegetation to predict the residence indices for the different artificial vegetation types. I then used these residence indices to predict the distribution of individuals among the artificial vegetation types in the arenas.

Finally, I compared the observed and predicted distributions of individuals. In paper I I studied if movement patterns of nymphs observed in homogeneous vegetation produced the distribution of individuals observed in heterogeneous vegetation. In paper III I studied if the predicted differences in motility on the different artificial vegetation types explained the observed distribution of individuals.

Results

Host plant species impact on movement and spatial distribution of *L. rugulipennis* nymphs

Host plant species markedly affected movement patterns of *L. rugulipennis* nymphs (I). Net displacements of the nymphs were clearly higher on wheat than on *T. inodorum*, but turning angles did not differ between host plants. Also, the motility of the nymphs was clearly higher on wheat than on *T. inodorum*.

The host plant-induced movement patterns clearly affected the distribution of the nymphs in heterogeneous vegetation (I). The observed distributions of nymphs among wheat and *T. inodorum* were in accordance with the distribution predicted using the biased random walk models. At equilibrium distribution about 95% of individuals were predicted and observed to be on *T. inodorum*, in the arenas where the area covered by the two plant species was equal.

The redistribution of nymphs in the arenas was fast (I). For example, in 60×60-cm arenas the distribution of nymphs was predicted and observed to be close to equilibrium after only three hours of redistribution.

Within species variation in host plant quality and movement behavior of *L. rugulipennis* nymphs

Within species variation in host plant quality influenced movement behavior of *L. rugulipennis* nymphs (II). The time that the nymphs allocated in movement clearly increased with the level of nitrogen fertilization applied to wheat.

The difference between movement behavior on the wheat fertilized with the lowest and the highest nitrogen levels was great. In fact it seemed to be as great as the difference in movement behavior on two different host plant species, wheat and *T. inodorum* (I). The total time spent moving on the wheat fertilized with the highest nitrogen level was not different from the total time spent moving observed earlier on wheat (U = 155.0, P = 0.336, N = 39). But, the total time spent moving on the wheat fertilized with the lowest nitrogen level was significantly lower than the total time spent moving observed earlier on *T. inodorum* (U = 153.0, P = 0.034, N = 44).

Vegetation architecture and redistribution of insects moving on the plant surface

I derived a model for predicting the impact of vegetation architecture on the speed of population redistribution through vegetation by insects moving on the plant surface in paper III. I described vegetation architecture using two parameters, (1) the proportion of the total length of connecting plant parts in relation to the total length of all plant parts, and (2) the proportion of the horizontal projection of connecting plant parts in relation to the total length of connecting plant parts. First, I quantified the influence of each parameter on mean squared displacement separately. Then, I combined the influences of the two parameters in a model for predicting the influence of vegetation architecture on motility through vegetation.

The positive influence of 'the proportion of connecting structures' (parameter 1) on rate of displacement was quantified by considering diffusion along the backbone of comb like structures as done by Weiss & Havlin (1986). The positive influence of 'the proportion of horizontal direction' (parameter 2) on the rate of displacement was quantified simply by translating displacements on the plant surface into displacements in horizontal direction. The model combined of the two parameters is

$$\mu_V = \mu K H^2$$

Here μ_V = motility through vegetation, μ = motility on plant surface, K = 'the proportion of connecting structures' (parameter 1), and H = 'the proportion of horizontal direction' (parameter 2). If the motility on the plant surface is known the model can be used to predict motility through vegetation. If the motility on the plant surface is not known the model can be used to predict the relative influence of vegetation architecture on motility by using a value of one for motility on the plant surface.

I tested the model by solving the diffusion equation numerically on example structures that differed in architecture. The motilities predicted by the model corresponded very well with the numerical solutions. The mean difference between the predicted and numerically acquired motilities was only 2.8%. I also tested the model by observing redistribution of *L. rugulipennis* nymphs on small arenas of artificial vegetation. The model was successful in predicting which vegetation type would have the higher insect density, although it did not always predict the distribution of nymphs exactly.

