Habitat connectivity and fragmented nuthatch populations in agricultural landscapes

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Habitat connectivity and fragmented nuthatch populations in agricultural landscapes

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WAGENINGEN

STELLINGEN

1 De ruimtelijke variabelen 'oppervlakte van habitatplekken' en 'afstand tussen habitatplekken' zijn van wezenlijk belang voor het begrijpen van de populatiedynamiek.

P. Kareiva (1990). Population dynamics in spatially complex environments: theory and data. Phil. Trans. R. Soc. Lond. B 330: 175-190

Dit proefschrift

2 Bij het bepalen van effecten van de mate van verbinding van habitatplekken op processen in populaties dient men de ruimtelijke schaal waarop dit wordt gedaan expliciet in beschouwing te nemen.

Dit proefschrift

3 Habitatplekken die niet bezet zijn door boomklevers hebben een hogere kolonisatiekans naarmate de afstand tot omliggende bezette plekken kleiner is.

J. Verboom, A. Schotman, P. Opdam en J.A.J. Metz (1991). European nuthatch metapopulations in a fragmented agricultural landscape. Oikos 61: 149-156

Dit proefschrift

4 In tegenstelling tot hetgeen Matthysen *c.s.* hebben gevonden, is de selectie van territoria door boomklevers voor reproductie slechter naarmate het habitat meer versnipperd is.

E. Matthysen en D. Currie (1996). Habitat fragmentation reduces disperser success in juvenile nuthatches Sitta europaea*: evidence from patterns of territory establishment. Ecography 19: 67-72 en E. Matthysen en F. Adriaensen (1998). The effects of forest size and isolation on the reproductive success of Eurasian Nuthatches* Sitta europaea*. Auk 115: 955-963*

Dit proefschrift

5 In versnipperd habitat is de relatie afwezig tussen het populatieniveau en de kwaliteit van de bezette territoria en daarmee het gemiddelde broedsucces; dit kan worden beschouwd als het ontbreken van een negatieve feedback op het populatieniveau, waardoor de kans op het uitsterven van lokale populaties hoger is.

Dit proefschrift

6 De combinatie van ruimtelijke optimaliseringsmodellen voor de allocatie van nieuwe natuurgebieden en simulatiemodellen voor populatiedynamiek is een bruikbaar instrument voor de ondersteuning van de ruimtelijke planvorming.

Dit proefschrift

7 Wegen van lagere orde leveren een grotere bijdrage aan de versnippering van natuur dan tot op heden werd aangenomen; het beleid dient zich derhalve minder eenzijdig op de hoofdwegen te richten.

C.F. Jaarsma en F. van Langevelde (1998). Strategie tegen versnippering. Lagere orde wegen en auto(snel)wegen in één strategie. Landschap 15, 2: 111-120

8 Theologische leerstukken in de gereformeerde traditie zoals over de drie-eenheid van God, de uitverkiezing, de voorzienigheid, de ware kerk, zijn slechts een middel om de Bijbel te begrijpen; theologen dienen zich hiervan rekenschap te geven bij deelname aan publieke discussies.

9 Het belangrijkste doel van simulatiemodellen is het begrijpen van processen, niet het voorspellen van toekomstige situaties.

10 De postmoderne stellingname dat aan de waarheid van elk groot verhaal dient te worden getwijfeld, wordt zonder enige twijfel aangenomen.

Stellingen behorende bij het proefschrift

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van Frank van Langevelde

Wageningen, 9 april 1999

Abstract

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In this thesis, the effects of habitat connectivity on processes in populations, especially on colonization and habitat selection, are investigated. Therefore, habitat patches and the distances between these patches were modelled as networks. Given that in fragmented habitat these networks consist of several disjointed subsets of patches for a certain species, parameters to measure the connectivity of the patches were first derived. The colonization frequency of unoccupied patches by nuthatches could be best explained by the degree of connectivity measured for threshold distances between patches of approximately 2.4 to 3 km. This indicates that dispersal is a problem for nuthatches in habitat fragmented at that spatial scale. Second, the selection of territories in fragmented and contiguous habitat was compared. Based on a theoretical and empirical study, it is concluded that selection of territories is limited in fragmented habitat compared to contiguous habitat. The quality of the occupied territories in fragmented habitat is lower than in contiguous habitat. This is especially the case when the population level is low. A lower average breeding success can be found in territories with low degree of connectivity. The results indicate the absence of a negative feedback between population level and the average breeding success in fragmented habitat, which contributes to the increased extinction probability of populations. Finally, two spatial allocation models are presented that mitigate effects of habitat fragmentation. These models plan new habitat considering ecological guidelines of minimum patch size and maximum threshold distances and the suitability of the land for competing land uses. The model MENTOR adds new patches that may act as stepping stones between existing patches. The model ENLARGE enlarges existing sites. Both models result in a higher percentage of occupied habitat.

Key words: habitat fragmentation, patchiness, connectivity, colonization, habitat selection, nuthatch, *Sitta europaea*, reserve site selection, metapopulation

Voorwoord

In dit proefschrift wordt verslag gedaan van een onderzoek naar de effecten van de mate van verbinding van het habitat op processen in populaties. Het onderzoek is tot stand gekomen in de periode 1993-1998 bij de leerstoelgroep Landgebruiksplanning van de Landbouwuniversiteit Wageningen. Veranderingen in het landgebruik hebben geresulteerd in versnippering van het habitat van veel dieren. Wat zijn de effecten van deze versnippering op populaties? Kan de ruimtelijke planvorming door het wijzigen van de inrichting van de ruimte bijdragen tot het verminderen van deze effecten? Deze vragen hebben in het onderzoek centraal gestaan. Hoe logisch deze vragen elkaar ook lijken op te volgen, ze vormden voor mij de twee polen waartussen ik mijn weg heb gezocht. Zoals uit het proefschrift blijkt, hebben vragen vanuit de populatie-ecologie mijn grootste belangstelling gehad.

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Tijdens het onderzoek heb ik van 13.583 bomen de stamdiameter gemeten, 10.535 keer de afstand tussen bomen bepaald en van 725 territoria de aanwezigheid en het paar- en broedsucces van boomklevers vastgesteld. Dit hoefde ik gelukkig niet alleen te doen. Mijn dank gaat uit naar iedereen die me hierbij heeft geholpen. Daarbij wil ik ook degenen hartelijk bedanken die hun gegevens ter beschikking hebben gesteld: Frans Post en de vogelwerkgroep Midden Brabant, Arend van Dijk, Alex Schotman, Geoske Sanders en de KNNV vogelwerkgroep Wageningen, Rob Vogel en DLG Noord-Brabant.
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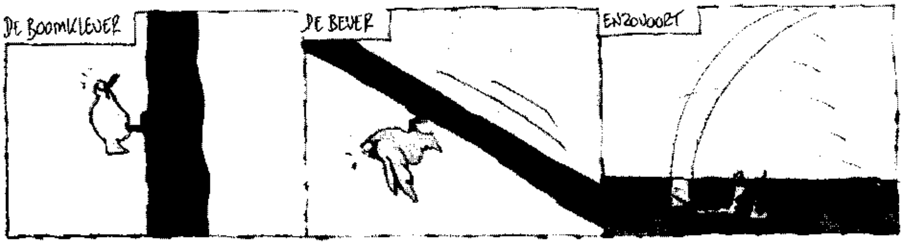

CONTENTS

1 INTRODUCTION

Introduction

1 Research topic

Rural areas provide space for all different kind of land uses, such as economic activities, residential areas and recreation. As a result, the landscapes of the rural areas appear as mosaics of spatially or functionally related systems. Dynamic developments, especially in agriculture and transportation, have transformed the land and its use drastically. In the future, the dynamics in land use will rather increase than decrease. This dynamic and multiple land use had considerable consequences for the ecology of the landscapes. The human-dominated landscapes changed so fast that species were not able to adapt to these changes and populations declined or disappeared. Habitat alteration, loss and isolation lead to this decline in biodiversity. Habitat loss and isolation are often referred to as habitat fragmentation (Burgess and Sharpe 1981, Lord and Norton 1990, Saunders *et al.* 1991, Opdam *et al.* 1993, Andrén 1994). The alteration, loss and isolation of habitat and the effects on population sustainability, and therefore, on biodiversity, depend upon the spatial claims and intensity of the other land uses.

This thesis focuses on habitat fragmentation in the rural areas of the Netherlands. Since the beginning of this century, a lot of attention is given to the decline in biodiversity and the causes for this decline (Weinreich and Musters 1989, Bink *et al.* 1994, H+N+S 1996). A recent report indicates that biodiversity decreases despite the activities of nature conservation, although, the rate of this trend declines (RIVM *et al.* 1997).

I studied effects of habitat fragmentation at population and individual level and opportunities to mitigate these effects by planning ecological networks. The study was restricted to the rural areas in the Pleistocene sandy regions of the Netherlands. Due to the dominance of agriculture, especially dairy farming, these rural areas appear as agricultural landscapes. In these landscapes, agriculture is expected to be still the dominant land use in the future (De Groot *et al.* 1994, Van Eck *et al.* 1997). The majority of the large and small natural areas in the agricultural landscapes in the Pleistocene sandy regions consists of woodlots and hedgerows. In these regions, the wooded area has decreased, especially from the 1950s until the 1970s (Kerkstra and Vrijlandt 1990, Vos and Zonneveld 1993). The remaining elements can be characterized as relatively small, disjunct and sharp bounded. A lot of species can be found in these wooded elements and at the border with the farmland. However, the farmland is often unsuitable or inhospitable to reproduce or find food, and may act as barrier for movement. The biodiversity of the woodlots and hedgerows still decreases due to environmental stress, lowering of the groundwater table and fragmentation (RIVM *et al.* 1997).

Approximately 80% of the natural areas in the Netherlands is dissected in elements smaller than 10 hectares (RIVM *et al.* 1997). For many species, especially for birds and mammals, the amount of habitat in these elements is not sufficient for viable populations (Kalkhoven *et al* 1995, Verboom *et al.* 1997). When the habitat of species is fragmented, their local populations are small and extinctions may occur (Harrison 1991). Small populations have a higher probability of extinction due to processes that have a stochastic character, like low reproduction, genetic inbreeding or environmental fluctuations. Regional survival of these species requires several habitat patches. Then, the connectivity of these habitat patches becomes crucial (Opdam 1990, Hansson 1991, Taylor *et al.* 1993). Extensive theoretical and empirical research shows the importance of sufficient habitat connectivity in landscapes with fragmented habitat for several species (*e.g.*, Fahrig and Merriam 1985, Van Dorp and Opdam 1987, Henein and Merriam 1990, Gilpin and Hanski 1991, Opdam 1991, Saunders and Hobbs 1991, Verboom *et al.* 1991, Arnold *et al.* 1993, Andrén 1994, 1996, Wahlberg *et al.* 1996, Hanski and Gilpin 1997). Local populations of a species that are connected by dispersing individuals constitute a metapopulation (Levins 1970, Hanski and Gilpin 1997; see chapter 2 for definition). Constrained dispersal may affect processes at population and individual level such as a reduction of the probability of successful colonization of unoccupied patches from surrounding local populations and of the opportunities for optimal habitat selection. Due to the low amount of habitat and its widespread fragmentation, the habitat connectivity in human-dominated landscapes may often be not sufficient for viable metapopulations (Hanski *et al.* 1995, 1996).

Since population dynamics depend upon the spatial structure of the landscape (Kareiva 1990, Fahrig and Merriam 1994, Hanski 1994, Wiens 1995), increase in habitat amount or connectivity may positively affect population survival. Several (applied) landscape ecological research efforts indicate possibilities to address fragmentation of habitat by a network approach (*e.g.*, Noss and Harris 1986, Margules *et al.* 1988, Saunders and Hobbs 1991, Smith and Hellmund 1993, Vos and Opdam 1993, Cook and Van Lier 1994, Hanski and Thomas 1994, Arts *et al.* 1995). I define an ecological network as a set of habitat patches in which local populations of a species can act as a metapopulation. The habitat patches in the network are accessible to a certain degree when they are located sufficiently close together. However, a part of the suitable habitat patches can be unoccupied due to the dynamic balance between survival and colonization probability of local populations (Hanski 1994, Hanski *et al.* 1995). This definition of ecological networks has a starting point in population ecology. In this context, they are also called habitat networks or patch networks. In spatial planning, the term ecological network is also often used. Then, it refers to a structural property of landscapes that may have a function for species or other processes (chapter 2).

Spatial planning can play a role in nature conservation by means of defragmentation of habitat and optimization of land use allocation. Defragmentation intends to mitigate the effects of habitat fragmentation: an increase of the size or of the degree of connectivity of habitat patches. In this context, the notion of ecological networks is used as a spatial concept (chapter 2). The spatial concept of ecological networks indicates how the land and its use can be organized to preserve biodiversity and to provide space for developments in land use. A well-known example of the spatial concept of ecological networks is the Dutch National Ecological Network as proposed in the Nature Policy Plan (Min. LNV 1990).

2 Research hypothesis and questions

The objective of the research is to contribute to an improved knowledge about the effects of fragmentation and defragmentation of habitat on populations, in particular effects of differences in the degree of habitat connectivity on colonization and habitat selection. Therefore, the main question of the research was: do networks of patches contribute to population sustainability of species in fragmented habitat? To address this question, I focused on the effects of spatial variables on population processes. The hypothesis was that the degree of habitat connectivity is a crucial feature to constitute an ecological network since it determines processes at population and individual level in fragmented habitat.

The main research question was split up in three questions:

1) What variables can measure the degree of connectivity of the habitat patches? When insufficient connectivity constrains dispersal in fragmented habitat, it will be reflected by the colonization patterns of the species. Are differences in the degree of connectivity related to the probability that patches are colonized?
2) When insufficient connectivity constrains dispersal in fragmented habitat, habitat selection will deviate from optimal selection. Is habitat selection limited in landscapes with fragmented habitat?
3) When networks of patches can mitigate effects of habitat fragmentation by enhancement of the degree of connectivity, how can they be optimally allocated in agricultural landscapes that both meets the requirements for population sustainability and takes into consideration the suitability of the land for competing land uses?

The research is restricted to forest fragments in agricultural landscapes of the Dutch Pleistocene sandy regions. A species-oriented approach was used since effects of habitat fragmentation and defragmentation are species specific. I focused on the European nuthatch *Sitta europaea*. The nuthatch is a songbird of mature deciduous forests. Pairs have strong site tenacity and defend their territory the year round. Although the nuthatch was used as a model species to study effects of fragmentation and defragmentation, I can advance three arguments for selecting the nuthatch. First, research efforts provide evidence that nuthatch populations are sensitive for habitat fragmentation (Opdam *et al.* 1985, Van Dorp and Opdam 1987, Verboom *et al.* 1991, 1993, Enoksson *et al.* 1995, Matthysen and Currie 1996, Bellamy *et al.* 1997, 1998, Schotman in prep.). Populations of the nuthatch in a landscape with fragmented habitat may act as a metapopulation (Verboom *et al.* 1991). At this moment, interesting questions are addressed about consequences of reduced dispersal success of nuthatches in landscapes with fragmented habitat (Matthysen *et al.* 1995, Matthysen and Currie 1996, Bellamy *et al.* 1997, 1998, Matthysen and Adriaensen 1998, Schotman in prep.). This thesis joins in this discussion. It adds to spatially explicit theory in population ecology since nuthatches represent a group of species with relatively small populations, a density-dependent growth and a limited dispersal success. These species may show similar responses when their habitat is fragmented. Second, the nuthatch can be considered as an umbrella species (*sensu* Simberloff 1998) which presence indicates that the forest ecosystem is mature and a high degree of biodiversity can be expected (Siepel 1992). The third argument is that good data on the presence and absence of nuthatches and the location of their territories were available for several regions in the Netherlands.

3 Research context

This thesis contributes to knowledge for substantive planning theory: understanding into the phenomena with which planning is concerned (cf. Faludi 1973, chapter 2). This knowledge is embedded in both a scientific and societal context: an increase in scientific understanding and the application of scientific understanding to the societally defined problem of nature conservation (Pickett *et al.* 1994).

3.1 Scientific context

Extensive research is done to the effects of habitat fragmentation for species of forests. Many forest species appear to be sensitive to fragmentation. Most of the empirical evidence for this has been related to forest birds (*e.g.*, Lynch and Wigham 1984, Opdam *et al.* 1985, Askins *et al.* 1987, Van Dorp and Opdam 1987, Opdam 1991, McCollin 1993, Enoksson *et al.* 1995, Bellamy *et al.* 1996). These research efforts demonstrate the role of habitat amount and connectivity in the presence of populations of forest birds. The effects of habitat fragmentation on species richness have usually been studied with the theory of island biogeography (MacArthur and Wilson 1967). In studies of single species, the metapopulation theory has been applied (Hanski and Gilpin 1997). The theories are related since they assume the same population processes: colonization and extinction of populations in islands or habitat fragments. A debate is going about the questions 'if, or when, effects of habitat fragmentation are solely due to habitat loss (the random sample hypothesis) or to both habitat loss and isolation (the theory of island biogeography and the metapopulation theory)?' (Haila *et al.* 1993, Andrén 1994, 1996, Bellamy *et al.* 1996). In contrast with the theory of island biogeography and the metapopulation theory, the random sample hypothesis implies that local extinction and colonization in small fragments are a reflection of changes in territory location from year to year and disconnected from population dynamics (Haila *et al.* 1993). It is argued that small habitat patches can be considered as random samples from large ones (Connor and McCoy 1979, Haila 1983). When the random sample hypothesis is true, habitat selection is optimal, *e.g.*, as assumed in Fretwell and Lucas (1970) and Pulliam and Danielson (1991). This thesis provides a contribution to this debate by investigating the effects of the degree of connectivity on colonization of unoccupied patches (chapter 4) and on habitat selection (chapter 5 and 6).

Crucial in the research to population dynamics in landscapes with fragmented habitat is the acknowledgement that habitat patches differ in size and quality, and that they are not equally accessible (Fahrig and Merriam 1994). There is a need for more understanding in the importance of spatial variables in the population ecology of species (Kareiva 1990, Fahrig and Merriam 1994, Wiens 1995). For example, the way a certain amount habitat is arranged appears to be a key scientific question (Adler and Neurnberger 1994, Harrison and Fahrig 1995, Andrén 1996, chapter 4, 5 and 6). Another important variable is the spatial scale. It is important to assess the effects of habitat fragmentation at the scale that agrees with the scale of movement of the concerning species (Levin 1992, Wiens 1995, chapter 4 and 5). A fundamental question that often appears in literature about developments in landscape ecology is 'how and at what scale does the complex spatial structure of landscape mosaics affects ecological patterns and processes?' (*e.g.*, Forman and Godron 1986, Turner 1989, Forman 1995, Wiens 1995). This question was the starting point for the three research questions in this thesis.

3.2 Societal context

The key issue in planning is "how knowledge should be properly linked to action" (Friedmann 1987, pp. 73-74). The action in spatial planning already exists, *e.g.*, see chapter 2, Cook and Van Lier (1994), Arts *et al.* (1995), Jongman and Kristiansen (1998). Landscape ecology provides useful theory, data and experiences for spatial planning (Forman and Godron 1986, Vos and Opdam 1993, Noss *et al.* 1997, chapter 2, 7 and 8). The knowledge provided by this thesis can be applied as scientific support for spatial interventions.

Effective planning includes a clear problem detection and exploration of possible solutions. In the praxis of planning, there is an increasing need to utilize guidelines that can mitigate effects of habitat alteration, loss and isolation. However, this requires a clear understanding of the quantitative relationships between landscape characteristics and the response of populations (Saunders *et al.* 1991, Soulé 1991, Verboom *et al.* 1993). In this thesis, the problem detection is conducted as the analysis of the effects of the degree of habitat connectivity on processes at population and individual level (the first and second research question). When the causes for the decline in biodiversity are mapped and modelled, knowledge is needed about 'what interventions should be applied, on which locations, how should they be conducted, and how should the suitability of the land for competing land uses be taken into consideration?' (the third research question).