Pest movement, trap crop area and pest distribution

I present and explore a model in paper IV for assessing, how pest movement influences the equilibrium distribution of pests among crop and trap crop in fields differing in the proportion of trap crop area of the total field area. The model utilizes the concept of residence index (Turchin, 1991) and it is based on two assumptions: (1) the pests move by undirected random walk with spatially variable motility, and (2) the total number of pest individuals is distributed among two habitats, crop and trap crop. The model is

$$u_C = \frac{N}{\dfrac{A_T}{s} + A_C}$$

Here u_C = pest density in crop, N = total number of individuals, A_T = trap crop area, A_C = crop area, and s = the ratio of the pest's residence indices calculated so that the residence index in the crop is divided by the residence index in the trap crop. Because the configuration of the environment, such as the spatial arrangement of trap crops, has no influence on the equilibrium distribution of organisms moving according to the considered type of random walk (Turchin, 1991; Vail, 1993) the model applies to all field configurations.

Not surprisingly, the model predicts that the proportion of the pest population in the crop decreases as the proportion of trap crop area of the total field area increases. However, when the residence index in the trap crop is clearly higher than in the crop the proportion of pest population in crop decreases very sharply for small trap crop proportions. In contrast when the residence index in the trap crop is closer to that in the crop the proportion of pest population in crop decreases much more gradually with increasing trap crop cover.

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Pest movement, crop patch shape and pest distribution

I present and explore a model in paper IV for evaluating, how the speed of pest redistribution from crop to trap crop is affected by crop patch size and shape. Although the configuration of the environment has no impact on the equilibrium distribution of organisms that move according to random walk (Turchin, 1991; Vail, 1993), it may have an impact on the speed of the redistribution process. Thus it may also influence the efficiency of trap crops. The presented model is an analytical solution of the two-dimensional ecological diffusion equation in a rectangular area, with absorbing boundary conditions and uniform initial density of individuals. It models pest redistribution in a situation where rectangular crop patches are surrounded by trap crops. When several such crop patches are brought together they compose fields differing in configuration.

Not surprisingly, the model predicts that the proportion of the pest population in crop, after a given time of redistribution, increases with crop patch area for all patch perimeters. However, the proportion of the pest population in the crop also decreases with increasing crop patch perimeter for all patch areas. A variable combining both area and perimeter of the crop patch, *i.e.* perimeter to area ratio of crop patch, explains the proportion of pest population in the crop better than either patch area or perimeter alone. The proportion of pest population in crop after a given time of redistribution decreases with increasing perimeter to area ratio of crop patch.

Because of the absorbing boundary conditions used in deriving the model, the model describes a situation where pests that have entered the trap crop never return to the main crop. This is highly unrealistic and hence the model cannot be used to predict true pest redistribution. However, if parameterized with pest motility observed on a crop species the model can be used to predict the maximum speed of pest redistribution from crop to trap crop. This information may be used to aid in determining if an aspired speed of reduction in pest density is achievable with even a highly effective trap crop.

Discussion

Host plant impact on movement behavior of *L. rugulipennis* nymphs

Both host plant species (I) and within species variation in host plant quality (II) clearly affected movement behavior of *L. rugulipennis* nymphs. Net displacements of the nymphs were clearly lower on *T. inodorum* than on wheat (I), and on wheat the time spent moving by *L. rugulipennis* nymphs was positively correlated with the nitrogen fertilization applied to the wheat. The time moving by the nymphs was the lowest on low nitrogen wheat and on *T. inodorum*, it was intermediate on the intermediate nitrogen wheat, and the highest on high nitrogen wheat.

The dependence of movement patterns on internal state variables, such as physiological condition, are considered to be central to searching behaviors of foragers (Kareiva & Odell, 1987; Bell, 1990; Grünbaum, 2000). Starving foragers tend to move long distances along relatively straight paths, whereas the movement paths of satiated foragers are more sinuous (Jones, 1977; Bond, 1980; Bell *et al.*, 1985; Kareiva & Odell, 1987). Because the satiation level of the forager is likely to depend on the amount of resources it has encountered in the recent past the described behavior will cause foragers to aggregate in high quality patches (Kareiva & Odell, 1987). Thus the internal state variables provide animals a simple and profitable means for assessing patch quality. The internal state variables can be used to compare the quality of the present patch with the quality of previously experienced patches. Also, they could be used to assess the quality of the natal patch, as would be the case in the papers I and II, where the nymphs experienced only one host plant type.

Because *L. rugulipennis* has been shown to favor *T. inodorum* over wheat for both food and oviposition (Varis, 1972), *T. inodorum* may be a superior host compared to wheat. If this inference were correct the movement patterns observed on *T. inodorum* and wheat could reflect host plant quality in the manner described above. The movement patterns would cause the nymphs to aggregate on the superior hosts, and therefore be beneficial to the nymphs.

Most of the favored hosts of *L. rugulipennis* are nitrophilous (Holopainen & Varis, 1991), and the growth rate of its nymphs has been positively related to nitrogen concentration in the host plant (Holopainen *et al.*, 1995). Hence suitability of plants to *L. rugulipennis* may be positively correlated with nitrogen content of the host plant. If this were true the observed positive correlation between movement activity and nitrogen level of wheat would be somewhat puzzling. Movement patterns would not categorically reflect the host quality in the expected manner, and they would cause the nymphs to aggregate in areas of low profitability. However, it is possible that the low nitrogen wheat was so low in quality that the nymphs had no other choice except to stay where they were.

In fruitflies (Bell *et al.*, 1985) and in blowflies (Green, 1964) the relationship between habitat quality and the percentage of time spent moving has been reported to be bell-shaped. The time moving was very low in unstarved flies, higher in moderately starved flies and again very low in more severely starved flies (Bell *et al.*, 1985; Green, 1964). Bell *et al.* (1985) suggested that when the energy reserves of the foragers are still relatively high they can gamble and invest energy in moving in order to find more resources. But, foragers suffering from severe food depletion have no other choice but to stay where they are, and wait for renewal of the local resources or wait until they detect appropriate stimuli such as food odor.

It is clear that the availability of nitrogen to plants may influence several plant factors, such as concentration and composition of amino acids, nitrogenous secondary chemicals, or carbohydrates (Mengel & Kirkby, 1987; Bernays & Chapman, 1994), that may contradict the influence of the plant nitrogen content. For example, nitrogen fertilization has been shown to have a negative influence on the concentration of water-soluble carbohydrates in wheat (Frank, Bauer & Black, 1989), and sucrose, glucose and fructose have been reported to be feeding

stimulants to *e.g. L. lineolaris* (Hatfield, Frazier & Ferreira, 1982). However, because I did not analyze plant factors other than nitrogen, and because I have no data on the times spent feeding on the different wheat, linking the observed behavior to actual food quality, such as concentration of feeding stimulants or deterrents, is not possible.

Redistribution of *L. rugulipennis* nymphs in heterogeneous vegetation

Redistribution of *L. rugulipennis* nymphs in heterogeneous vegetation was successfully modeled as simple random walk with motilities determined by local conditions (I). This implies that the nymphs were engaged in area-restricted search, and that the nymphs were searching for superior hosts by random movement coupled with sensitivity to local host quality.

The experiments were not clever enough to rule out the possibility that the nymphs might have a tactic component, *i.e.* orientation towards *T. inodorum*, in their movement behavior. However, the fact that the redistribution of the nymphs in heterogeneous vegetation was very fast suggests that no such tactic behavior is needed for *L. rugulipennis* nymphs to locate preferred hosts in heterogeneous vegetation composed of small patches. Instead it seems likely that the nymphs could successfully locate superior hosts merely by random movement coupled with sensitivity to local host quality.

It should also be pointed out that in non-continuous environments, such as vegetation is to insects moving on the plant surface, tactic behavior may actually slow down redistribution. This is because following a strong cue in a non-continuous environment may cause foragers to spend a lot of time going back and forth in dead ends (Johnson, Hatfield & Milne, 1995; Gustafson & Gardner, 1996). If patch size is small drifting far away from the superior host is unlikely, and thus the good patches are likely to be reached faster by moving randomly than by following cues.