When scientific knowledge is used in planning, it can be seen as a tool to realize certain objectives. Since the application of scientific knowledge has pretentions of understanding, prediction and control of the studied phenomena (Schuurman 1989), the use of this tool has limitations (as in fact, the use of each tool has limitations). These pretentions are both useful and problematic. They are useful in terms of a scientific foundation of interventions (Noss *et al.* 1997). However, it can be problematic due to the forceful claims made about it. Often, decisions are made based on knowledge that is insufficiently founded. Moreover, scientific knowledge is not the only type of knowledge needed in planning. Normative knowledge or knowledge about proper procedures is also essential, *e.g.*, a relevant aspect in spatial planning is to increase the participation of interest groups in the process.

The possibilities and limitations for application of the knowledge provided by this research are discussed in chapter 9.

4 Methods and outline of thesis

Landscape ecology became a basis for spatial planning for the rural areas. For the Dutch planning tradition, this is illustrated in chapter 2. This chapter provides an overview of developments in spatial planning and spatial concepts related to the rural areas in the Netherlands. It can be regarded as an introductory chapter.

Chapter 3 and 4 address the first research question about the degree of habitat connectivity and the effects on colonization. Therefore, habitat patches and the distances between these patches are modelled as networks. In landscapes with fragmented habitat, these networks appear as nonconnected networks. In chapter 3, parameters are derived that measure the degree of connectivity of networks and their elements concerning the size (in terms of the number of elements) and the spatial configuration of the networks. The parameters are used in a study that relates the degree of connectivity of habitat patches with colonization data (chapter 4). I studied the process of colonization using pattern data of distribution and abundance of nuthatches in three regions in the Netherlands: Midden Brabant, Zuidwest Drenthe and Noordoost Twente.

Chapter 5 and 6 address the second research question about limited habitat selection in landscapes with fragmented habitat. In chapter 5, the results of a spatially explicit, stochastic model are presented. The model simulates the occupancy of sites in landscapes with differences in the amount and spatial configuration of the breeding habitat. Also, landscapes with a relatively large amount of breeding habitat were included. This study deduced hypotheses about limited habitat selection, which are tested with empirical data of nuthatch populations (chapter 6). This study was conducted by comparison of the distribution patterns and breeding success in a region with contiguous habitat and regions with fragmented habitat: Midden Brabant, Zuidwest Drenthe, Noordoost Twente and Veluwezoom. The latter region has contiguous habitat and can be considered as a reference region where the ideal distribution can be expected.

The third research question about allocation of ecological networks in agricultural landscapes is addressed in chapter 7 and 8. The model MENTOR was developed for allocating stepping stones between existing habitat patches. The use of the allocation model resulted in a set of landscapes with different amount and configuration of habitat (chapter 7). For these landscapes, the spatially structured population model METAPHOR, developed at the Institute for Forest and Nature Research in Wageningen (Verboom 1996), was used to evaluate the population performance. The effects for the agricultural use were assessed in terms of changing spatial conditions for farming. In chapter 8, models for two strategies for conservation planning in human-dominated landscapes are discussed and compared: the first model ENLARGE enlarges existing habitat patches, and the second model MENTOR connects the patches with stepping stones. Both chapters 7 and 8 use scenarios with probable developments in the rural areas of the Pleistocene sandy regions in the Netherlands.

Finally, chapter 9 provides a discussion about the relationships between the degree of habitat connectivity and the response of nuthatches, especially colonization (at population level) and habitat selection (at individual level), and about possibilities to increase the degree of habitat connectivity realized by allocating networks of habitat patches to enhance population sustainability.

Due to the structure of the thesis in chapters that are written as separate papers, different terms are used for the same subject: *e.g.*, landscape planning in chapter 2, spatial planning in chapter 3 and conservation planning in chapter 7 and 8. All these terms refer to planned spatial interventions inherently related to the use of the land. They are not directly linked to the Dutch planning instruments.

2 CONCEPTUAL INTEGRATION OF LANDSCAPE PLANNING AND LANDSCAPE ECOLOGY, WITH A FOCUS ON THE NETHERLANDS

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Conceptual integration of landscape planning and landscape ecology, with a focus on the Netherlands

1 Introduction

In recent decades, landscape planners became aware of planning for nature. Several authors have linked (landscape) ecology and planning in a preliminary way and have documented examples of applications. Ecological approaches of landscape planning are developed as useful planning frameworks, including guidelines for the way data should be collected, analyzed and presented, for participation of interest groups and for implementation and monitoring plans (*e.g.*, McHarg 1969, Fabos 1979, Vink 1983, Ruzicka and Miklos 1990, Steiner 1991). These approaches require a focus on interactions between landscape components and processes, and on the context in which the plan area is placed. This approach is more or less based on ecological theories, such as theories about biocybernetics and the hierarchical organization of nature. However, ecology is becoming well integrated in planning and design, it appears that ecology is considered as an attitude, rather than a substantive contribution to planning. For example, Hackett (1971, p. 18) summarizes the dilemma of applying ecology in planning as "the growing acceptance of the need for an ecological basis in planning large areas of landscape is an encouraging fact to set against the insatiable demands of a materialistic industrial society. But, whereas acceptance of a principle is one thing, the question of putting it into practice is quite another matter". Yet, there is a need for a deeper understanding to use (landscape) ecological principles and spatial concepts in landscape planning, which contribute to use the collected data in planning and design, and to recognize how to intervene in the landscape.

To enhance the ecological integrity of the landscape and achieve sustainable land use, landscape planning should consider natural and social processes and their spatial relationships in a comprehensive way. This approach offers the challenge to design landscapes that are beautiful, ecologically healthy, as well as productive of goods and services required by society. Also, it should include a framework to assess and protect landscapes for their intrinsic values (after Golley 1987).

The relationships between people and the land change over time as a result of a changing perception of the land and spatial transformations. The changing perception of the land is expressed in spatial concepts, which in turn may lead to interventions induced by planning. This chapter will show that planning the landscape and its spatial concepts have become landscape ecology based, called landscape ecological planning. It provides an overview of developments in landscape planning and spatial concepts related to the rural areas in the Netherlands. Several problems will be addressed: (1) what are the developments in landscape planning for nature and landscape ecology in the Netherlands; (2) what are the key connecting issues between landscape planning and landscape ecology; (3) what is the role of landscape ecology in landscape planning; (4) what spatial concepts are used in landscape planning for nature; (5) what is the content of the spatial concept of ecological networks, and what are the substantive landscape ecological principles for planning ecological networks?

2 Landscape ecological planning in the Netherlands

Planning is a human activity inherently related to the use of land. Planning is defined as "the use of scientific and technical knowledge to provide options for decision making as well as a process for considering and reaching consensus on a range of choices" (Steiner 1991, p. 4). According to Faludi (1973), two main types of planning theory can be identified: procedural and substantive theories. Procedural planning theories, or theories of planning, focus on methodological issues, such as purposes, principles and characteristics of the planning process. These theories provide guidelines for the way planners operate in formulating objectives and planning goals, inventory and assessment of the land, development of spatial concepts, generation and evaluation of scenarios, participation of interest groups and implementation of plans. For example, a working method for landscape planning was presented by Steiner and Osterman (1988) applied to a case study of soil erosion, and Duchhart *et al.* (1988) for agroforestry. Substantive planning theories, or theories in planning, provide insights into the phenomena with which planning is concerned. They lead to better understanding of the landscape as the interface between natural and social processes, and may legitimate interventions in the landscape. Substantive planning theories provides guidelines for spatial concepts and interventions in the landscape. These theories can be both descriptive and predictive. They originate from natural and social sciences, such as geography, ecology, economics, anthropology and sociology. The distinction between theory in planning and theory of planning should not result in an entirely separate development of the two. Clearly, both types of theory are needed for effective planning (Faludi 1973, Ndubisi 1997). This chapter does not provide a discussion about planning theories, but rather use them to discuss landscape ecological planning and the spatial concepts.

Planning the landscape involves decisions about alternative futures focus on the wise and sustained use of the landscape to accommodate human needs. Landscape planning provides an opportunity to influence spatial practices and to create new landscape structures. It attempts to allocate land-use activities while minimizing the disturbance effects of these activities on other land uses and the environment. In this context, landscape planning is a process of managing transformations of the landscape to bring land use in harmony with natural processes, based on knowledge of the reciprocal relationships between people and the land. An ecological approach has been globally accepted and advocated in planning and design literature. The historical link between ecology and planning is documented by, for example, Hackett (1971), Naveh and Lieberman (1984), Steiner *et al.* (1988) and Ndubisi (1997). Planning became ecologically based because of a growing environmental consciousness in society about pollution, destruction of nature, loss of amenity and the depletion of resources. The increasing environmental concerns changed the landscape planning paradigm. Pepper (1986) states that to understand the actual situation of environmentalism (*i.e.*, ideologies and practices which inform and flow from a concern with the environment), one should study how people perceive the environment, and the nature of the — economic, social and cultural — presuppositions which colour these perceptions. The question of how landscape planners perceive and act to change the landscape is not free from these notions. In the subsequent sections, a historical overview of an ecological approach in landscape planning for nature in the Netherlands is provided, exploring some of these presuppositions.

2.1 Retrospective analysis of the evolution of an ecological approach in landscape planning for nature

In areas with a relatively high density of human activities and conflicting land uses, the need for landscape planning is evident. European and North American countries (especially the United States and Canada) have a long tradition of landscape planning. A number of themes and issues have emerged as ecological planning has developed in Europe and North America. For example, the incorporation of the ideas of multiple land use, sustained yield and carrying capacity into planning, and the acceleration of the movement towards holistic planning for environmental issues (Steiner *et al.* 1988). The shifting landscape planning paradigm incorporating an ecological approach is described for the USA by Steiner *et al.* (1988) and Ndubisi (1997). The latter distinguishes several stages in the paradigm shift and changes in the perception of land. Ndubisi described how an awaking of a belief for guiding the wise use of the landscape for human use was beginning to emerge. This belief was primarily based on faith and intuition of the intrinsic character of land as a basis for guiding. Its tenets were not yet founded on rigorous proof. Next, a formative period appeared in which planning based on the belief system seemed innovative and rather successful attempts. In the 1960s consolidation occurred, characterized by the explicit linkage between ecology and planning, the articulation of ethical principles governing human relations to the land, and the refinement of techniques for applying ecological ideas in landscape planning efforts. This was followed by the acceptance of a paradigm for the ecological approach in landscape planning (see Hills 1961, Lewis 1969, McHarg 1969). More recently, a landscape ecological planning approach matured, which characterizes a majority of current work in landscape planning in the USA.

Land use and landscape planning in the Netherlands is characterized by scarcity of land. The landscape types of the Netherlands have been drastically changed by human interventions, such as reclamation of land, construction of drainage systems, expansion of road patterns, urbanization, and intensification of agriculture. The evolution of landscape planning in the Netherlands reflects several social, economic and political developments and a change in the perception of land (Van Lier 1981, Van der Valk 1982, Groeneveld 1985, Grossman and Brussaard 1989, Driessen 1990). Two periods can be distinguished: the period from the beginning of this century until 1954 and the period from 1954 until now.

(1) Period from the beginning of this century until 1954

Reclamation and optimal allocation of land for agricultural use has been evident for a long time in the Netherlands. Originally, landscape planning was primarily mono-objective. Land consolidation projects with an agricultural purpose aimed to a spatial re-arrangement of farmlands, enhancement of the accessibility of field parcels and farm households by building and improvement of roads, construction of drainage systems, improvement of soils and relocation of farm buildings. Land consolidation was needed because of the unfavourable agricultural land structure that existed in many areas of the country. The first law for regulation of these projects, the Land Consolidation Act, became effective in 1924. An increased demand for space to exploit the land for agriculture occurred. Agricultural (re)allotment and land reclamation projects provided a strong stimulus for structural agricultural adaptations to economic and technological developments. Especially after the Second World War, landscape planning was aimed to increase agricultural production and productivity.

In the period from the end of the 19th century until the 1950s, the importance of protection of natural and scenic values was also recognized. Nature conservation organizations arose in the Netherlands around 1900. By the 1930s, the State Forest Service became advisor in land consolidation projects for issues related to the natural and scenic aspects of the landscape. The then nature conservation activities were primarily focused on protection of 'untouched' natural areas, such as wetlands, forests and meandering brooks. For some other areas a compromise was made with other interests, such as outdoor recreation and forestry. Nature conservation organizations have bought and managed nature reserves since the beginning of this century. The biologist Dr. Jac. P. Thijsse, one of the leaders of the then nature conservation movement, proposed in 1938 that the Land Consolidation Act should not only promote agriculture, but also nature conservation and housing. However, his idea was rejected.

The period from the beginning of this century until 1954 can be described as a period in which land consolidation was developed to reallocation and improvement of lands for agriculture. Landscape planning had mainly a single purpose. An awaking of nature conservation appeared during this period.

(2) Period from 1954 until now

Land consolidation projects, which evolved into land development projects, tended towards a multi-objective approach. Societal developments, such as the expansion of towns, increasing mobility, higher recreational needs and the enhanced value assigned to nature and landscape, led to changes in the perception of the land. The notion was accepted that the landscape is not only an agricultural production space, but also to provide space for multiple use. The legitimacy and acceptability of landscape intervention was changed. The Land Consolidation Act was revised in 1954 to adapt the planning procedure to pay more attention to the protection and restoration of the landscape. Several public interests, such as outdoor recreation, nature conservation and forestry, were increasingly taken into account. In this context, the demand for land consolidation and development grew during the 1950s. However, the priority in landscape planning remained an increased agricultural production.

During several decades of land reclamation and consolidation, large parts of the Netherlands have changed tremendously in terms of the structure of farmlands, resulting in a considerable increase in agricultural productivity and profits. Reallotment projects were stimulated by the government to meet the needs of modern mechanized agriculture. These projects have changed the formerly small-scale agricultural landscapes, especially in the sandy regions. Irregularly shaped plots have been adjusted and adjoining parcels have been merged. Many small landscape elements were eliminated during this process. Developments in the rural areas, such as mechanization, specialization and intensification of land use, gave rise to serious environmental problems with a loss of diverse natural values (Weinreich and Musters 1989, Bink *et al.* 1994).

Since the late 1960s and 1970s, nature conservation has received more attention. The developments after the Second World War, especially in modern agriculture, were seen as great threats to nature and landscape. A growing concern about environmental quality from the public appeared. Several European national governments accepted responsibility for nature conservation (Bischoff and Jongman 1993). During the 1960s, the conservation approach changed: the definition of nature widened and its appreciation increased. A revaluation of agricultural areas occurred. Nature conservation values were recognized and the preservation of natural values within agricultural landscapes became an important policy objective. For example, the decline of small landscape elements, such as wooded banks and hedgerows, was noticed. Protection and enhancement of these elements increased. The arguments for nature conservation also changed. Not only rare and endangered species had to be conserved, but also human's experience of the landscape, especially visiting the natural areas, became an important argument. These developments can partly be explained by an increase in ecological knowledge. Moreover, the societal basis of nature conservation grew: the valuation of the beauty of nature, the love for nature and the recognition of its opportunities for outdoor recreation increased. This trend was expressed in an increase of members in non-governmental nature conservation organizations (Van der Valk 1982, Dekker and Van der Windt 1992).

The 1954 law for land consolidation was increasingly criticized. In 1972, the national government initiated a new law to replace the 1954 law, the Land Development Act, which was implemented in 1985 after a lengthy parliamentary debate. The new law was broader in scope to recognize the multiple use of the rural areas. It also established a stronger connection between physical planning and land development. Several forms of land development were proposed, and participation of interest groups and inhabitants involvement was regulated. The broadened purpose of the Land Development Act is stated as follows: Land development strives toward the improvement of the countryside in conformity with the functions of that area, as these are specified in the framework of physical planning. In this context, the nature of landscape planning in the Netherlands became multi-objective. Planning included measures and provisions for agriculture, forestry, nature conservation, outdoor recreation, traffic and landscape maintenance. Indeed, agriculture still characterizes the structure of the rural landscapes since sufficient farmland remains important for the Netherlands. Multiple land use requires a thorough landscape planning approach, which provides well-considered spatial solutions. Different interests in landscape planning may conflict, especially uses with competing land claims. Moreover, each land use may have its own problems. The economic and technological developments in agriculture, wherein since 1960 the policy of the European Community and recently the General Agreement on Tariffs and Trade (GATT) play an important role, forced farmers to continually improve farm management and the layout and structure of the farmlands. The decline of area for agriculture, as a result of claims from other land uses, requires improved farmland and a well-suited parcelling, while reducing negative impacts on the environment. Modern agriculture will be limited in the use of manure and pesticides. Landscape planning can contribute by means of reallotment and rural development to both an increase in the economic benefits and enhancement of the social and working climate in agriculture. The complicated planning process of land development is designed to make the best use of the limited amount of available land and to deal with several interest groups. In an early stage of this process, involvement of several sectors are required — agriculture, nature conservation, landscape maintenance and outdoor recreation — containing consequences of the plans. Grossman and Brussaard (1989) explain this planning process. Nowadays, the emerging multiple land-use approach is still discussed (*e.g.*, CLMI 1990, Min. LNV 1992).

Since the perception of nature reflects people's fundamental attitudes towards the land (*e.g.*, Philipsen 1995), changes in the perception of nature will lead to different nature conservation strategies. In the Netherlands, a debate developed on the question what is nature, and what natural values should be protected: untouched nature, semi-natural areas or a maximum biodiversity? These objectives require different spatial strategies, which can be placed within a continuum from segregation to integration of land uses (see section 5.2). In this period, the definition of nature was restricted and renewed, in which the emerging discipline of landscape ecology played an important role. In this context, restoration of natural processes was advocated (Dekker and Van der Windt 1992). New nature conservation strategies were formulated in the Nature Policy Plan on the preservation of natural areas and restoration of former or potential natural areas (Min. LNV 1990). The keynote of this plan is to realize a robust national ecological network of sustainable ecosystems considered of (inter)national importance. As Harms *et al.* (1993) state, landscape planning for nature recently changed to incorporate both nature preservation and restoration. Landscape planning is considered as an essential tool to implement this new policy. Most planning projects have a direct relationship with the national ecological network. Moreover, since 1994 new land development projects are obliged to make an environmental impact assessment.

The period since 1954 can be characterized by an awaking and consolidation of an ecological approach in Dutch landscape planning. In the 1980s and 1990s, this approach matured in landscape planning. Extensive landscape planning and design studies have been based on (landscape) ecological theories, data and experiences (*e.g.*, Schoorl *et al.* 1987, Helmer and Smeets 1990, Kadaster 1992, Harms *et al.* 1993).

2.2 Emerging landscape ecology based landscape planning

The close relationship between landscape planning and landscape ecology is pointed out by several authors (*e.g.*, Brandt and Agger 1984, Forman and Godron 1986, Schreiber 1988, Zonneveld and Forman 1990, Vos and Opdam 1993, Smith and Hellmund 1993, Jongman 1993). Bischoff and Jongman (1993) note that nature conservation in Europe became landscape ecology based in the last decade. Landscape ecology is a relatively new discipline and has been influenced by ecology, geography and vegetation science. The term "landscape ecology" was introduced by

Troll (1939). It is the study of spatial relationships and functional interactions between component ecotopes of a kilometres-wide heterogeneous area, and the way in which these bring about changes of structure and function in the ecological mosaic over time (Forman and Godron 1986, Brandt and Agger 1984, Naveh and Lieberman 1984, Turner 1987). In this context, landscape is defined as "a heterogeneous land area composed of a cluster of interacting ecosystems that are repeated in similar form throughout. Landscapes vary in size, down to a few kilometres in diameter" (Forman and Godron 1986, p. 11). This heterogeneous land area contains a mosaic of land forms, vegetation types and land uses. The emphasis on patterns and processes and their interactions over time within a landscape scale mosaic, is what differentiates landscape ecology from other ecological disciplines. Several authors describe landscape ecology, its origin and paradigms (*e.g.*, Zonneveld 1982, 1990, Naveh and Lieberman 1984, Forman and Godron 1986, Turner 1989). For the Netherlands, Opdam (1993) describes twenty years of landscape ecology and its connection to landscape planning. For a short overview, Opdam distinguishes three periods of time: the period of the 1970s, the period of the 1980s and the period of the late 1980s to the present.