When the non-continuous structure of vegetation is considered it is actually no surprise that the nymphs seem to be searching for superior hosts by random movement coupled with sensitivity to local conditions. Such area-restricted search has been shown to efficiently cause foragers to concentrate in areas of high resource density (Hassell & May, 1974; Kareiva & Odell, 1987), and it has been observed in numerous insect taxa, including coccinellid adults and larvae (Carter & Dixon, 1982; Nakamuta, 1985; Kareiva & Odell, 1987), lacewing larvae (Bond, 1980), syrphid larvae (Chandler, 1969), adult houseflies (White, Tobin & Bell, 1984), anthocorid nymphs (Evans, 1976), and butterfly caterpillars (Jones, 1977).

Redistribution in non-continuous environments

From works in physics and chemistry we know that the rate of displacement in complex environments is slowed down compared to diffusion in uniform continuous environment, and that the rate can be predicted using fractal and fracton dimensions of the structure (Halvin & Ben-Avraham, 1987; Orbach, 1986).

Landscape ecology has also put considerable effort into studying the impacts of complex landscape patterns on rate of displacement in heterogeneous landscapes (Gardner *et al.*, 1989; Johnson, Hatfield & Milne, 1995; Gustafson & Gardner, 1996; Schumaker, 1996; With, Gardner & Turner, 1997; With & King, 1999; King & With, 2002). Landscape ecological studies have employed simulations of movement on neutral landscape maps or on maps representing real landscapes. Dispersal success in the landscapes has been related to indices of landscape pattern, such as patch cohesion (Schumaker, 1996), and lacunarity index (With & King, 1999). However, population redistribution at the landscape level is a complex process. It is not determined only by the pattern of the optimal habitat but also at least by the biology of the dispersing species, and by the quality and spatial pattern of the sub-optimal habitat matrix (With & Crist, 1995; With, 1997). Thus landscape ecological studies relating landscape patterns to population processes have not been aimed at yielding exact analytical relationships between rate of movement and landscape structure.

In paper III I derived and tested an analytical model for predicting rate of diffusion through complex random structures, such as vegetation is to insects moving on the plant surface. Because the model is analytical it is not surprising that it predicted the rate similar to numerical analysis. In fact, the small difference between the rate of diffusion obtained using the model and using numerical computation is likely to be due to the error in the numerical method.

The qualitative predictions of the model presented in paper III agree with results of simulations of organism movement on percolation clusters and other heterogeneous landscapes (Gardner *et al.*, 1989; Johnson, Hatfield & Milne, 1995; King & With, 2002). For example, a simulation of random walk on river networks showed that as height of river tributaries, that are analogous to non-connecting structures, increased the rate of displacement along the river's main channel decreased (Johnson, Hatfield & Milne, 1995). Yet, properly relating the predictions of my model with results of these simulations would require quantitative measurement of the model parameters from the studied landscapes.

It should be noted that because the structures used in developing and in testing the model were quite simple, the model does not necessarily predict correct motility in real complex vegetation. However, the model could be used for comparisons of vegetation types with a relatively simple structure, for example vegetation of grasses. Also, because the model employs simple diffusion, *i.e.* uncorrelated random walk, the motility it predicts is not affected by the number of connections or by the width of the connecting structures. Yet, for real organisms whose subsequent move directions are often correlated these variables may make a difference. Nevertheless, the model was rather successful in predicting the distribution of *L. rugulipennis* nymphs in artificial vegetation, even when the contrasted vegetation types differed in the number of connections among artificial plants.

Modeling in the design of trap crop systems

The efficiency of any trap crop system depends on the interplay between the physical design of the trap crop system and pest population processes. Unraveling this interplay and its impact on the within field distribution of the pest is central for the development of efficient trap crop systems. Finding the most efficient trap crop layout in field experiments even for one pest, crop, trap crop combination is likely to be very laborious and costly. And, unfortunately generalizing the patterns seen in field studies is not safe unless the population processes governing the pattern of pest distribution are known.

Modeling provides a handy method for studying the interplay between the physical design of trap crop systems and pest population processes. Modeling can be used to reveal patterns created by the different population processes, to provide insight about the importance of the different processes, and to create testable predictions about pest distribution in different situations. Unfortunately, modeling has not been extensively used in trap cropping studies.

The existing trap crop models that have considered pest colonization, local movement and emigration (Banks & Ekbom, 1999), pests' oviposition behavior (Åsman, 2001), and pest movement by biased random walk (IV) have all demonstrated one common pattern. When the pest's preference for the trap crop is strong the proportion of pest population in crop decreases sharply for small trap crop proportions. Yet, if the preference is weak the decrease in pest pressure with increasing trap crop cover is much more gradual. These results strongly suggest that finding a trap crop that the pest distinctly prefers over the crop is vital for the efficiency of any trap crop system.

It is clear that, when pests move according to random walk with motility that depends only on the quality of the present patch type, the configuration of the environment, such as the spatial arrangement of trap crops, has no impact on the equilibrium distribution of insects (Turchin, 1991; Vail, 1993). Yet, if the movement behavior of the forager does not change immediately after it has moved from one patch type to another, for example because its motility is mediated by its hunger level, the spatial configuration of the environment may affect the equilibrium distribution of the foragers. Walsh (1996) showed that if the searching behavior between patches depends on the quality of the patch from which the forager has most recently departed the equilibrium distribution of foragers among good and poor patches is influenced by interpatch distance. His results suggest that the patch quality discrimination may peak at the intermediate interpatch distances. The system studied by Walsh (1996) differs from a typical trap crop scenario, where a true interpatch space is lacking because good and poor patches are next to each other. Nevertheless, considering pest redistribution by movement behavior that is mediated by the physical state of the forager instead of mere patch quality might prove worthwhile.

I also studied the impact of crop patch size and shape on pest redistribution. The model suggests that when the pests move by random walk in crop patches surrounded by trap crop, pest redistribution accelerates with increasing perimeter to area ratio of crop patches. This suggests that using elongated instead of

rectangular crop patches may be beneficial if a rapid reduction in pest pressure is important. However, if pest movement is mediated by its physical state instead of mere patch quality, the optimal crop patch shape is not necessarily as highly elongated. This is because, if motility is mediated by satiation, pests leaving the trap crop have low motility also in the crop. This will increase the forager's changes of reentering the trap crop, but it will also lead to increased pest density in the crop near the trap crop edges.

When modeling trap crop systems one is faced with the tradeoff between simplicity and realism. Simple models ignore most of the details related to the studied system, while realistic models tend to include a lot of details. The aim of a simple model is often merely to assist in understanding the process. Yet, a simple model can also be realistic if the factors that are included in the model dominate the studied system, and the details that are left out are only of minor importance. The trap crop models presented in paper IV are very simple. They ignore pest reproduction, changes in plant and insect phenology, density dependence of pest behavior etc. Also, they assume that pest movement is simple random walk with spatially variable motility, *i.e.* the pest is not attracted to the trap crop. These restrictions could possibly limit the applicability of the models to a few cases. Naturally, trap crop models could include all the above details. However, obtaining reliable estimates for all the parameters needed for such complex models would be practically impossible. This in turn would seriously hinder the testability of the models.

None of the discussed trap crop models (Banks & Ekbom, 1999; Åsman, 2001; IV) has been tested in field experiments. This is at least partly because field scale experiments are laborious and costly. Small-scale experiments, on the other hand, cannot safely be scaled up to apply at field scale, because the pest's responses to landscape heterogeneity may be scale-dependent (Kareiva, 1982; Banks, 1989; Walsh, 1996). Instead of merely testing the models one may at the same time test the efficiency of a promising trap crop system. In order to save resources in such studies the trap crop models may be used to limit the field experiments into the trap crop designs that appear to have the highest potential for controlling the pest attacks.