(1) Period of the 1970s

Dutch landscape ecology originated in the 1970s. The development was induced by demands for an integrative environmental survey of the Dutch rural areas. To prevent the increasing destruction of nature and landscape, it was decided that the natural values should be mapped. Several landscape characteristics, such as geomorphology, geology, hydrology, vegetation, fauna and land use, were mapped and combined (Burggraaff *et al.* 1979). These environmental surveys mapped several landscape patterns, which were overlaid to search for coherence between the landscape patterns. It resulted in maps with relatively homogeneous land units (Zonneveld 1989). Such surveys provided principles for landscape planning, such as gradients, natural equilibrium and ecological functions. For example, for the entire Netherlands an environmental survey (GEM) was done (Van der Maarel and Dauvellier 1978). It mapped several ecotopes of the Netherlands as related to the potential natural vegetation. Yet, spatial relationships between elements in the landscape were hardly investigated.

(2) Period of the 1980s

In the next period, landscape ecological research became more concerned about natural processes and interactions between landscape patterns, for example, nutrient cycles, hydrological flows and movement of species. A shift from the study of static patterns and of community composition towards dynamic phenomena such as population extinction, colonization, isolation, migration and dispersal appeared. The landscape ecological research was divided into several topics. In the Netherlands, this shift stimulated a resumed biological and landscape ecological interest for the isolation of most nature reserves, and for small landscape elements and their function in the agricultural surroundings of these reserves (*e.g.*, Opdam *et al.* 1986).

(3) Period from the late 1980s to the present

In the current period, the fragmentation of landscape ecological research and the need for synthesis was recognized (*e.g.*, Vos and Stortelder 1988, Vos and Opdam 1993). The way environmental surveys are carried out and the collected data is interpreted changed. In the beginning, the conservation of existed natural values was emphasized. In later years, possibilities to restore natural processes are explored. Landscape ecology matured. For example, the Nature Policy Plan of the Netherlands is based on recent landscape ecological research. This plan emphasized the necessity of addressing environmental problems, such as habitat fragmentation, acidification and eutrophication. In turn, the implementation of this policy in landscape planning may lead to broader and deeper problem inquiry in landscape ecology. In the Netherlands, several researchers have played a role in the explicit integration of landscape ecological principles and methods in landscape planning, for example, Vink (1983), Zonneveld (1989), Harms and Opdam (1990) and Jongman (1993).

Several key connecting issues between landscape planning and landscape ecology can be distinguished.

3 Key connecting issues between landscape planning and landscape ecology

3.1 Landscape and its processes as subject of study

In landscape planning, the landscape and its processes are the subject of study (material object). A key attribute of this subject is the spatial form. The subject is shared with other disciplines, such as landscape ecology, geology and geography. A range of definitions of the term landscape exists, depending upon the phenomena under consideration and presuppositions of each discipline. A common element in most definitions is, that landscapes are the tangible and visual parts of earth's surface consisting of a complex of living and non-living entities. The spatial character of landscapes is treated as a fact of nature, in which all objects exist and move, and space as a measurable attribute of these objects. It can be measured by parameters such as area, volume, direction, pattern, shape, distance and position.

Through representation and imagination (Harvey 1989), people give meaning to the landscape, as space for agriculture, nature conservation or recreation. Each of the mentioned disciplines may have its own point of view, theory and jargon, and therefore its own representation of landscape (Toth 1988). In this sense, the term landscape is differently interpreted as, for example, landscape scenery and the landscape as a conglomerate of land attribute units. Imaginations are mental inventions that imagine new meanings or possibilities for spatial practices. These imaginations may contain codes, signs, plans for the future and imaginary landscapes (*e.g.*, depicted as designs or paintings). Imagination of spaces is pre-eminently the domain of planning that may lead to interventions in the landscape.

The landscape is interpreted as the interface of natural and social processes. Many human practices involve decisions that alter landscape patterns to facilitate desired functions. Landscape ecology deals with landscapes as the total spatial and functional entity of natural and cultural systems. A definition of landscape from the landscape ecological point of view was given in the previous section. A tenet of landscape ecology is that the juxtaposition of ecosystems or landscape elements regulates the distribution of species, nutrients and energy (Forman and Godron 1986).

The spatial nature of both landscape planning and landscape ecology indicates a common bond. However, the way of regarding the landscape (the formal object) of both disciplines differs. The nature of landscape planning is to intervene purposively in the landscape. Planners are agents of change (F. Steiner pers. comm. 1994). To bring about transformation based on imaginations, planning is considered fundamentally as an art, and is inherently normative and value laden. The formal object of landscape ecology is to understand and describe the landscape, its structure, function and changes. Ecologists and geographers are scientists using the landscape to generate and test hypotheses in theory building. In identifying what distinguishes planning and design from landscape ecology and other spatial sciences, planning goes beyond the mere explanation of spatial phenomena. It has primarily to do with synthesis, rather than analysis. In this sense, planners wish to know what motivates the objects of their planning, and what forces bring about changes. Based on this knowledge, among which knowledge of ecological processes, planners propose interventions.

3.2 An holistic and interdisciplinary approach

An important presupposition of landscape planning and landscape ecology is that people, plants, animals and the abiotic substrate, all become understood as interdependent parts of a larger system. It is proposed that the holistic approach provides a better appreciation and understanding of the intricate web of interactions between people and the land. The holistic axiom that "the whole is more than the sum of its parts" was first stated by Smuts in 1926, and introduced to ecology by Egler in 1942 as the concept of the hierarchical organization of nature. Holism has become a basic philosophical concept in landscape ecology. It provides the basis for studying entities without knowing all the details of their internal functions. In essence, the holistic approach in landscape ecology and landscape planning "viewed the landscape not just as an aesthetic asset (as by most landscape architects) or as part of the physical environmental (as by most geographers), but as the total spatial and visual entity of human living space, integrating the geosphere with the biosphere and the noöspheric man-made artefacts" (Naveh and Lieberman 1984, p. 21). Regarding landscapes as complex systems, landscape ecology has a principal holistic problem definition.

As is stated before, landscape planning requires a similar synthesis of knowledge about processes and patterns and their mutual interactions. This synthesis is necessary to understand the landscape, because different disciplines may investigate different topics, such as flows of water, species, nutrients, disturbances in the landscape and ecotones. Such holistic approach essentially goes beyond reductionism (Hall 1988, Zonneveld 1990, Opdam 1993).

Inherent to this holistic approach is the interdisciplinary character of both landscape ecology and landscape planning. The field of landscape ecology demands the contribution and interactions of a range of disciplines, for example, population ecology, ecosystem ecology, geography, hydrology and soil science[1]. Many of these disciplines have contributed to recent developments in landscape ecology (Toth 1988). Since landscape planning and design are based on the understanding of how complex landscapes originate, how they currently exist, and how they will change, they also require an interdisciplinary approach. Problem solving at the landscape level requires knowledge and awareness of the complex interactions between social and natural components in the landscape. This analysis depends on the contribution of various disciplines, because no profession by itself can fully understand all the intricacies involved in making decisions about the wise and sustained use of the land.

3.3 Scale issues and the hierarchy paradigm

Several authors have written about scale and the interactions within and between different scale levels in the landscape (*e.g.*, Young *et al.* 1983, Meentemeyer and Box 1987, Urban *et al.* 1987, Turner 1989, Hall 1991). The structure, function and change of landscapes are scale-dependent. The measurement of spatial patterns and heterogeneity is dependent upon the scale that is considered. A landscape may appear to be heterogeneous or fine-grained at one scale, but quite homogeneous or course-grained at another. Natural and social processes occur in a specific time and spatial scale. The scale questions in landscape planning parallel those in landscape ecology. The hierarchy paradigm as applied to landscape ecology, provides guidelines for defining the functional components of a system, and defines ways components at different scales are related to one another (Urban *et al.* 1987, Van den Aarsen 1994). The complexity of landscapes can be partially simplified by decomposing them into a hierarchical framework, in which each scale level may have its own properties and mechanisms.

Table 1 *A proposed hierarchical set of ecosystem classifications at various spatial scales (Klijn and Udo de Haes 1994)*

	Indicative mapping scale	Basic mappable unit
Ecozone	1: >50,000,000	>62,500 km^2
Ecoprovince	1: 10,000,000-50,000,000	2,500-62,500 km^2
Ecoregion	1: 2,000,000-10,000,000	100-2,500 km^2
Ecodistrict	1: 500,000-2,000,000	625-10,000 ha
Ecosection	1: 100,000-500,000	25-625 ha
Ecoserie	1: 25,000-500,000	1.5-25 ha
Ecotope	1: 5,000-25,000	0.25-1.5 ha
Eco-element	1: <5,000	<0.25 ha

Spatial and temporal scales are also important in landscape planning. In general, three scale levels are distinguished in landscape planning: site, local and regional level (Haber 1990, Zonneveld 1989). Table 1 gives a terminology proposal by Klijn and Udo de Haes (1994) for a hierarchical set of ecosystem classifications at various spatial scales. The elements at site level, called eco-elements or ecotopes, are areas less than a few hectares. An ecotope is the smallest and relatively homogenous landscape element that can be mapped at scales of 1: 5,000 to 1: 25,000. The elements at a local level are called ecosections and ecodistricts. The regional level contains ecoregions or regional natural units. The landscape mosaic corresponds with the regional scale. Especially the regional or landscape level is the strategic planning level where landscape planners are looking for opportunities and constraints to direct the current land-use patterns, to link possible landscape interventions with costs and benefits to people and nature, as well as to configure land-use changes over time.

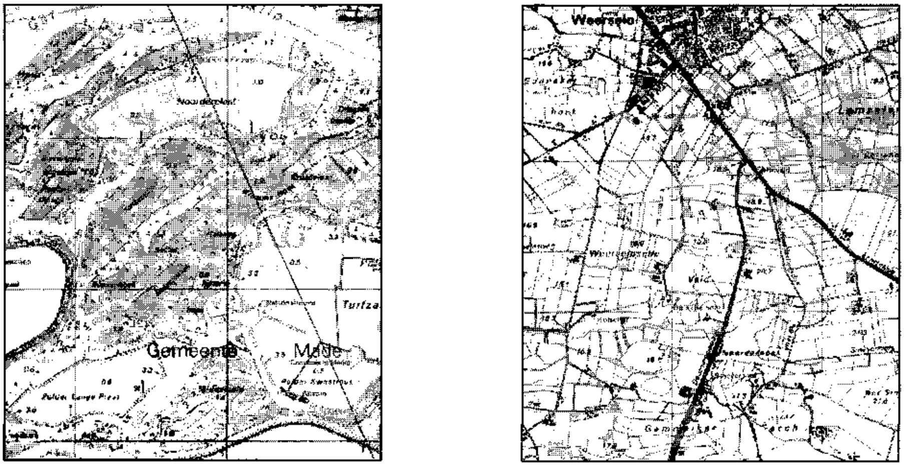
3.4 Recognition of human influences in the landscape

As an interface of natural and social processes, the landscape reflects the history of the dialogue between people and the land. Both the continuity and the variability of land use are present in the landscape. Nowadays, most landscapes have been more or less influenced by human practices. The resulting landscape mosaic is a mixture of natural and human-managed patches that vary in size, shape and arrangement. Landscape planning addresses those issues that concern the interactions between people and the land. A substantial amount of landscape ecological research, however not necessarily each part, pays attention to human influences in the landscape. Naveh and Lieberman (1984, p. 9) state that "one of the central features in the theory of landscape ecology is the recognition of the dynamic role of man in the landscape and the quest for the systematic and unbiased study of its ecological implications". Impacts of human activities on landscapes are discussed by a number of researchers, for example, Burgess and Sharpe (1981), Forman and Godron (1986), Jongman (1993) and Vos and Opdam (1993). Recognition of human influences is particularly apparent in the Dutch landscape. A central feature in Dutch landscape ecology and planning is the acceptance of the dynamic human role in creating heterogeneous landscapes (Vink 1983). Several authors describe the changes in the Dutch landscapes resulting from human influences (*e.g.*, Kerkstra and Vrijlandt 1990, Vos and Zonneveld 1993). They provide an overview of the developments in modern land use which have led to changes in natural patterns and processes in the landscape.

Spatial scale and dynamics of land use may be different from the original natural process. Human-dominated landscapes may change according to economic and social factors such as price regulation, mechanization, or transfers of land ownership. Changes in land use may result in different types of landscape. A human landscape modification gradient can be described, from natural, managed or semi-natural, agricultural, suburban, to urban landscapes (see figure 1). This gradient is based on increasing impact of interventions, from shifting cultivation, extensive agriculture, industrial agricultural, to urbanization. Landscape ecology should study the whole range of human-dominated landscapes. Then, it can provide knowledge for interventions in landscapes such as can be found in the Netherlands.

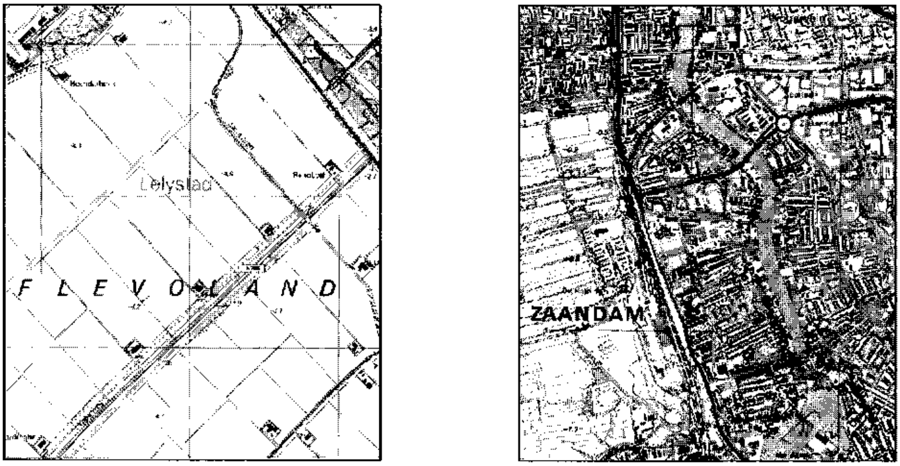
4 Landscape ecology and its role in landscape planning

The application of landscape ecology in planning landscapes is relatively new. For the Netherlands, the evolution of landscape ecological planning is discussed in section 2. Also in other countries, this issue is gaining interest, for example, in Germany (*e.g.*, Woebse 1975, Haber 1990, Jedicke 1990), France (*e.g.*, Burel and Baudry 1990), the Czech and Slovak republics (*e.g.*, Ruzicka and Miklos 1990) and the USA (*e.g.*, Noss and Harris 1986, Soulé 1991, Smith and Hellmund 1993).



Semi-natural landscape of the Biesbosch in the middle of the Netherlands

Small-scaled agricultural landscape of Twente in the east of the Netherlands



Large-scaled agricultural landscape of the Flevopolders in the middle of the Netherlands

Urban landscape of the Randstad in the west of the Netherlands

Figure 1 *Gradient of several landscape types in the Netherlands, from a semi-natural landscape to an urban landscape*

The emergent discipline of landscape ecology contains both a scientific and a philosophical stream. For example, Zonneveld (1982) regarded landscape ecology as a formal bio-, geo- and human science, and as an holistic attitude or state of mind. He states that everyone who has the attitude to approach the environment — including all biotic and abiotic values — as a coherent system, as a kind of whole that cannot be really understood from its separate components only, is a landscape ecologist. Landscape ecology as a philosophy is also advocated by Naveh and Lieberman (1984), since they make an attempt to show how landscape ecology can contribute to the active role of people in design and further constructive evolution through self-reflection and human consciousness. Increasingly, ecology is seen as an answer to a growing need for direct human relationships with the land. Naveh and Lieberman state that since landscape ecology is a basis for human concern with the total landscape, it has overstepped the purely natural realm of classical bio-ecological sciences and has entered the realm of human-centred fields of knowledge (social, economic and geographic sciences) connected with modern land uses. In this context, landscape ecology is considered as part of human ecology. Human ecology focuses on the way people interact with each other and with the land (Young 1984, Berger 1987). Landscape planning is one of the interactions of people and the land. More of the literature of ecology based planning is oriented toward planning as applied human ecology rather than just incorporating ecological principles into land-use and landscape planning (Steiner *et al.* 1988, Hall 1988, 1991).

Since planning is normative containing choices for future land uses, planning is anthropocentric (in terms of being human-responsible, rather then being human-centred; Vink 1983). On a moral basis of environmental ethics, landscape planners and designers may reconcile the inherent worth of nature with needs and demands of society, and legitimize interventions in the landscape. For both human-centred (anthropocentrism) and nature-centred (biocentrism) points of view, norms for planning and design are perceived by people. In society, these norms will be debated. The integration of landscape ecology and landscape planning should be viewed from the notion of people's responsibility for nature, rather than from the emerging ecological insights. To set norms for landscape planning assumes both knowledge of landscape function and a value judgement about the rightness of this knowledge and its underlying paradigms. For example, preservation of a maximum degree of biodiversity cannot be solely argued from biological and ecological research. At the utmost, these disciplines may point to the necessity of preserving a certain degree of biodiversity. Landscape planning objectives often have an ecological character. However, society should make decisions about norms, while balancing nature conservation issues with other land uses. Therefore, landscape ecology is not able to determine norms, but is rather viewed as one of the major scientific bases or substantive theories in landscape planning and design.

The central prerequisite for wise landscape planning is understanding of natural and social processes and their influences on the landscape, the relevant parameters and to which extent these parameters influence the landscape. Landscape planners deal with questions as, for example, which landscape structure or spatial configuration of ecosystems will concurrently optimize soil conservation, biodiversity, wildlife populations, scenic quality, outdoor-recreation opportunities and other interests? Landscape ecology contributes to an understanding of heterogeneous landscapes and the changes associated with natural processes and human interventions. Landscape ecology provides the planner with a set of theories, knowledge and experiences of landscape study, especially related to the spatial structure of landscapes, their origin, and the processes that alter the spatial structure. It also provides a conceptual framework within which planners can explore how the structure of land evolves with relevant natural processes. Examples include the modelling of natural processes such as flows of individuals (Merriam 1984, Verboom *et al.* 1993) and landscape heterogeneity and disturbances (Turner 1987). In this context, landscape planning is also called applied landscape ecology (versus theoretical landscape ecology; Vink 1983, Golley and Bellot 1991, Jongman 1993). Since landscape planning and design bring about change in the landscape, the application of landscape ecological knowledge in spatial concepts for planning and design is necessary. The main challenge in landscape ecological planning is to articulate guidelines for the optimal pattern of landscape structure that will manage landscape function while accommodating sustainable use of land (Van Langevelde 1993). Such applied landscape ecology intends to solve environmental problems which have a spatial component, and to plan how landscapes should be organized in the future. It may lead to a substantial and noticeable improvement of landscapes, and more balanced policies and decision making. Landscape ecological research helps to legitimize and justify the importance of planning and design for large areas and in long term perspectives (Hall *et al.* 1989).

Landscape ecology may also structure the planning process. It contributes to procedural planning theories in two ways: as a basis for generating forms and developing guiding principles in planning and design, and as an evaluative tool (Hall *et al.* 1989). Landscape ecology may guide what data should be collected, how should these data be interpreted, how should these data and insights be used to address the problems and explore the opportunities, and how should environmental impacts of future developments be predicted. Opdam (1993) noted three fields of landscape ecological knowledge for landscape planning. Pattern analysis may discern environmental problems. Substantial process knowledge can be used to address these problems. In turn, translation of the process knowledge to spatial patterns is necessary for comparing and evaluating plan scenarios.

Landscape ecology may provide answers for landscape planning. Basically, landscape ecology is problem inquiry oriented. However, demands for problem solving from the field of landscape planning is considered a positive stimulus for integrating and deepening of pattern and process knowledge in landscape ecology (Naveh 1991, Opdam 1993). For the landscape ecologists, the planned and designed landscape may serve as field experiments to test hypotheses and acquiring knowledge (Golley and Bellot 1991). The increasing recent landscape ecological knowledge may provide a strong scientific basis for future landscape planning.