Modeling population redistribution as diffusion

Modeling is central in studies of spatial population dynamics (see *e.g.* Tilman & Kareiva, 1997; Turchin, 1998; Hanski, 1999). Consequently, both the number and variability of spatial population models is impressive. The models can be spatially implicit or explicit. In spatially explicit models the population density, space and time can be treated as discrete or continuous variables. The environment can be composed of separate habitat patches, or it can be considered as a mosaic of habitat fragments. Movement of animals can be simulated based on self-defined rules, it can be simulated according to one of the standard random walks, or it can be modeled using one of the many diffusion equations. Clearly, the choice of modeling technique will influence the predictions of the model. Thus effort should be put into choosing a technique that adequately mimics the modeled phenomenon.

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Use of diffusion models has been promoted because comparison of studies using well-defined diffusion equations is easier than comparison of individual based simulations (Turchin, 1991). Also, diffusion models are appealing because they can be neatly presented with one equation while simulation models often require a lengthy description. However, diffusion models are clearly not the best models for all situations. This is because diffusion models imply an infinite speed of propagation, which is bound to affect the dynamics predicted by the models (Durret & Levin, 1994). Especially when studying dynamics of inter- or intraspecific interaction models that treat individuals as distinct entities are likely to mimic the real dynamics better than diffusion models. Also, if local stochasticity is important diffusion models may result in predictions different from the more realistic stochastic models (Durret & Levin, 1994).

When the aim is merely to study population redistribution by organism movement diffusion models are often a suitable method. They have been successfully used to describe, for example, insect redistribution (references in Okubo, 1980; Kareiva, 1983; Corbett & Plant, 1993; and Turchin, 1991; I; III). Yet, if movement paths of an organism cannot be divided into infinitesimal segment lengths diffusion models will not properly predict redistribution in heterogeneous landscapes. Thus diffusion models cannot be used to model movement of organisms, such as Pierid butterflies, that tend to move for a fixed minimum path length before stopping (Fahrig & Paloheimo, 1988; Walsh, 1996). This is because diffusion models assume that organisms always change movement behavior immediately after encountering a patch.

Sometimes using simulations of random walk instead of the equivalent diffusion equation may be advantageous. Because diffusion models are deterministic they predict the mean behavior of the studied phenomenon but give no estimate of the variance around the mean. This may sometimes impede comparison of model predictions with results from the field or laboratory experiments, especially if variation in the studied phenomenon is great.

Concluding remarks

The results of this thesis suggest that trivial movements and the subsequent distribution *L. rugulipennis* nymphs may be influenced by host plant species (I), host plant quality (II), vegetation architecture (III), and composition and configuration of the environment (IV). Consequently, for example, the presence of weeds (I), heterogeneous availability of nutrients to plants (II), plant density (III), and composition and configuration of agricultural fields (IV) may influence the damage a pest population causes to the crop plants.

The behavior of *L. rugulipennis* adults, the life stage most damaging to field crops, is likely to differ from the behavior of the nymphs studied in the first two papers of this thesis. Thus these results cannot propose any direct pest control applications, yet they do illustrate some points that may be of interest. The host plant induced movement patterns of *L. rugulipennis* nymphs appeared to explain the distribution of nymphs in heterogeneous vegetation (I). This suggests that pest movement patterns on a plant species may indicate the trap crop potential of the

plant species rather accurately. However, because host plant quality may also strongly influence movement behavior (II) using movement patterns observed on homogenous plant material, for example, to predict the trap crop potential of plant species, may be seriously misleading.

The model of the impact of vegetation architecture on motility through vegetation presented in paper III, in itself, is not especially interesting. But, it could be used to study some exciting questions, for example, the impact of plant density on motility through vegetation. If plant density affects motility the spatial distribution of individuals and the dynamics of predator-prey systems may also be affected by the plant density.

The trap crop models presented in paper IV are very simple, and they do not even begin to grasp the complexity of pest population dynamics. Testing the models in situations where they might apply is one of the many things yet to be done. *L. rugulipennis* is a reasonable candidate for a model species in such studies. Because most of the damage caused by *L. rugulipennis* is done by the overwintered adults, including population growth in the models is not essential. Obviously models predicting the efficiency of different trap crop systems could include many more details about the pest population processes. Yet, I believe that regardless of the multitude of factors affecting pest population dynamics, understanding the interplay between pest movement and trap crop physical design is important.

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