5 Spatial concepts in landscape planning for nature

5.1 Spatial concepts and their functions in landscape planning

In the planning process, spatial concepts connect planning objectives and interventions. Following the inventory and problem analysis, the first step of plan development involves spatial concepts for the plan area. "A spatial concept expresses through words and images in a summarized way, the view of a planning subject in respect of the desired spatial development of society and the nature of the interventions which are considered necessary" (Zonneveld 1991, p. 222). Spatial concepts are related to the formal object of planning, *i.e.*, to intervene purposively in the landscape. Therefore, they come under the acting concepts. Acting concepts express a certain gap between an actual and an imaginary situation. They present suggestions to bridge this gap. Spatial concepts in landscape planning may have five functions (as distinguished by Zonneveld conforming to Habermas' theory of communicative action): the cognitive, the intentional, the institutional, the communicative and the action functions:

- The cognitive function of spatial concepts refers to an organized thinking about the spatial form of the planned landscape. Spatial concepts contain a synthesis of knowledge related to the plan area coming from several disciplines, such as landscape ecology, geology and economics. This knowledge may provide understanding of the local problems and the way they can be solved. Planners need spatial concepts which link the tools of planning with the view of how people use, perceive and shape the landscape.
- Spatial concepts contain the (wittingly or unwittingly formulated) vision for the future developments in the area. This is the intention function, by which spatial concepts expresses the imagination of landscape planners and designers.
- The planning process is embedded in legislative and institutional structures. The institutional function refers to control of the land: spatial concepts should go into the authority of decision making by individuals, interest groups and governmental agencies. This is especially important when landscape planning is confronted with multiple land claims. For land development in the Netherlands, these institutional issues are articulated in the Land Development Act 1985.

- Spatial concepts may benefit communication among the various interest groups. Via word and images, discussion about the representation and imaginations of the landscape can take place.
- The action function of spatial concepts refers to the interventions in the landscape which are necessary to address the planning objectives. The content of spatial concepts give guidance to achieve the planning objectives.

Each spatial concept should more or less perform these functions. Regarding these functions, spatial concepts form the final landscape plan, which can be realized after discussion about the planning objectives, scenarios and interventions. Spatial concepts should be viewed as a basis for discussion where choices are made by the community about its future. Spatial concepts structure the planning process (*e.g.*, Steiner 1991, Hall *et al.* 1989)[2].

Spatial concepts cannot be viewed as having an independent existence, as being universal abstractions true for all time. In the same way that changes in scientific concepts are discussed, for example, the development and shift in paradigms by Kuhn (1970), Zonneveld (1991) describes the process of conceptualization in planning. Conceptualization is the process of making, adapting and changing the content of a spatial concept. Changes in spatial concepts occur when certain groups in society no longer accept the main spatial concepts, the context of planning changed, or new knowledge developed. The history of conceptualization processes can be seen as an alteration of conceptual complexes and shifts. The spatial concepts in a certain period form conceptual complexes, *i.e.*, a coherent structure of spatial concepts. Throughout the ongoing alteration in spatial concepts, some basic principles can be discerned which remain stable. Basic principles are spatial concepts that have proven to be successful or are considered as too important to become rejected. In the next section, the process of conceptualization will be discussed for spatial concepts in landscape planning for nature related to the rural areas in the Netherlands. Especially the cognitive and intentional functions of these concepts will be focused on.

5.2 Development of spatial concepts in landscape planning for nature in the Netherlands

The development of spatial concepts is related to the evolution of a landscape ecological approach in landscape planning in the Netherlands as described in section 2. The conceptualization process reflects the representation and imagination of the land through time. Several conceptual complexes and shifts can be distinguished in the history of Dutch landscape planning (Zonneveld 1991, Gorter 1986). It is notable, that most of the spatial concepts refer to multiple use: nature conservation, landscape maintenance, agriculture and outdoor recreation. The spatial concepts with different spatial strategies for planning the rural landscape in the Netherlands can be placed within a continuum from segregation to integration of land uses[3]. In the following, the successive phases will be briefly reviewed. Also in other countries, spatial concepts in landscape planning for nature have been developed. In North America recently the spatial concept of greenways appeared (Little 1990, Smith and Hellmund 1993). Steiner *et al.* (1988) and Ndubisi (1997) provide the first step to describe the conceptualization processes in the USA for spatial concepts in landscape planning for nature related to both the urban and rural landscape.

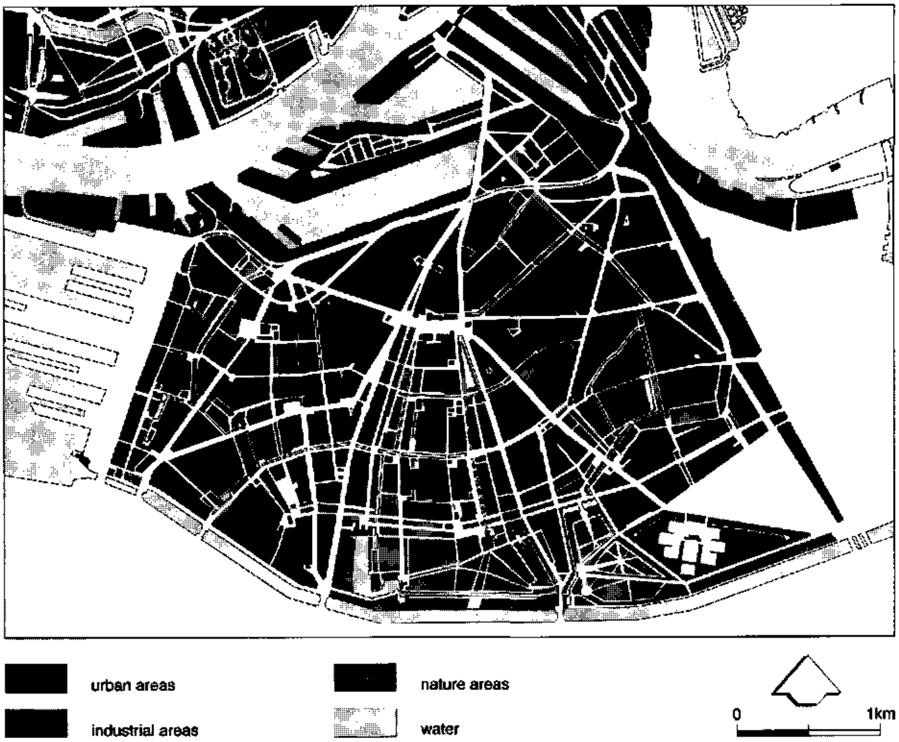


Figure 2 *Design for parkways in a development plan of the 'Linker-Maasoever' of Rotterdam from 1926 (Witteveen 1926)*

(1) Period from the beginning of this century until 1954

In the period from the beginning of this century to the 1920s, several motives for landscape planning for nature appeared. Nature and landscape had to be protected against the spreading urbanization and land reclamation. Although the cities grew, the urban dwellers were offered opportunities to experience nature. The increasing recreational use emphasized the quality of the rural landscape. The then spatial concepts reflected a symbiosis between nature conservation and outdoor recreation. In 1926, the spatial concept of parkway was introduced in a development plan for the 'Linker-Maasoever' of Rotterdam (Witteveen 1926, see figure 2). The spatial concept of parkways had an American origin (Cleyndert 1924, 1932, see Smith and Hellmund 1993). Parkways aimed to create greenways in the city and bring nature back to town via greenwedges. They connect the countryside with the innercity. Parks and greenwedges should divide the cities into areas of a relatively small scale.

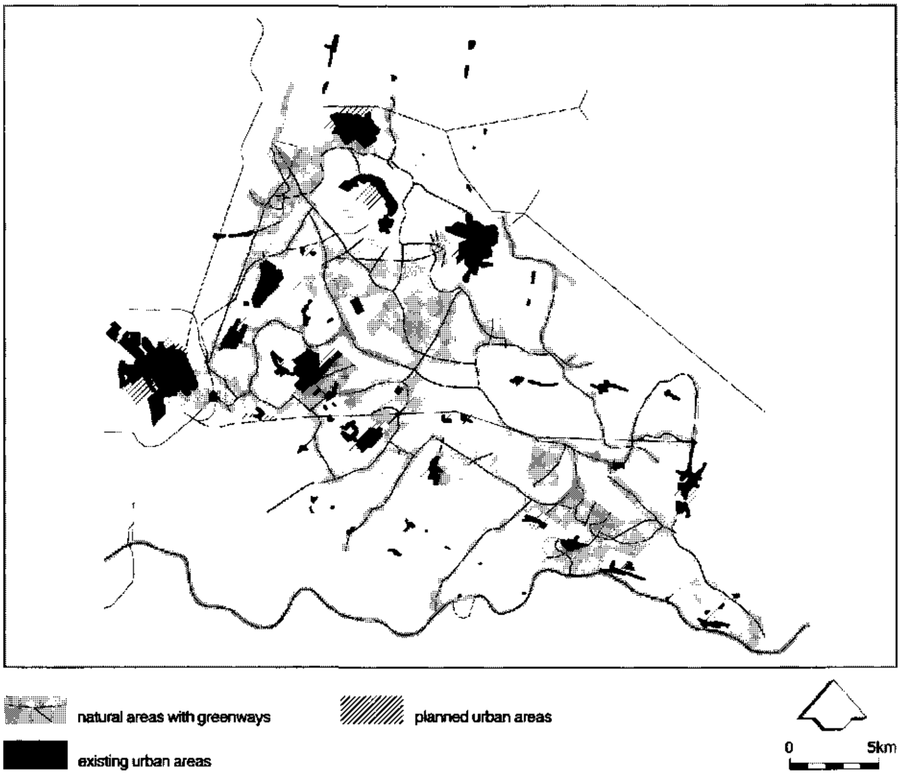


Figure 3 *Regional plan with a system of greenways for 'Oost-Utrecht' from 1935 by Granpré Molière (Van der Cammen and De Klerk 1986)*

For planning the rural landscape, the spatial concept of parkway provided a network of afforested ways for outdoor recreation. These parkways could accommodate (cycle) roads and walking paths in a naturalistic setting. In several regional plans, the spatial concept of parkway is worked out, for example, in the first draft Regional Plan 'Oost-Utrecht' from 1935 (Van der Cammen and De Klerk 1986, see figure 3). This plan contained a system of greenways connecting several natural areas. In 1938, the spatial concept of parkways is applied for the Regional Plan 'IJsselmonde' as a structure of cycle paths around the cities. This structure connects the suburbs with the countryside and provides opportunities for outdoor recreation in nature reserves (Van Boeijen 1938, see figure 4).

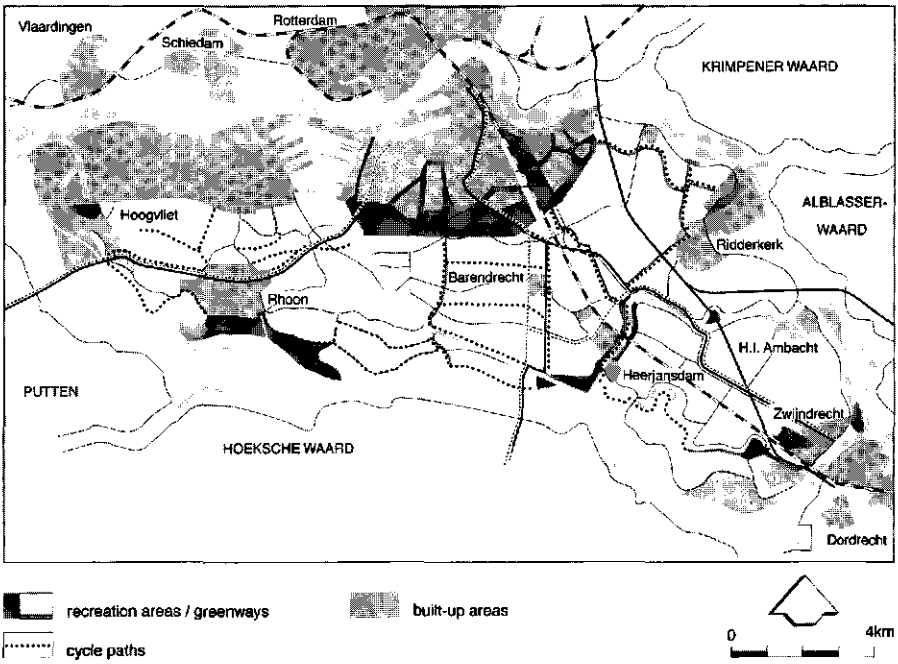


Figure 4 Regional plan for 'IJsselmonde' from 1938 (Van Boeijen 1938). The plan contains a network of cycle paths around the cities connecting the suburbs with the countryside.

Land consolidation was developed to reallocate and improve the land for agriculture. An awaking of nature conservation appeared. With the exception to land reclamation, land consolidation and urbanization, in the period from the beginning of this century to 1954 the relationship between agriculture and nature conservation and landscape maintenance was generally not considered as a dilemma (Zonneveld 1991). In this period, the spatial concepts were characterized by integration of land uses, especially the connection of several nature reserves with a recreational function by cycle paths, and incorporating natural areas in cities. Therefore, natural areas should be ordered in a certain manner as an open-space network. The mentioned spatial concepts benefit the recreational and aesthetic experience of visitors, and protect endangered and rare species. These spatial concepts are based on a kind of intuition that connection between natural areas enhance the ecological integrity of the landscape. After the Second World War, these spatial concepts disappeared. However, the national government stated a list of areas, which were considered as a priority for nature conservation.

(2) Period from 1954 until the 1970s

After the implementation of the Land Consolidation Act in 1954, many rural areas were re-allocated and improved for a rational agricultural use. However, other land uses were also getting more attention. A conceptual shift occurred. The spatial concepts of this period can be characterized by segregation of land use and scale enlargement. The areas of land consolidation and development increased. Physical planning in the Netherlands, for example the Second Policy Document on Physical Planning in 1966, had a strong confidence in its possibilities to reconstruct the landscape[4]. The Nature Conservation Act was adopted in 1968 to protect nature reserves. This act was the basis for protection of large scale reserves. Besides, a higher recreational need led to the planning of several large-scale recreational areas. An example of a spatial concept of this period is the Green Heart of Holland, which intended to establish a buffer zone between the cities of the Randstad in the western part of the Netherlands.

(3) Period from the 1970s until the late 1980s

After the mid 1970s, the second conceptual shift appeared. The large-scale spatial concepts of the sixties and early seventies vanished. In this period, the Land Development Act of 1985 became operative. The concern for the environment was gaining importance. The capacity of planning to intervene in the landscape was widely discussed. Increasing attention was paid to nature conservation and enhancement of the aesthetic, recreational and historic values of the landscape. Natural values in agricultural lands were recognized. With the Memorandum on Rural Areas in 1977 a new conceptual complex arose: integration of land use within diverse cultural landscapes. Integration of land uses was consolidated by agricultural surpluses. This allowed the set aside of marginal and unprofitable farmlands for nature reserves surrounded by buffer zones (Dekker 1990). Several instruments were proposed to regulate the dilemmas between land uses, for example, the Land Use Interaction Report. This Report was established in 1975 and provided opportunities for individual farmers to conclude management agreements with the government.

Increasing attention was placed on small landscape elements, with justification by use of the phrase "small is beautiful". However, it was recognized that integration of multiple land use could be a problem in planning.

In the beginning of the 1980s, the spatial concept of ecological infrastructure appeared. Ecological infrastructure was proposed in the Structural Outline Plan Nature and Landscape Conservation of 1980. From that moment on this spatial concept became the guiding principle in landscape planning for nature, for example, in the landscape development project 'Roden-Norg' (see figure 5). The hallmark of the spatial concept of ecological infrastructure is the necessity of establishing corridors between natural areas for the movement of species to address habitat fragmentation. In the early 1980s, the spatial concept of ecological infrastructure was used in the discussions about protection of small landscape elements and its species. Two differences with the former spatial concepts can be distinguished. First, the spatial concept of ecological infrastructure is considered to be scientifically based on conservation biology and landscape ecology. Secondly, this spatial concept is mainly focused on nature conservation.
However, the spatial concept of ecological infrastructure was criticized, especially by biologists and ecologists (*e.g.*, Dekker and Knaapen 1986, Opdam 1987, 1993, Gorter 1988). They discussed the scientific basis of the spatial concept. The spatial concept of ecological infrastructure was based on the theory of island biogeography of MacArthur and Wilson (1967), which was still an untested hypothesis and its application in continental situations disputed (Margules *et al.* 1982). Also, they emphasized its species-specific approach. Each species differs in habitat needs, tolerances and sensitiveness to habitat fragmentation. This corresponds with species-specific designs of ecological infrastructures. For these reasons, the spatial concept missed a clear definition and application in landscape planning. Several interpretations of ecological infrastructure occurred: a landscape structural approach with emphasis on protection of linear open-space systems, an ecotope approach neglecting the species-specific requirements and an overemphasis of dissolving habitat isolation rather than a comprehensive approach to consider both habitat patches and corridors (see section 5.4).

(4) Period from the late 1980s to the present

As is stated in section 2, landscape planning became landscape ecology based in the period from the late 1980s to the present. Zonneveld (1991) distinguishes a third conceptual shift about 1988. The integration of functions disappointed, and a new vision on the segregation of land uses appeared. It seemed difficult to reconcile the post-war industrial agriculture with nature conservation and landscape maintenance (Dekker 1990).

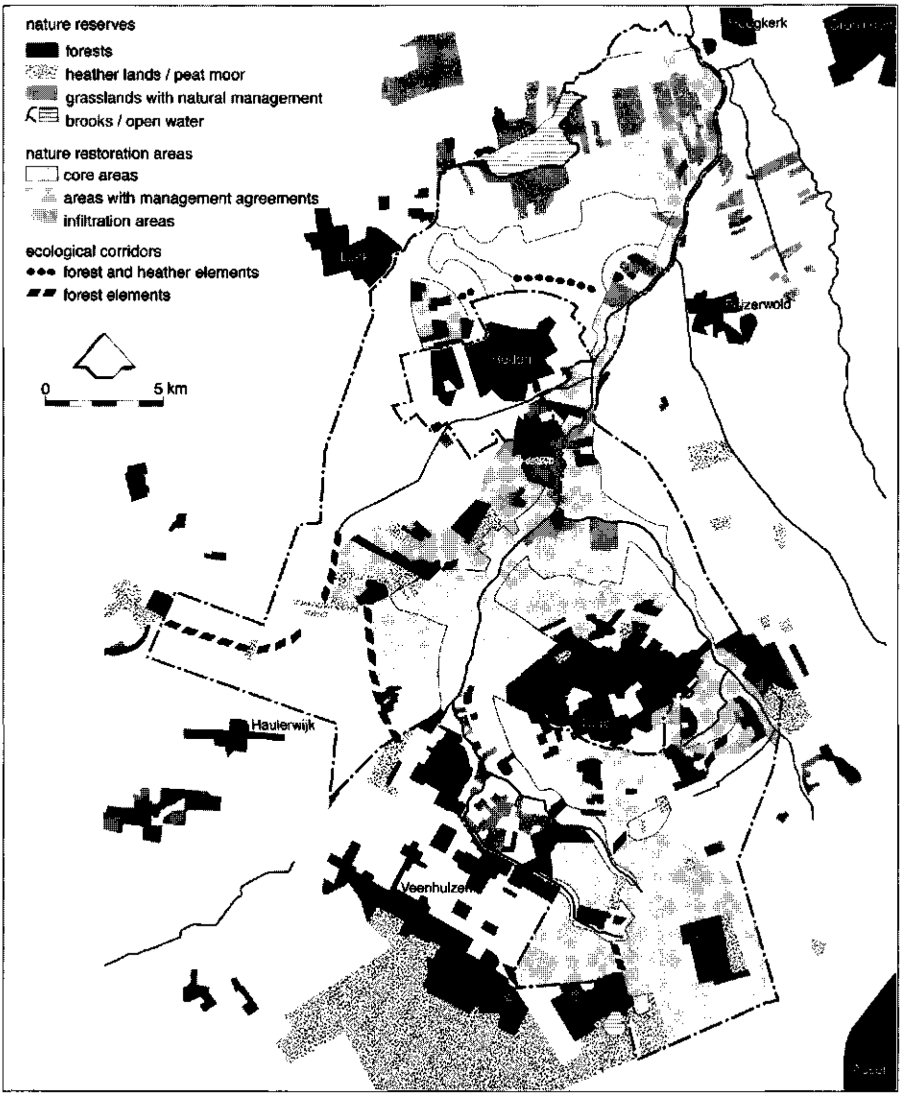


Figure 5 Preliminary sketch for the land development plan for 'Roden-Norg' in the north-eastern part of the Netherlands from 1990 (Landinrichtingsdienst 1990). The landscape plan consists of several ecological corridors between nature reserves for enhancing the movement and survival of several target species.

The Fourth Policy Document on Physical Planning of 1989 emphasizes spatial segregation of incompatible land uses based on planning robust landscape structures. Such landscapes permit flexible land development for agricultural use, and the realization of an integration of nature conservation, outdoor recreation, water control and forestry[5]. This was worked out in the spatial concept of landscape framework (Kerkstra and Vrijlandt 1990, Sijmons 1991, Van Buuren and Kerkstra 1993). For example, Kerkstra and Vrijlandt (1990) plan and design a landscape framework for industrial agriculture and nature conservation in the eastern part of the Netherlands. The spatial concept of landscape framework is based on spatial segregation of intensive land use requiring a flexible layout and the more extensive types of use requiring stability in time. The landscape framework is a network containing the extensive land use types, and will envelop large open areas for optimal agricultural production. Robust landscape structures are also advocated in the Nature Policy Plan of 1990 and the Memorandum on Landscape of 1992. The former presented a national ecological network (see section 2). The latter used the spatial concept of landscape framework for a high quality landscape. These spatial concepts are based on landscape ecological research and propose to enhance the ecological integrity of the landscape. Yet, these policy plans are merely intentions. Applications of these spatial concepts in landscape planning are now emerging.

Examples of basic principles in the conceptualization process of landscape planning in the Netherlands are regulated urbanization, and the connection between the innercity and the surrounding countryside. These have survived several conceptual shifts. Recently, the spatial concept of greenwedges returned. The greenwedges contribute to an attractive living and recreation climate, connect the city with the rural landscape, enhance ecological structure, and provide recreation infrastructure (Min. VROM 1989). These basic principles can also be found in the spatial concepts parkways and Green Heart of Holland. For example, the spatial concept Green Heart of Holland got more attention for regulated urbanization in the Randstad. Another basic principle in landscape planning is the emphasis on the connection of natural reserves through corridors. This principle was intuitively the basis of the early spatial concept of parkway. From the 1980s, the connectivity principle returned in the spatial concepts ecological infrastructure and landscape framework. Landscape ecological research pointed the necessity of this principle. The application of these spatial concepts in recent planning efforts for nature are characterized by the principle of an ecological network. The Regional Plan for Noord-Brabant presented the spatial concept green network. This network contains nature reserves, nature restoration areas, ecological corridors and multifunctional forests (Prov. Noord-Brabant 1993, see figure 6).

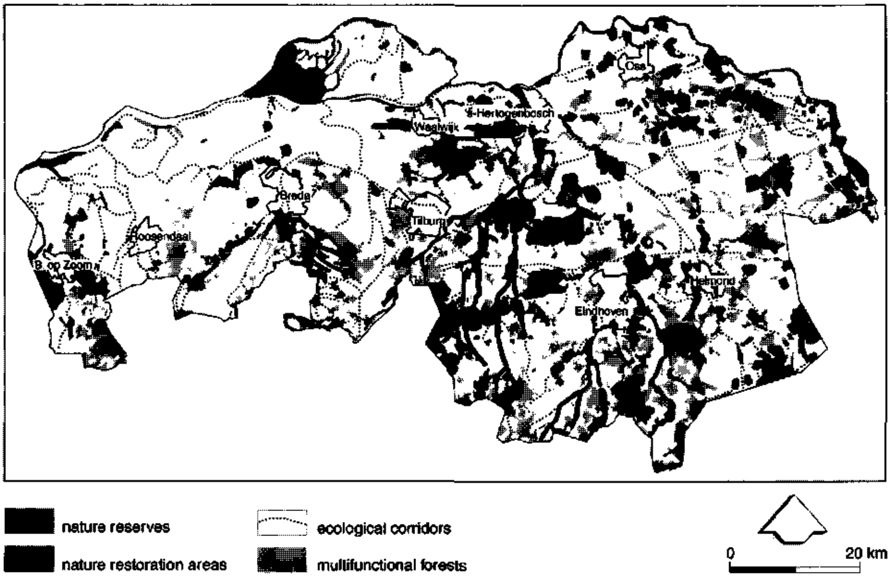


Figure 6 Regional plan for 'Groene Hoofdstructuur' in Noord-Brabant in the south of the Netherlands from 1993 (Prov. Noord-Brabant 1993). The plan consists of a network of nature reserves, nature restoration areas, corridors and multifunctional forests.

Planning ecological networks is based on the presuppositions that it is impossible to protect all natural values, rather choices should be made, and that natural values can be restored and developed. These presuppositions provide a renewed, but modest, conviction to enhance the dialogue between people and the land. The basic principle of ecological network may inspire the development of a new conceptual complex.

5.3 Spatial concept of ecological networks

During the last decades, the effectiveness of the management of nature areas increased under the influence of (landscape) ecological research. Interventions to protect solely nature areas seemed insufficient to preserve all natural values. In fragmented landscapes, the viability of remnant local populations is limited. Whereas large reserves are the spine of long-term preservation of natural values, these reserves cannot be considered in isolation from their context. Between the components of the landscape several interactions take place such as hydrological relationships and species movement. An important concern in both landscape ecology and landscape planning and design, is the enhancement of such processes. For example, McHarg (1969) pointed that "the distribution of open space must respond to natural processes. (...) The problem lies not in absolute area but in distribution" (p. 65). Especially movement and survival of species is gaining importance in landscape ecological research, since it is recognized that habitat fragmentation affects the movement and survival of species. Extensive research has been done to various species, their population dynamics in fragmented landscapes and the role of corridors (*e.g.*, Den Boer 1981, Merriam 1984, Forman and Godron 1986, Van Dorp and Opdam 1987, Burel and Baudry 1990, Soulé 1991, Saunders and Hobbs 1991, Verboom *et al.* 1993, Opdam *et al.* 1993). Several (applied) landscape ecological research efforts indicate possibilities to address fragmentation of habitat by a network approach in landscape planning (*e.g.*, Noss and Harris 1986, Saunders and Hobbs 1991, Smith and Hellmund 1993).

The network approach in landscape ecology distinguishes nodes, associated with hospitable habitat patches, and links, associated with corridors between these habitat patches. Such habitat networks may be essential for the survival of populations of species, which are poorly adapted to human-dominated landscapes. Networks provide opportunities for an efficient migratory route, as well as to alter the flow of nutrients, water and energy across the landscape (Forman and Godron 1986). This can be viewed as a basic principle for landscape planning for nature, at any scale and any context. In recent land development projects in the Netherlands, the spatial concept of ecological networks is gaining importance. For this reason, there is a need for a deeper understanding to use the spatial concept of ecological networks in landscape planning. Current landscape ecological research provides substantive theories for framing ecological network planning.

In the case of habitat networks, which form a part of the spatial concept ecological network, the theory of metapopulation dynamics is useful as substantive planning theory. In a fragmented landscape the habitat of many native species is dissected into small, isolated patches with sharp boundaries, separated by unsuitable area for the species concerned. Each habitat patch may contain a population of these species, but local extinctions appear and led to (temporally) empty patches. As long as dispersal is frequent, local extinctions will be prevented or the empty habitat patches will be recolonized. This system of spatially and functionally structured populations in heterogeneous landscapes is called a metapopulation. Metapopulations are defined as "any set of spatially defined local populations, which are demographically affected by the spatial arrangement of habitat patches and the resistance of the non-habitat of the landscape matrix" (Opdam *et al.* 1993, p. 165). Extensive research has been done to the dynamics of metapopulations (*e.g.*, Levins 1970, Merriam 1984, 1990, Lefkovitch and Fahrig 1985, Opdam 1987, 1991, Henein and Merriam 1990, Hanski and Gilpin 1991, Opdam *et al.* 1993, Verboom *et al.* 1993). Besides the theory of metapopulation dynamics, another spatial population theory is developed: the source-sink theory

(Wiens and Rotenberry 1981, Pulliam 1988). Both theories can be regarded as a follow up at the population level of the island biogeography theory of MacArthur and Wilson (1967). Two aspects determine the function of metapopulations: carrying capacity (size and quality) and connectivity of the habitat patches. These aspects are subject of biological and landscape ecological research. For example, several studies examine the influence of carrying capacity and connectivity at the dynamics of populations in heterogeneous landscapes (*e.g.*, Lefkovitch and Fahrig 1985, Fahrig and Merriam 1985, Gilpin 1987, Van Dorp and Opdam 1987, Opdam 1991, Verboom *et al.* 1993). In this context, connectivity refers to the qualities of the landscape that facilitate interaction among local populations of habitat patches, so that these populations act as local populations into a metapopulation and individuals can move among the habitat patches (Merriam 1984, 1990, Baudry and Merriam 1988).

Planning habitat networks implies the selection of target species since the perception of the landscape pattern, and hence the response to the fragmentation process of a population, will vary widely among species. The utility of particular landscape elements as habitat or corridor depends on the behaviour of the targeted species (Soulé 1991, Opdam *et al.* 1993). Habitat-network structures will differ between species (see also the previous section). In this context, the spatial concept of ecological networks is a way in which society can protect and preserve specific natural values. Therefore, a well-considered selection of target species is crucial.

Ecological networks should not only provide suitable habitat and facilitate species movement between habitat patches, also protection of water resources, providing forestry opportunities and other ecological functions may be of the spatial concept of ecological networks[6]. It also provides opportunities for integration of social functions, which are more or less compatible with the ecological functions, such as outdoor recreation, and protection of cultural and historic resources. The spatial concept of ecological networks implies multiple land use and is based on segregation of incompatible land use. Ecological networks may agree with the spatial concept of greenways in landscape planning and design in North America (Hall *et al.* 1989, Little 1990, Smith and Hellmund 1993).

The spatial concept of ecological networks may lead to a differentiation in natural values in the human-dominated landscape. Within the robust network, several sensitive species, meandering brooks and other natural values can occur, which are valued by society for preservation. However within the agriculturally used land, habitat for several species is also considered as valuable for protection, for example, ditches, verges and hedgerows. These elements provide habitat and corridors for several plant and animal species (*e.g.*, Forman and Baudry 1984, Fahrig and Merriam 1985, Van Dorp and Opdam 1987, Baudry and Burel 1990, Verboom *et al.* 1993).

5.4 Landscape ecology based spatial guidelines for planning ecological networks

Planning ecological networks requires spatial guidelines, based on the existing knowledge of landscape ecological processes and patterns. Spatial network layout can be defined at several scale levels, in terms of size, nature and configuration of landscape elements for the species concerned. Such guidelines for habitat-network planning should minimize local extinction rates and maximize opportunities for (re)colonization. As a result of research of biogeography, conservation biology and landscape ecology, several authors have discussed planning guidelines (*e.g.*, Diamond 1975, Helliwell 1976, Lovejoy and Oren 1981, Margules *et al.* 1982, Noss and Harris 1986, Opdam 1987, Soulé 1991, Smith and Hellmund 1993). It is proposed that the theory of metapopulation dynamics and its models are useful for impact assessment of (de)fragmentation effects on populations, and guidelines for landscape planning of habitat networks (Verboom *et al.* 1993, Opdam *et al.* 1993).

To enhance the survival chance of metapopulations of threatened species, several interventions on a local scale may be taken: (1) improve the quality of habitat and (2) enlarge patch size to stabilize and enlarge the local population size and to diminish the risk of extinction; (3) increase the number of habitat patches to improve the possibility for exchange and (re)colonization, and to lower the change of stochastic extinction of the metapopulation; and (4) decrease barriers between habitat patches and/or establishment of corridors to enable the possibility of dispersal. The advantages and the feasibility of habitat improvement, the extension of patches, and the establishment of corridors should be considered and balanced simultaneously in landscape planning. Only advocating the establishment of corridors — using the spatial concept of ecological infrastructure — for the benefit of a species' survival is an oversimplification, neglecting the role of habitat quality and patch size in the survival of metapopulations.

However, the theory of metapopulation dynamics should be considered as a relatively new and hardly tested hypothesis (Simberloff *et al.* 1992). Resulting data and models of metapopulations may be hardly applicable in regions with different abiotic and biotic conditions. Moreover, metapopulation dynamics is limited to a specific group of species, *i.e.*, species with a growth rate depending on density and a low mobility, which are sensitive to habitat fragmentation. It is only focused on population processes, rather than taking into account several interspecies relationships, such as predation and concurrence. With respect to these limitations, metapopulation theory may provide rules of thumb to help planners to layout the spatial network structure and decide among alternative spatial configurations (Van Langevelde 1993). These rules of thumb should reflect the present state of knowledge. Therefore, they should be constantly evaluated. Knowledge about species behaviour is increasing, but still insufficient to plan for all species. For example, the minimum critical size of populations to preserve is hardly known. More landscape ecological research is necessary. Establishing and monitoring existed and planned ecological networks may increase knowledge. Such adaptive management can provide a strong partnership between planners and ecologists (Holling 1978, Walters 1986).

(1) Planning guidelines for habitat patches

Vulnerability of patches to function as habitat must be examined for each species. Several parameters define the function as habitat patch: size, number, shape, position in the landscape and quality of the patches. Guidelines should concern these parameters. The quality of the patches may be influenced by several factors, such as the agricultural use of the matrix and recreational activities. The size of habitat patches is one of the most important spatial parameters in preserving viable populations of plant and animal species. Low local extinction rates can be achieved if patches are large and contain good quality habitat. In other words, local population growth rate should be optimized and local carrying capacity should be high (Verboom *et al.* 1993). The occupation of a habitat patch by a particular species depends on both the size of the population with fluctuations as a result of local processes, and the interaction with other local populations in the habitat network. In this context, important is what number of interacting habitat patches with a certain size and quality, is necessary for a viable population (Opdam 1987, Gilpin 1987). The choice between several large or many small patches (*i.e.*, the SLOSS-discussion — Single Large or Several Small nature reserves; Gilpin and Diamond 1980, Higgs and Usher 1980) can only be made after consideration of the species' particular characteristics, the role of inter-patch dispersal, and the relative merits of spreading risk and local density dependent effects. There are no general rules here (Verboom *et al.* 1993). In general, large fragments can support a larger number of individuals for a particular species. Large fragments minimize edge influence of the matrix. Large nature reserves in the agricultural and urban matrix may be important as both source and refuge of species. Especially patches that due to their size and habitat quality serve as stable source for dispersing propagules, may play an important stabilizing role in metapopulations and should be preserved (Verboom *et al.* 1993). In general, as many as possible suitable (occupied and unoccupied) habitat patches for the species concerned should be protected. For smaller fragments, buffer zones may protect the edges of the patch and minimize or eliminate negative impacts from the surrounding landscape matrix.

(2) Planning guidelines for corridors

Colonization rates are high when the distance between habitat patches can be bridged over. This can be stimulated by dispersal corridors, stepping stones, or devices that counteract effects of barriers (*e.g.*, badger tunnels; Verboom *et al.* 1993). However, questions about the role of corridors have also been posed (*e.g.*, Simberloff and Cox 1987, Simberloff *et al.* 1992). Although, there has been some research on optimal corridor design (*e.g.*, Forman and Baudry 1984, Fahrig and Merriam 1985, Forman and Godron 1986, Henein and Merriam 1990, Baudry and Burel 1990, Saunders and Hobbs 1991), little is known about how individuals actually move through the landscape. Do they use linear elements as corridors or simply follow a straight or random route, and how do they react to boundaries. In general, connecting elements may be introduced to enhance dispersal between habitat patches. On the other hand, barriers have to be minimized for species movement. The connecting elements can function as corridor and secondary habitat for the species concerned, and as barriers or filters to the movement of other species as well.

6 Discussion and conclusion

A synthesis of the developments in landscape planning and landscape ecology in the Netherlands can be summarized by five topics: (1) the emerging concern that human practices progressively degrade the landscape and that people should plan for nature; (2) the consolidation of the idea of landscape planning for nature in numerous large-scale planning efforts and the emerging incorporation of ecological principles into spatial concepts; (3) the explicit linkage between landscape ecology and landscape planning in policy, research and planning practice; (4) the changing perception of nature and the land as expressed in the evolution of landscape planning and spatial concepts, embracing the notion of multiple land use; and (5) a diversity in the scope of spatial concepts in landscape planning for nature at several scale levels. It is shown that landscape planning for nature became landscape ecology based. The landscape ecological planning approach reflects the existence of an environmental ethic or set of moral principles that governed people's relationships to the land. As Steiner (1991) advocates, landscape ecological planning is focused on the appropriate fit between people and the land.

Several motives are obvious for incorporating landscape ecology as substantive theories in landscape planning. Landscape ecology provides landscape planners and designers with a conceptual framework within which they can include knowledge about relevant patterns and processes. Since both landscape ecologists and landscape planners and designers focus on the ecology of a landscape, a close relationship can be distinguished between these disciplines. Four key connecting issues can be noted: the landscape and its processes as subject of study, the interdisciplinary and holistic approach, the consideration of scale and scale-related parameters, and the recognition of human influences in the landscape. The combination of these related interests makes the emergent discipline of landscape ecology a promising basis for landscape planning and design. Adopting landscape ecology and its representation of the landscape as a way of knowing has many profound consequences for landscape planning. It forces planners to ask questions. Landscape ecology may also structure the planning process. In turn, applied landscape ecology orients the research to both problem inquiry and problem solving.

Landscape ecology provides principles as substantive theories for landscape planning. Landscape ecology is not unique in this role. Recognition of human influences in the landscape and the intention to direct both natural and social processes, implies a need for understanding both the natural and human sides of the dialogue. It is assumed that knowledge related to landscape patterns and processes, and human influences on these, is provided in landscape ecology by integrating natural sciences, such as geology, soil science, hydrology and vegetation science. Knowledge about social processes and the resulting land use patterns should be provided by social sciences, such as economics, sociology, geography and anthropology.

Spatial concepts are the interface between substantive planning theories and plans to intervene in the landscape. Substantive planning theories should provide some basic principles in the process of conceptualization. In the Netherlands, several spatial concepts are used in landscape planning for nature, such as parkway, greenwedge, greenway and ecological infrastructure. Ecological networks forms a basic principle in the evolution of these spatial concepts. The shifts of spatial concepts in landscape planning are caused by both a changing perception of nature and nascent landscape ecological insights. However, these causes cannot be viewed separately, since the increasing environmental concern has stimulated scientific research and vice versa. Two motives were used in the emerging planning approach with changing priorities: the protection of ‘untouched’ natural areas, which is advocated as an ecological argument, and the enhancement of the aesthetics of natural landscapes or the protection of nature for outdoor-recreational use.

Spatial concepts may contain several presuppositions with respect to the representation and imaginations of the landscape. Spatial concepts reflects the planners’ perception of the land and the signification assigned to the landscape. As shown in the conceptualization process, different conceptions of nature exist, related to different spatial strategies of landscape planning for nature. Therefore, a systematic evaluation of current spatial concepts is proposed (Dekker and Knaapen 1986). The evaluation should discuss the criteria that are used to confirm the validity of the spatial concept, for example, its cognitive basis or scientific legitimacy of the spatial concept, and its applications in planning. Such evaluation of conceptual complexes is a crucial step in a progressive conceptualization process, which result in useful spatial concepts for landscape planning (Zonneveld 1991).

Spatial concepts are the domain of planning and design. Planning and design are focused on creating images and plans. Research, policy and decision making contribute to the conceptualization process. Research may provide substantive planning theories to support the spatial concept. Policy and decision making refers to an acceptance and elaboration of the spatial concept. Landscape planning needs societal support since intervention in the landscape is limited, for example, as a result of land ownership and private properties, claims from several land uses and scarcity of land, and limited financial resources. Landscape planning occurs via deliberations and involvement of interest groups to reach consensus about future developments. Spatial concepts may have an important communicative function in landscape planning and design. Therefore, metaphors as 'thinkable' images in spatial concepts are used, for example, the spatial concepts of the Green Heart of Holland, greenways and greenwedges (Zonneveld 1991, Boogert 1992, Steiner 1991).

Recent landscape ecological research supports the spatial concept of ecological network. This research emphasizes that nature reserves should be contain sufficient, high quality areas of habitat, connected by corridors. The spatial concept of ecological network may motivate landscape planners and designers to plan landscape structures that enhance natural processes, especially the movement of particular species. Such habitat-network planning should be based on the theory of metapopulation dynamics. It is shown that the use of landscape ecological knowledge in landscape planning and design is limited. Several questions in applying the spatial concept of ecological networks should be addressed: what species or species group are focused on, what is its minimum viable population size, what is the necessity for establishment of corridors or enlargement of patches, what landscape elements are crucial to enhance population survival, what is the configuration, quality, shape and area of these landscape elements, and what interventions should be necessary?

Inherent to landscape planning for multiple use is the dualism between segregation and integration. The dilemmas between agriculture and nature conservation are reflected in the shifting emphasis on segregation or integration of land uses (Dekker and Van der Windt 1992). Such dilemmas are not only related to agriculture, but also to forestry and outdoor recreation. At the basis of these dilemmas is the dialogue between people and nature. In the Netherlands, the position towards agriculture seemed mainly competitive, but sometimes more co-operative. This competitive position combined a pessimistic view on agriculture with a preference for segregation of land use. In turn, the co-operative position had an optimistic view on agriculture with a preference for integration. Recently, planners are considered to contribute substantially to conservation by nature restoration and development. Segregation of incompatible land uses and integration of compatible land uses form the underlying perception of nature from the network perspective. However, discussion about natural values of the agricultural landscape recently returned in the Netherlands.

The need for landscape planning in the Netherlands has increased with rising competition for scarce land and its resources, and the need to preserve natural values. Taken into account the complexity and different spatial and time scale of the interacting processes, landscape planning is an essential tool. In the intensely managed landscape, there is a need for a planning approach that can assist planners, designers and decision makers in analyzing and plan the landscape. This approach requires a systematic integration of planning social and natural processes and their spatial relationships. In this chapter such approach is discussed: landscape ecological planning.

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Notes

[1] In this context, Naveh and Lieberman (1984) called landscape ecology a transdisciplinary science, because it is not just a combination of the methods and knowledge of various sciences, but an integration on a higher level that in turn influence other disciplines in basic philosophy and application.

[2] Zonneveld (1991) and Boogert (1992) distinguish several types of spatial concepts.

[3] Crucial in considering the notion of segregation versus integration is the scale at which integration or segregation of land uses take place. Segregated land use on a low scale level may appear as an integrative pattern on a higher scale level.

[4] This confidence is also expressed by technological optimism in land development projects to transform the landscape for human use (see Groeneveld 1985).

[5] However, integration of agriculture and nature conservation is also advocated in the 'ecological' agriculture or 'integrated' agriculture. This type of agriculture reflects a wide perception of nature: natural values adapted to land use are included, for example, meadow birds. Also natural values which are beneficial to the running of farms are included, for example, wind breaks and hedgerows (Dekker and Van der Windt 1992).

[6] Note that the definition of an ecological network differs from the definition as used in the other chapters of this thesis.

3 COMPARING CONNECTIVITY IN LANDSCAPE NETWORKS

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Comparing connectivity in landscape networks

1 Introduction

One of the primary concerns in spatial analysis is the position of locations in a region relative to one another, because locations adopt their roles in the region as a function of their connectivity to the system as a whole (*e.g.*, Taaffe and Gauthier 1973, Lowe and Moryadas 1975, Tinkler 1977, Haggett *et al.* 1977, Hillier and Hanson 1984, Cantwell and Forman 1993). Differences occur in the connectivity of locations, and hence in their function, owing to differently spaced and sized systems.

We define connectivity as a property of locations to maintain spatial or functional relationships with other locations in terms of flows of entities (materials, energy, information, people, animals, etc.). This definition embraces other terms such as accessibility of locations, so long as they emphasize spatial characteristics that direct relationships between locations. The locations in a region constitute landscape networks as a result of these relationships. Graph theory provides parameters to quantify the degree of connectivity in such networks. These parameters have a long history and have been widely applied in geographical research, especially for analyzing communication and transportation networks (Allen *et al.* 1993, Garrison and Marble 1965, Ingram 1971, Taaffe and Gauthier 1973, Shimbel 1953, Mackiewicz and Ratajczak 1996). The values of these parameters are dependent upon the size of networks (we define the size of a network as the number of locations in it). These parameters are thus unsuitable for comparing the connectivity in networks that have different numbers of locations (Allen *et al.* 1993, Teklenburg *et al.* 1993).

Our objective is to extend the existing parameters, so that the degree of connectivity of elements in a variety of networks can be compared. We do not apply these parameters to explain certain observed patterns in landscapes. The background to this paper is our study of fragmentation effects in animal populations, where we dealt with locations in different (subsets of) networks whose relative position in the network may determine colonization processes. As we wish to explain the relationships between the relative position of the elements and colonization processes, the relative positions should be measured so that they can be compared. In our opinion, however, the issue of comparing the connectivity in landscape networks can also be relevant to other fields in spatial analysis.

We address two questions:

1) Does the size of networks affect the degree of connectivity measured by the parameters?
2) Does variation in the parameters concur with the variation in the spatial configuration of the network?

2 Comparing the degree of connectivity of locations

Connectivity parameters can be used to assess the function of a location. For example, for economic purposes, the parameters can be used to determine whether a location is an element with high degree of inward and outward traffic in the transportation network or is a centre for economic activities (Allen *et al.* 1993, Dupuy and Stransky 1996). These parameters can also be applied in studies with other objectives. For example, locations may act as a point of attraction in a network of tourist movements (Van der Knaap 1997), or as source for dispersal of species in the region (Hanski and Gilpin 1997). To test and compare these relationships across several locations in different regions as well as in one location in time, the degree of connectivity of elements should be measured and compared with the degree of connectivity measured in other networks (figure 1).

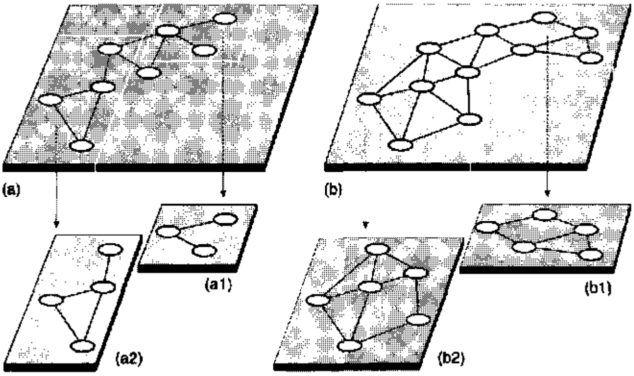


Figure 1 *Measuring the degree of connectivity of elements in two networks (a) and (b) should enable us to compare the elements of these networks with each other. The elements of the nonconnected subsets (a1) and (a2) or (b1) and (b2) of the decomposed networks (a) and (b) should also be compared. It is obvious that network (b) and its subsets are more complex than network (a) and its subsets, and that most elements in network (b) and its subsets have a higher degree of connectivity.*

A special case in such comparisons is when the elements belong to different subsets in one network (figure 1). Networks decomposed into different subsets of elements can be considered as disconnected or non-connected (Wilson and Watkins 1990). It may be relevant to test the degree of connectivity of elements in different subsets, *e.g.*, when the accessibility of a location by different types of transportation systems needs to be determined (*e.g.*, either by bus, by train, or a combination of both; Tinkler 1977), or in the analysis of the position of large cities in the European highway network related to their position as elements in the national network (Dupuy and Stransky 1996). Subsets of elements also occur in analyses where relationships between certain sets of elements are restricted, *e.g.*, in the study of effects of habitat fragmentation in population ecology (Taylor *et al.* 1993, Hanski and Gilpin 1997) where population survival in subsets of habitat patches depends upon the number and spacing of the elements in the subset. The function of an element in a subset may depend upon relationships with all other elements in the subset.

Relevant questions in spatial analysis concern whether differences in the degree of connectivity of locations in different (subsets of) networks are related to their function. To address such questions where comparison among elements in different (subsets of) networks comes up, we extend the existing parameters. For those who are less familiar with graph theory, we first introduce the matrix-based approach to measure connectivity of elements in networks.

3 Matrix-based approach for connectivity analysis

3.1 Definition of distance

Matrix-based parameters measure the degree of connectivity of network elements as a function of the number of (direct and indirect) neighbouring elements and the distance between these elements. Connectivity may be defined in various ways. The main distinction between matrix-based parameters depends on the use of space to define distance. Topological and geometric approaches exist. In the topological approach, the presence or absence of an edge between vertices is considered. In this context, the cardinality t_{ij} of a path between two vertices in a graph is the number of edges between these vertices. In the geometric approach, positive numeric weights, w_{ij}, are assigned to each edge in the graph, *e.g.*, the costs of movement, Euclidean distance, time required to move between elements, amount of flow, etc. The weights offer additional information about the relationships between elements. In the context of this paper, we use high values of w_{ij} between two vertices to indicate a low degree of connectivity, and vice versa.

Two matrix-based parameters can be distinguished for both the topological and the geometric approaches: those for direct connections and those for shortest paths. These parameters can be applied to nondirected and directed graphs that are either connected or nonconnected.

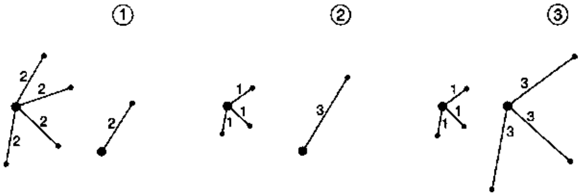
3.2 *Connectivity in nondirected graphs*

First, we consider a nondirected graph $G(V,E)$ with vertex set $V(G)$, $V(G) = \{v_1, v_2, ..., v_n\}$, with n vertices, and edge set $E(G)$, $E(G) = \{e_1, e_2, ..., e_m\}$, without self-loops and multiple edges. The topological connectivity matrix **C**, $\mathbf{C} = (c_{ij})$, of $G(V,E)$ is defined as: $c_{ij} = 1$, if a direct connection between the vertices v_i and v_j exists in $G(V,E)$; $c_{ij} = 0$, otherwise. The geometric equivalent of **C** is the weighted-distance matrix **P**, $\mathbf{P} = (p_{ij})$, defined as: $p_{ij} = w_{ij}$, if a direct connection between v_i and v_j exists in $G(V,E)$; $p_{ij} = 0$, otherwise. The weighted length p_{ij} of direct edges of v_i provides a measure for the geometric proximity of all neighbouring v_j. Matrix **D**, $\mathbf{D} = (d_{ij})$, is the shortest-path distribution between vertices: d_{ij} is the cardinality t_{ij} of the shortest path between v_i and v_j. The diameter δ of the graph is defined as δ = maximum $\{d_{11}, d_{12}, ..., d_{nn}\}$. Matrix **S**, $\mathbf{S} = (s_{ij})$, provides the shortest-weighted paths between pairs of vertices: s_{ij} is the cumulative edge length w_{ij} of the shortest path between v_i and v_j. To obtain **S**, a heuristic algorithm is applied (Taaffe and Gauthier 1973, Tinkler 1977). As a result, the paths generated are not necessarily the shortest paths, but approximations. We define the geometric diameter σ of the graph as σ = maximum $\{s_{11}, s_{12}, ..., s_{nn}\}$.

The four matrix types can measure three characteristics of networks and their elements: the relative position of elements, their relative importance, and the network dispersion. Each matrix type provides a quantitative measure for the relative position of elements in terms of highly connected elements versus badly connected elements in the network. This is obtained by the vector that sums the elements of each row or column in the matrix. For nondirected graphs, the vector $\boldsymbol{c}$ can be obtained by multiplying matrix **C** with the vector $\boldsymbol{l}$:

$$\boldsymbol{c} = \mathbf{C}\,\boldsymbol{l} \qquad (1)$$

where $l_i = 1$, $i = 1, 2, ..., n$. The elements c_i of $\boldsymbol{c}$ provide a measure for the relative position of v_i. For **D**, **P**, and **S**, the corresponding vectors $\boldsymbol{d}$, $\boldsymbol{p}$, and $\boldsymbol{s}$ can be obtained by an analogous process to that shown in equation (1). For the elements of vector $\boldsymbol{p}$ we advocate a modification. One may expect that low values of p_i refer to v_i with a high degree of connectivity. However, if more than one edge is connected to v_i, p_i can be misleading. For example, we assumed that a vertex connected with four edges and $w_{ij} = 2$ has a degree of connectivity four times higher than that of a vertex connected with one edge and $w_{ij} = 2$ [figure 2 (1)]. The same reasoning was applied for a vertex connected with three edges and $w_{ij} = 1$, which has a degree of connectivity three times higher than that of a vertex connected with one edge and $w_{ij} = 3$ [figure 2 (2)]. Therefore, each p_i should be modified. As connectivity declines with increasing distance w_{ij}, we used the reciprocal of w_{ij} to obtain a consistent measure. This is analogous to the commonly used population potential models (Pooler 1987). Matrix $\mathbf{P'}$ is then defined as: $p'_{ij} = 1 / w_{ij}$, if a direct connection between v_i and v_j exists in $G(V,E)$; $p'_{ij} = 0$, otherwise. Vector $\boldsymbol{p'}$ can be calculated in the same way as shown in equation (1). Figure 2 shows the comparison between c_i, p_i, and p'_i for different graphs.



c_i	4	1	3	1	3	3
p_i	8	2	3	3	3	9
p'_i	2	0.5	3	0.333	3	1
	← 4 x		← 9 x		← 3 x	

Figure 2 *Paired comparison of network patterns illustrating the modification of parameter p_i. The degree of connectivity of the large vertices i (•) is considered. The c_i, p_i, and modified p'_i values are given. High values of c_i and p'_i correspond to highly connected vertices. The arrows indicate the extent to which, in a given pair, the left vertex has a higher degree of connectivity (measured by p'_i) than the right vertex. It should be noted that comparisons between more complex patterns are difficult to interpret in simple terms.*

The elements d_i in $\boldsymbol{d}$ sum the shortest paths d_{ij} between v_i and all other vertices. For a given vertex v_i, each d_{ij} of length r ($1 \le r \le \delta$) occurs with a particular frequency $f_{i,r}$ (James *et al.* 1970). This frequency distribution is a finite, discrete set. Another formulation of d_i is thus

$$d_i = \sum_{r=1}^{\delta} f_{i,r}\, r \qquad i = 1,2,\ldots,n \tag{2}$$

We used this alternative formulation to derive our intended parameters.

The elements s_i in s sum the shortest-weighted paths s_{ij} between v_i and all other vertices. This parameter has been suggested as a suitable measure for analyzing variation in the spatial configuration of networks (Taaffe and Gauthier 1973). Because the frequency distribution $f_{i,u}$ of shortest-weighted paths s_{ij} of length u ($0 < u \leq \sigma$) for a given vertex v_i to all v_j is a finite discrete set, s_i can be represented by

$$s_i = \sum_{u>0}^{\sigma} f_{i,u}\, u \qquad i = 1,2,\ldots,n \tag{3}$$

Because s_{ij} is continuous, $f_{i,u}$ is often 1.

High values of c_i and p'_i correspond to a high degree of connectivity. For d_i and s_i, an inverse relationship exists: v_i with the lowest d_i or s_i has the highest degree of connectivity. A hierarchy embodying the relative importance of elements can be obtained by ranking the connectivity values. The network dispersion $\hat{c}$ of matrix $\mathbf{C}$ measures the connectivity or the compactness of the whole network (Shimbel 1953). It can be calculated by multiplying the transpose of $\boldsymbol{c}$ with $\boldsymbol{l}$:

$$\hat{c} = \boldsymbol{c}^T \boldsymbol{l} \tag{4}$$

The network dispersion $\hat{p}'$, $\hat{d}$, and $\hat{s}$ can be obtained by using their corresponding vectors $\boldsymbol{p}'$, $\boldsymbol{d}$ and $\boldsymbol{s}$ in the same way shown in equation (4).

3.3 Connectivity in directed graphs

We can also consider a directed graph or digraph $D(V,A)$ with vertex set $V(D)$, $V(D) = \{v_1, v_2, \ldots, v_n\}$, with n vertices, and arc set $A(D)$, $A(D) = \{a_1, a_2, \ldots, a_m\}$, without self-loops and multiple arcs. Arcs are directed edges. For a digraph $D(V,A)$, the same matrix-based parameters can be applied. However, in contrast to nondirected graphs, the matrices of digraphs are not necessarily symmetric about the principal diagonal. The rows of these matrices represent the origin locations for the connecting relationships, and the columns the destination locations.

For matrix $\mathbf{C}^D$ as derived from digraph $D(V,A)$, two vectors are distinguished. The vector $\boldsymbol{c}^{out}$ can be obtained by multiplying matrix $\mathbf{C}^D$ with the vector $\boldsymbol{l}$:

$$\boldsymbol{c}^{out} = \mathbf{C}^D \boldsymbol{l} \tag{5}$$

The vector $\boldsymbol{c}^{in}$ is given by

$$\boldsymbol{c}^{out} = \boldsymbol{l}^T\ \mathbf{C}^D \tag{6}$$

in which $\boldsymbol{l}^T$ is the transpose of the vector $\boldsymbol{l}$. The elements c_i^{out} provide a measure for the relative position of v_i concerning outward relationships; the elements c_i^{in} provide measures for the inward relationships. For $\mathbf{D}^D$, $\mathbf{P}'^D$ and $\mathbf{S}^D$ as derived from digraph $D(V,A)$, the corresponding vectors can be obtained as demonstrated in equations (5) and (6). Here, unless otherwise specified, we will focus on nondirected graphs, without self-loops and multiple edges.

3.4 Connectivity in nonconnected graphs

We advocated that if g different graphs are considered we should be able to compare the degree of connectivity of the elements among different graphs $G_j(V,E)$ and $G_k(V,E)$, where j and k are elements of g. When a network is decomposed into nonconnected subsystems, the graph $G(V,E)$ of this network consists of several disjointed subgraphs. In graph theory, nonconnected graphs are distinguished as graphs with specific properties. In our study of fragmentation effects on animal populations, we dealt with nonconnected networks (Van Langevelde *et al.* chapter 7). We argued that comparison among different graphs is equivalent to the comparison among different subgraphs in a nonconnected graph (see figure 1).

A graph $G(V,E)$ is connected if there is at least one direct or indirect path between any pair of vertices; otherwise, it is nonconnected. Graph $G(V,E)$ of a nonconnected network is the union of g subgraphs. We define a subgraph $G_k(V,E)$ as the kth component of $G(V,E)$. The vertex subset $V(G_k)$ with n_k vertices and edge subset $E(G_k)$ of $G_k(V,E)$ of a nonconnected network are defined as

$$V(G_k) \subset V(G) := \{V(G_1), V(G_2), \ldots, V(G_g)\}$$
$$E(G_k) \subset E(G) := \{E(G_1), E(G_2), \ldots, E(G_g)\}$$

and

$$G_k(V,E) \subset G(V,E) := \{G_1(V,E), G_2(V,E), \ldots, G_g(V,E)\}$$

In nonconnected graphs,

$$V(G_j) \cap V(G_k) = \{\varnothing\} \text{ and } E(G_j) \cap E(G_k) = \{\varnothing\} \qquad \text{for } j \neq k.$$

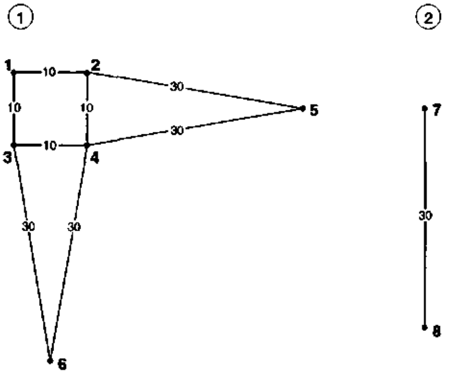
The vector $\boldsymbol{c}_k$ of subgraph k can be obtained by multiplying $\mathbf{C}$ by the vector $\boldsymbol{l}_k$:

$$\boldsymbol{c}_k = \mathbf{C}\,\boldsymbol{l}_k \qquad k = 1,2,\ldots,g \tag{7}$$

where $l_{i,k} = 1$ for $v_i \in V(G_k)$, and $l_{i,k} = 0$ for $v_i \notin V(G_k)$. Then for $v_i \in V(G_k)$, $c_{i,k} \neq 0$, unless $n_k = 1$. The network dispersion $\hat{c}_k$ of each subgraph k is obtained from

$$\hat{c}_k = \boldsymbol{c}_k^T\,\boldsymbol{l}_k \qquad k = 1,2,\ldots,g \tag{8}$$

The vectors p'_k, d_k, and s_k and the network dispersion $\hat{p}'_k$, $\hat{d}_k$, and $\hat{s}_k$ can be calculated as shown in equations (7) and (8).



Graph 1					Graph 2				
v_i	d_i	order	s_i	order	v_i	d_i	order	s_i	order
1	8	5	120	4	7	1	1.5	30	1.5
2	7	2.5	110	2.5	8	1	1.5	30	1.5
3	7	2.5	110	2.5					
4	6	1	100	1					
5	8	5	200	5.5					
6	8	5	200	5.5					
	$\hat{d}_1 = 44$		$\hat{s}_1 = 840$			$\hat{d}_2 = 2$		$\hat{s}_2 = 60$	

Figure 3 *Two graphs (k = 1, 2) with values of the connectivity parameters d_i and s_i per vertex v_i, the hierarchy numbers (order) of the vertices per graph related to d_i and to s_i, and the network dispersion $\hat{d}_k$ and $\hat{s}_k$ of the two graphs. Low values of d_i and s_i correspond to highly connected vertices. For both d_i and s_i, the best connected vertex has the lowest hierarchy number.*

In the next section, we derive parameters that are suitable for comparing the degree of connectivity of elements in g different graphs where each graph $G_k(V,E)$ consists of vertex set $V(G_k)$ with n_k vertices and edge set $E(G_k)$. The parameters should also allow comparison of the degree of connectivity of elements in g subgraphs of a nonconnected graph where each subgraph $G_k(V,E)$ consists of vertex subset $V(G_k)$ with n_k vertices and edge subset $E(G_k)$.

4 Parameters to compare the degree of connectivity in different networks

4.1 Problem with comparing the degree of connectivity

Figure 3 illustrates the problem of using either ***d*** or ***s*** for comparing the degree of connectivity of elements in different networks. The d_i and s_i values of the vertices are listed in the figure. For each graph, the lowest values of both d_i and s_i represent the best connected vertices. However, the values returned for d_i and s_i reveal that v_4 is better connected than v_7. This is a counterintuitive notion when the size and spacing of the networks are considered. Elements in large networks are likely to have a higher degree of connectivity than elements in smaller networks. Also, when the distances between vertices increase, the degree of connectivity of the vertices is assumed to decrease.

Two methods correct for the size bias of different networks. Allen *et al.* (1993) argue that the normalized mean spatial separation E_k among the set of vertices in graph k overcomes the size effects; E_k of graph k is obtained by

$$E_k = \frac{1}{n_k(n_k - 1)} \sum_{i=1}^{n_k} \sum_{j=1}^{n_k} s_{ij}$$

The value E_k converges quickly to a stable value as the size n_k of the vertex set $V(G_k)$ increases. Teklenburg *et al.* (1993) propose a standardization of their integration measure by using complete bipartite graphs. They show that its value is independent of the size of the vertex set $V(G_k)$. This method is used only in the topological approach (Teklenburg *et al.* 1993).

Both methods advocate a standardization of the network dispersion that relates to the degree of connectivity of the network as a whole. They place networks on a more or less fixed range of normalized degrees of connectivity. This range goes from completely connected networks with the highest degree of connectivity through to branching networks with the lowest degree of connectivity. Completely connected networks always have the same normalized value for the network dispersion, regardless of the size of the set $V(G_k)$. However, these methods neglect our assumption that locations in large landscape networks (with numerous elements) function differently from locations in small networks (with a small number of elements), and fail to meet our objective to measure the connectivity of the individual elements. When applied to individual vertices, the measure proposed by Allen *et al.* (1993) is calculated as

$$E_i = \frac{1}{n_k(n_k - 1)} \sum_{j=1}^{n_k} w_{ij} \tag{9}$$

In figure 4, E_i is shown for the vertices v_i indicated by large dots. It appears that E_i cannot differentiate between vertices in differently sized graphs.

When vertices in subgraphs of nonconnected networks are considered, another problem arises if the degree of connectivity of elements in different subgraphs is compared. The parameters d_i and s_i measure shortest paths from v_i to all others. In order to calculate **D** and **S**, d_{ij} and s_{ij} are assigned values of infinity if there is no path between v_i and v_j (Taaffe and Gauthier 1973). This will not occur in connected graphs. For nonconnected graphs, the values of infinity in the matrices will dominate the connectivity values in $\boldsymbol{d}$ and $\boldsymbol{s}$. For these reasons we advocate a modification of the connectivity vectors $\boldsymbol{d}$ and s for the influence of the size n_k of the vertex set $V(G_k)$.

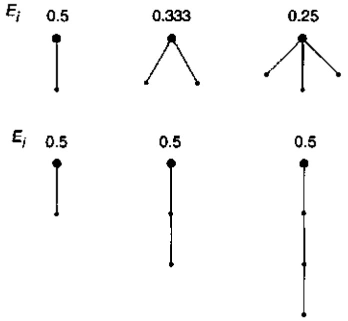


Figure 4 Calculation of the values for the normalized mean spatial separation E_i for vertex v_i based on equation (9). In the six graphs, $w_{ij} = 1$. The degree of connectivity of the large vertices i (•) is considered. Low values of E_i correspond to highly connected vertices. In the upper three graphs, E_i decreases. However, one should expect that the degree of connectivity of the vertex indicated in the first graph is twice the degree of the vertex in the second graph, and so on. In the lower three graphs, the degrees of connectivity of the indicated vertices do not differ in contrast to what can be expected when the shortest paths of all vertices are considered.

4.2 Topological approach

For d_i to be a suitable measure for comparing the degree of connectivity of vertices in a single graph, a prerequisite for modification is that the relative importance of vertices within each graph is constant. The d_i values should be modified for the influence of n_k because we assumed that vertices in a large graph k have higher degree of connectivity than vertices in a smaller graph l ($n_k > n_l$). However, the opposite can also be true. Vertices with low c_i values within a large graph (such as a branching network) will have a lower degree of connectivity compared with vertices in a small, completely connected graph. We therefore introduce critical points. For what conditions do vertices within a small graph k have higher degree of connectivity than vertices within a large graph l?

The effect of size on the connectivity parameters is ambiguous. How can the problem of comparing d_i values of vertices in differently sized graphs be resolved? As is shown by equation (2), d_i is based on the summation of $f_{i,r}$ multiplied by r. If more vertices are added to the vertex set $V(G_k)$, then either the maximum value of r will increase, the frequency $f_{i,r}$ for high values of r will increase, or both will increase. Therefore, the value of d_i increases when the size n_k of the set $V(G_k)$ is increased. For conformance with the calculation of p'_i, we used the reciprocal of r to obtain a modification of the influence of r, and therefore of the size n_k of $V(G_k)$, in d_i. The modified d'_i value can be calculated by

$$d'_i = \sum_{r=l}^{\delta} f_{i,r} \frac{1}{r} \qquad i = 1,2,\ldots,n \tag{10}$$

High values of d'_i represent highly connected vertices. The network dispersion $\hat{d}'_k$ of a connected nondirected graph k can be obtained as shown in equation (4) using $\boldsymbol{d'_k}$. From equation (10) it can be easily understood that an additional path $d_{ij} = 1$ (or direct edge) increases d'_i by 1, an additional path $d_{ij} = 2$ adds at least 0.5 to d'_i, etc. Therefore, vertices connected to large graphs have higher degree of connectivity. This is generally true, except if for vertex v_i in graph k, and vertex v_j in graph l, with $n_k > n_l$, it can be stated that $d'_i \leq d'_j$. The condition for this critical point can be defined as $f_{i,r} < f_{j,r}$ for low values of r. As the network dispersion $\hat{d}'_k$ is the sum of the degree of connectivity d'_i of all vertices v_i in k, critical points can also be defined for the measures of the network dispersion.

Table 1 presents the results of the modified parameter d'_i for the graphs in figure 3. Comparison of table 1 and figure 3 shows that the relative importance of vertices measured by the hierarchy numbers are constant.

4.3 Geometric approach

In correspondence with the topological approach, the s_i values are suitable measures for the degree of connectivity of vertices in one graph. The same reasoning as for d'_i can be applied for the modification of s_i. The modified s'_i value can then be calculated by

$$s'_i = \sum_{u>0}^{\alpha} f_{i,u} \frac{1}{u} \qquad i = 1,2,\ldots,n \tag{11}$$

High values of s'_i represent highly connected vertices. The network dispersion $\hat{s}'_k$ can be obtained as shown in equation (4) by using s'_k. Table 1 presents the results of the modified parameter s'_i for the graphs in figure 3.

Table 1 *The modified connectivity parameters d'_i and s'_i per vertex v_i, the hierarchy numbers (order) of the vertices per graph related to d'_i and to s'_i, and the network dispersions $\hat{d}'_k$ and $\hat{s}'_k$ of the two graphs as presented in figure 3. High values of d'_i and s'_i correspond to highly connected vertices v_i. For both d'_i and s'_i, the best connected vertex has the lowest hierarchy number.*

Graph 1					Graph 2				
v_i	d'_i	order	s'_i	order	v_i	d'_i	order	s'_i	order
1	3.5	5	0.3	4	7	1	1.5	0.033	1.5
2	4	2.5	0.308	2.5	8	1	1.5	0.033	1.5
3	4	2.5	0.308	2.5					
4	4.5	1	0.317	1					
5	3.5	5	0.133	5.5					
6	3.5	5	0.133	5.5					
	$\hat{d}'_1 = 23$		$\hat{s}'_1 = 1.50$			$\hat{d}'_2 = 2$		$\hat{s}'_2 = 0.067$	

In the geometric approach, we can also define a critical point between two graphs. The condition for this critical point is: when vertex v_i in graph k, and vertex v_j in graph l, with $n_k > n_l$, fulfil the topological condition $d'_i \leq d'_j$, it can be stated that $s'_i \leq s'_j$ when $f_{i,u} < f_{j,u}$ for low values of u. The opposite holds when vertex v_i in graph k, and vertex v_j in graph l, with $n_k > n_l$, do not fulfil the topological condition; then $s'_i \leq s'_j$ when $f_{i,u} < f_{j,u}$ for low values of u or $f_{i,u} > f_{j,u}$ for high values of u. The geometric conditions for a critical point describe two effects. As s'_i measures the number and the weighted distance of shortest paths, the effect of the one (*e.g.*, increasing distance) in s'_i can be nullified by the effect of the other (more direct connections), and vice versa.

5 Simulations

5.1 Effect of size

We considered the effect of size n_k of the vertex set $V(G_k)$ on the parameters d'_i and s'_i. We used three topologically constant graph types which represent different landscape networks: the path graph as a linear landscape network, the completely connected graph as a compact landscape network, and the triangular graph as an extended landscape network (figure 5). For each type, we generated a series of g graphs with a systematic increase of the size n_k of the vertex set $V(G_k)$ for each graph k. For the path graph and the completely connected graph, n_k increases by 1 per graph k, starting with $n_1 = 1$. The triangular graphs increase with k (figure 5). All w_{ij} are considered to be equal.

We calculated d'_i for just one vertex of each graph. In figure 5 the vertices are indicated by large dots. Figure 5 also provides the equations to calculate d'_1 for these types. Figure 6 presents the d'_1 values of the first vertex of each graph k. The diagrams for s'_i (not presented) showed exactly the same pattern. Figure 7 shows the $\hat{d}'_k$ values for some graphs of the series. The $\hat{s}'_k$ (not presented) values showed the same pattern as the $\hat{d}'_k$ values.

Path graph

$n_k = k$

$$d'_1 = \sum_{i=1}^{n_k-1} \frac{1}{i} \qquad \forall \quad k \geq 2$$

Completely connected graph

$n_k = k$

$d'_1 = (n_k - 1)$

Triangular graph

$$n_k = \sum_{i=1}^{k} i$$

$$d'_i = \sum_{i=2}^{k} \frac{i}{(i-1)} \qquad \forall \quad k \geq 2$$

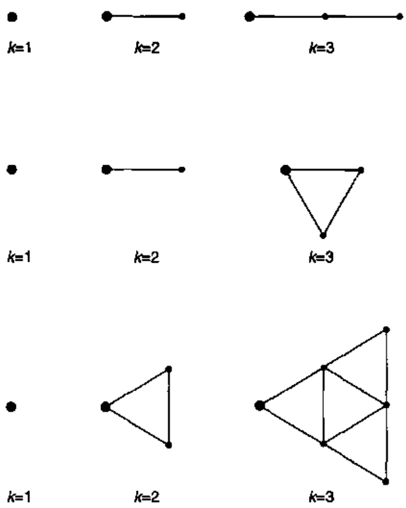


Figure 5 Three graph types with a topologically constant structure: the path graph, the completely connected graph, and the triangular graph. The large vertices (•) are used to illustrate the effect of size on the connectivity parameters. The equations for the size n_k of the vertex set $V(G_k)$ of graph k and for the connectivity parameter d'_1 for the indicated vertex are presented. For all three types, we defined $d'_1 = 0$ in graph $k = 1$.

5.2 *Effect of spatial configuration*

We also analyzed the effect of spatial configuration of the network on the parameters. For each graph type, we started with a limited number of differently sized graphs. The spatial configuration of each was independently changed by stretching w_{ij}. This provided a series of differently spaced graphs with constant sizes of the vertex set $V(G_k)$ and edge set $E(G_k)$. Hence, $\hat{c}_k$ and $\hat{d}'_k$ are constant. Because p'_i measures direct edges and s'_i both direct and indirect edges, we looked for the differences between the two parameters.

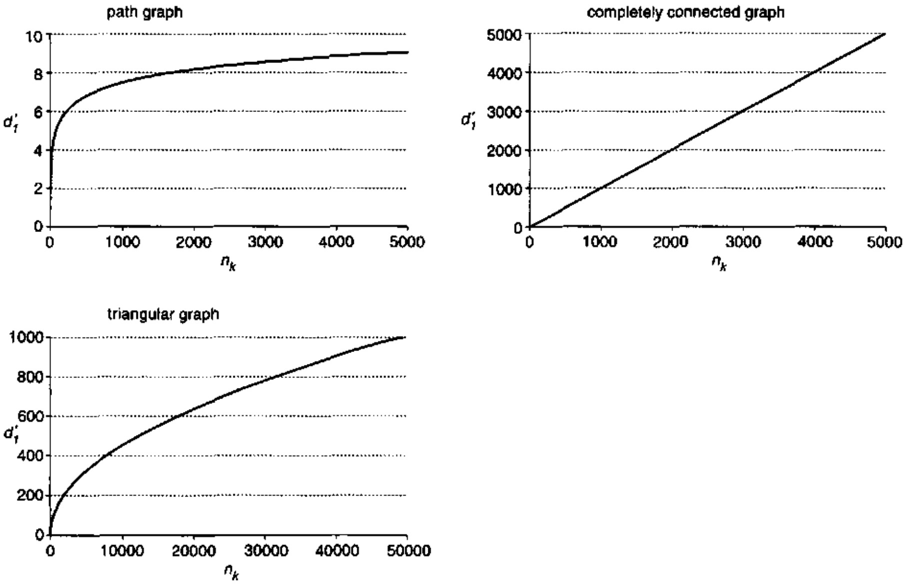


Figure 6 *The relationships between the size n_k of the vertex set $V(G_k)$ of each graph k and the connectivity parameter d'_1 of the first vertex (see figure 5). For the path graph and the completely connected graph, the number of graphs g = 5000. For the triangular graph, g = 1000.*

At the beginning, each graph had $w_{ij} = 10$ for all edges. The graphs changed because of one randomly selected edge which was stretched by $y = 3$ to $w_{ij} = 30$: graph 1 had one randomly stretched edge, graph 2 had one extra randomly stretched edge, etc. This was continued until all edges were stretched. Figure 8 presents the results of the series of stretched graphs. Critical points are indicated.

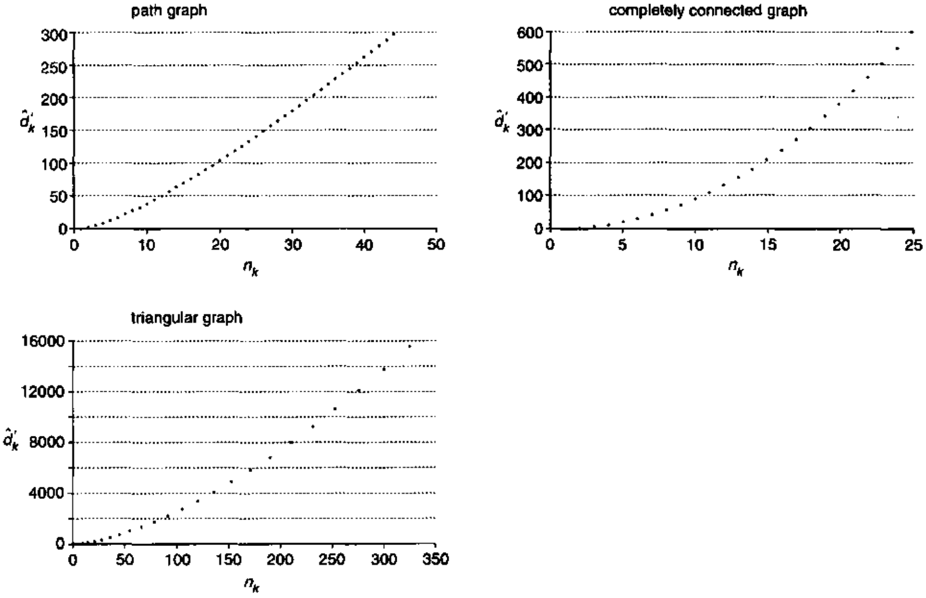
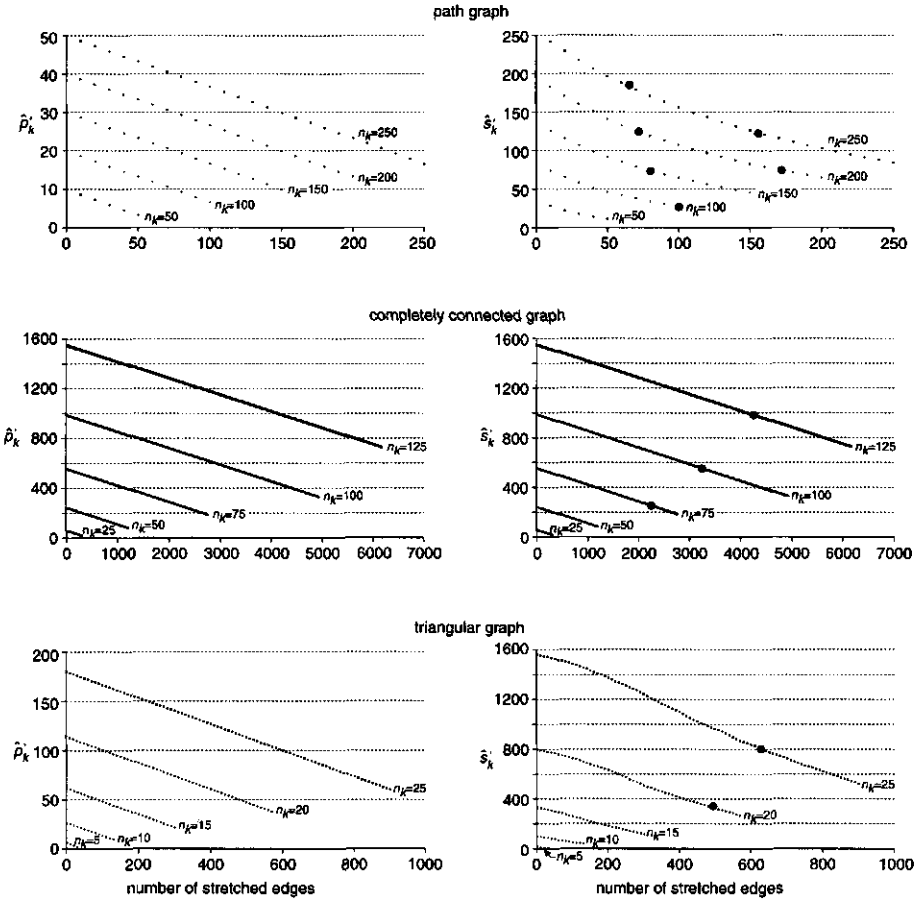


Figure 7 *The network dispersion* $\hat{d}'_k$ *per graph k for the three graph types. The graphs systematically increase in size* n_k *of the vertex set* $V(G_k)$ *(*$g = 44$ *for the path graph,* $g = 25$ *for the completely connected graph, and* $g = 25$ *for the triangular graph).*

6 Discussion and conclusion

The graph-theoretic parameters used frequently to quantify the degree of connectivity of network elements cannot be applied to compare the connectivity of these elements when they belong to different networks. This may not be problematic when the objective of the study is to analyze relationships between pattern and function within one (connected) network. However, a modification of the parameters appears to be necessary to compare the degree of connectivity of elements in different networks across regions as well as over time, or to analyze decomposed networks with nonconnected subsystems. We extended the existing parameters to overcome this problem. When applying these parameters, one should be aware that the results are dependent upon the number of locations that are accessed by the network or, in other words, by the boundaries of the delimited region. When the degree of connectivity needs to be measured independently of the delimitation of the region, the standardized parameters as derived by either Allen *et al.* (1993) or Teklenburg *et al.* (1993) should be used.



path graph

completely connected graph

triangular graph

Figure 8 *The relationships between the network dispersion $\hat{p}'_k$ (left) and $\hat{s}'_k$ of a limited number of graphs k of the three types, and the number of stretched edges (one randomly selected edge is stretched from $w_{ij} = 10$ to $w_{ij} = 30$). Graph 0 has zero stretched edges, graph 1 has one randomly selected edge, graph 2 has one extra randomly selected edge, etc. Critical points are indicated with dots. Critical points occur when the connectivity value of vertices in graph k is lower than for vertices in graph l ($\hat{s}'_k \leq \hat{s}'_l$), and $n_k > n_l$.*

The applications for these parameters can be encountered in comparing the relative position of any location to others over time or among regions, such as shopping centres, recreation facilities, hospitals, cities and natural reserves. The relationship between variables that represent the function of these locations (*e.g.*, number of visitors, telephone calls, passengers by bus, railway, or airline) can be tested against their degree of connectivity. Do differences between regions exist? Have the relationships been changed over time? Other applications in spatial analysis and planning are: as a measure of connectivity or accessibility in other models when such a quantity is required, *e.g.*, models of population potential (Pooler 1987), spatial interaction models, or spatially realistic models for animal populations (Hanski and Gilpin 1997); to indicate deficiencies of existing systems, to design new configurations, and to evaluate these new arrangements, *e.g.*, to address questions such as where facilities or resources may be located in a region so that they are accessible; to illustrate the effect on connectivity of changes in the observed system, *e.g.*, the impact of a new town, facility, or train station on relationships with other locations.

We used four types of matrix-based parameters to quantify the degree of connectivity of elements and the dispersion in networks. The parameters take into account only a few aspects of networks: measures for the number and weight of direct and indirect relationships between elements. We did not use other parameters such as the global indices from Kansky (1963), or density or shape indices (Haggett and Chorley 1969, Selkirk 1982) because they focus on the network as a whole rather than on individual locations. We also do not consider the size or weights of the locations (see Pooler 1987, 1995). However, the connectivity parameters can be combined with these characteristics of locations, such as population size and attractiveness.

Each parameter type has certain properties. The first simulation provides insight into the effect of network size on the relevant parameters. Figure 6 shows that size n_k of the vertex set $V(G_k)$ of graph k affects the degree of connectivity of the vertices concerned: when n_k increases, the value d'_i and, therefore, the degree of connectivity of the vertices increases. This agrees with our assumptions. As the graphs per type have the same topological structure, this effect can be explained solely by the increase in the size n_k. We compared the behaviour of d'_i with the original parameter d_i. As can be derived from equation (2), the degree of connectivity d_i of the first vertex of both the path graph and the triangular graph decreases exponentially with an increase in the size n_k of the vertex set $V(G_k)$. As low values for d_i correspond to a high degree of connectivity, this pattern cannot be correct. It implies that vertices connected to vertex sets $V(G_k)$ with larger size n_k have a lower degree of connectivity (see figure 3). In the completely connected graph, a linear increase of d'_i appears owing to its structure. This increase is equivalent as obtained by d_i, because for this graph type it can be stated that $d_i = d'_i = c_i$. For the other vertices in the graphs, we can expect the same effects of size because the graphs are topologically constant.

Network dispersion provides information about the degree of connectivity of individual elements. For example, for matrix **D**, the ratio $\hat{d}'_k$ / n_k is approximately d'_i, especially for large graphs. Therefore we calculated $\hat{d}'_k$ per graph k for the three types (figure 7). As can be expected, graph size n_k affects $\hat{d}'_k$. It appears that the increase in $\hat{d}'_k$ becomes linear when the size of large graphs increases. In accordance with the original parameter d_i, $\hat{d}_k$ decreases exponentially with an increase in the graph size n_k; two graphs which are almost equal in size may differ enormously in terms of the degree of connectivity measured by $\hat{d}_k$.

Figure 8 shows the relationships between the parameters $\hat{p}'_k$ and $\hat{s}'_k$ and the number of stretched edges. It is apparent that the diagrams of $\hat{p}'_k$ and $\hat{s}'_k$ for the completely connected graph are equal. In the beginning of the other series, only a few s'_i values are affected by stretched edges, especially in extended graphs where alternative shortest-weighted paths are available. When the number of stretched edges increases, two combined effects lead to the nonlinear variation of $\hat{s}'_k$ in the path graphs and the triangular graphs. First, the number of stretched edges increases in each shortest-weighted path s_{ij}. Second, the number of larger s_{ij} in each s'_i increases. The availability of shorter paths then decreases. In comparison with p'_i it appears that s'_i is sensitive to the multiplicity of edges with changing length. The connectivity parameters s'_i and $\hat{s}'_k$ provide refined measures when the spatial configuration is taken into account.

These results are confirmed by other types of graph we investigated: complete bipartite graphs with equal-sized subsets and rectangular graphs. Bipartite graphs belong to the type that represents compact landscape networks. The results were comparable with the completely connected graph. The rectangular graph type can be considered to be an extended landscape network. The results were comparable with those of the triangular graph.

We can conclude that the size of the graphs affects the values of the parameters d'_i and s'_i. However in contrast to d_i and s_i, the degree of connectivity of elements measured by d'_i and s'_i in a variety of differently sized networks can be compared. In accordance with our assumptions about effects of size on the degree of connectivity, the comparisons of the degree of connectivity provide useful results. We can also conclude that the variation in both $\hat{p}'_k$ and $\hat{s}'_k$ and, therefore, in p'_i and s'_i concurs with the variation in the spatial configuration of the network. The s'_i parameter of equation (11) and the resulting $\hat{s}'_k$ parameter can differentiate between differently sized and spaced networks. These parameters can be applied to compare the degree of connectivity of elements in digraphs and in nonconnected subsystems of decomposed networks. In this paper, we assumed a spatial definition of distance that resulted in emphasis on the relevance of the spatial configuration of networks in the analysis. These parameters can also be used for other definitions of space. The interpretation of the results of these applications are beyond the scope of our paper.

Acknowledgements

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4 HABITAT CONNECTIVITY AND COLONIZATION IN FRAGMENTED NUTHATCH POPULATIONS

Submitted

Habitat connectivity and colonization in fragmented nuthatch populations

1 Introduction

In human-dominated landscapes, the habitat of many species is subject to fragmentation. The degree of habitat connectivity is assumed to be an important landscape feature that determines the population dynamics (*e.g.*, Lefkovitch and Fahrig 1985, Fahrig and Merriam 1985, Gilpin and Hanski 1991, Verboom *et al.* 1991, Wu *et al.* 1993, Hanski 1994, With and Crist 1995, Gustafson and Gardner 1996, Schumaker 1996, Hanski and Gilpin 1997, With *et al.* 1997). In this context, connectivity is the property of habitat patches in the landscape to maintain flows of individuals with other habitat patches (cf. Merriam 1990, Taylor *et al.* 1993). Due to the low degree of connectivity, dispersal between habitat patches may be constrained. As predicted by the metapopulation theory, one of the effects of reduced habitat connectivity is a decrease of the colonization probability of patches (Verboom *et al.* 1991, Hanski 1994, Hanski and Gilpin 1997).

The objective of this paper is to investigate effects of habitat connectivity measured at different spatial scales on colonization in European nuthatch *Sitta europaea* populations in fragmented habitat. The nuthatch is a sedentary songbird of mature deciduous forests. In the agricultural landscapes of Northwest Europe, nuthatch habitat is often fragmented in small patches with large interjacent distances. For nuthatches, I conducted the degree of connectivity of a patch as a function of the number, size and location of the other patches occupied by nuthatches. There is empirical evidence that nuthatch populations are affected by habitat fragmentation (Van Dorp and Opdam 1987, Verboom *et al.* 1991, Enoksson *et al.* 1995, Matthysen and Currie 1996, Bellamy *et al.* 1997, 1998, Van Langevelde and Schotman chapter 6). Verboom *et al.* (1991) already showed that the presence of nuthatch populations in fragmented habitat differed from the predictions based on random distribution. They also showed that colonization of unoccupied patches is determined by the degree of habitat connectivity, although they do not include differences in the spatial scale.

The assessment of the effects of habitat fragmentation should be conducted at the spatial scale that agrees with the scale of movement of the species concerned (Wiens, 1995). However, there is often uncertainty about the movement distances of the species concerned, *e.g.*, for nuthatches see Matthysen *et al.* (1995). For three regions with fragmented habitat, I tested the null hypothesis that the degree of connectivity of patches does not explain colonization of unoccupied habitat patches.

If an effect of habitat connectivity on colonization is found, one should try to identify the spatial scale at which colonization can be best explained by the degree of connectivity of the fragments.

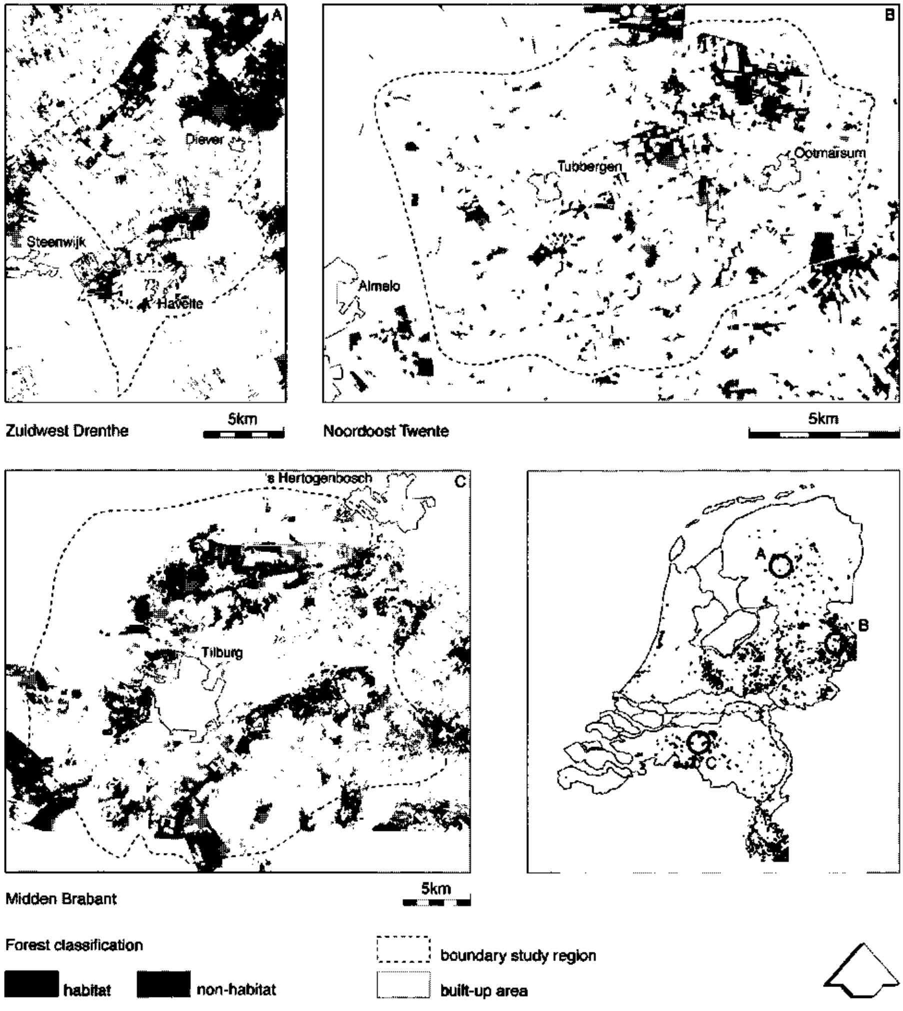

Figure 1 *The three study regions Zuidwest Drenthe (A), Noordoost Twente (B) and Midden Brabant (C) with fragmented habitat for the nuthatch* Sitta europaea*. The location of the regions is indicated on the map with deciduous forests in the Netherlands. In Midden Brabant, 178 habitat patches were distinguished, in Zuidwest Drenthe 66 and in Noordoost Twente 123.*

2 Materials and Method

Study regions and time series

The three study regions, Midden Brabant, Zuidwest Drenthe and Noordoost Twente, have forested patches in a matrix of farmland, predominantly grassland and maize (figure 1). In these regions, the area of suitable habitat is less than 5% of the total study area. To map the nuthatch habitat in the regions, we used the data of the Dutch national forest statistics (CBS 1984). This inventory provided detailed information about the location of the forests (the minimum-mapping unit is 0.2 ha). Comparisons between the actual situation and the forest statistics showed that the amount and distribution of the forests were hardly changed from 1984 until present.

Each woodlot with deciduous forest is considered as a habitat patch. When the woodlots are less than 200 m apart, they were joined to one patch. The size A_i of patch i was defined as the area covered by deciduous forest in the patch. Patches containing less than 1 ha habitat were considered too small and excluded from the analysis (cf. Verboom *et al.* 1991). Figure 2 shows the nearest-neighbour distances and the size of the patches.

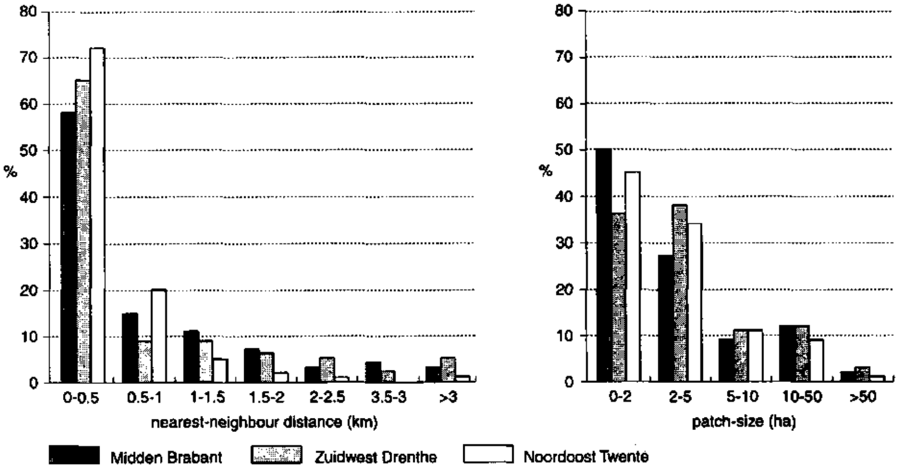

Figure 2 Percentage of patches per class of nearest-neighbour distances and of patch sizes in the three study regions

Time series of territory occupancy by nuthatches in the breeding season were available for the three regions: from 1990-1992 for Midden Brabant by F. Post *et al.* (unpubl.), from 1973-1995 in Zuidwest Drenthe by A. van Dijk (unpubl.), from 1988-1994 for Noordoost Twente by A. Schotman (Verboom *et al.* 1991, Verboom and Schotman 1994). I used these data to determine per year the presence or absence of nuthatches in a patch (patch occupancy) and the number of occupied territories per patch. The latter was considered as a measure for the local population size. For the surroundings of the regions in a range of 3 km, I estimated what patches can be expected to be frequently occupied, based upon data about the presence of nuthatches and the size of the habitat patches.

Based on the time series, I derived colonization patterns. A colonization was recorded when a patch was unoccupied in the breeding season of year t and occupied in the breeding season of year $t + 1$. In Midden Brabant, 72 colonizations were recorded for the observed period, 49 in Zuidwest Drenthe and 53 in Noordoost Twente.

Definition of habitat networks

To measure the degree of connectivity of the habitat patches, I used the mathematical graph theory (see Wilson and Watkins 1990 for an introduction). Therefore, the habitat patches in the regions were considered as elements of a habitat network connected by spatial or functional relationships between the patches. This network can be depicted as a graph in which the elements are the vertices and the relationships between the elements are the edges. I assumed that habitat patches are functionally connected when distances between the patches are less than a specified threshold distance. Then, an edge between a pair of vertices can be drawn. For a species, this threshold distance is the distance beyond which the probability of successfully bridging this distance by dispersing individuals rapidly decreases (see also Fahrig and Paloheimo 1988, With and Crist 1995, Keitt *et al.* 1997, Smith and Gilpin 1997). However, such a threshold distance is difficult to determine for species. Therefore, not one distance should be concerned. I analyzed a range of distances to determine what distance best explains the observed patterns.

Varying the threshold distances results in a different spatial scale of fragmentation (figure 3). With low threshold distance, disjointed subsets of habitat patches can then be distinguished. Between the patches in different subsets, no relationships exist as defined above. In graph theory, the disjointed subsets of patches are called subgraphs. The size of the subsets is the number of vertices in it. The graph to which these disjointed subgraphs belong is called nonconnected (Van Langevelde *et al.* chapter 3).

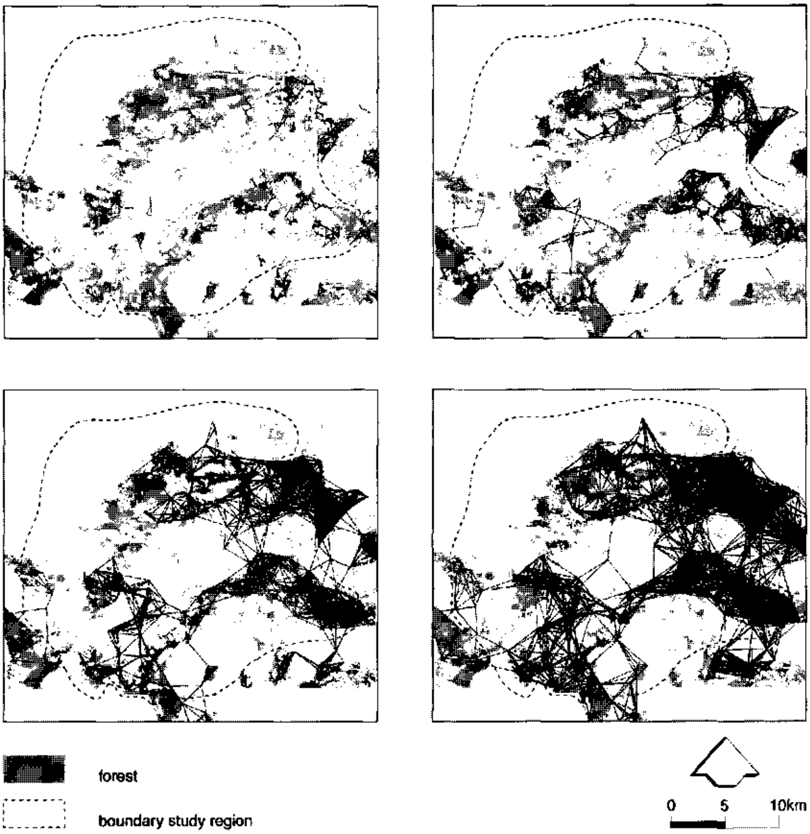

Figure 3 *Some graphs of the nuthatch habitat network in Midden Brabant for the threshold distances 1, 2, 3 and 4 km. The vertices in the graphs represent the centres of the habitat patches. An edge between two vertices indicates that the distance between the vertices is less than or equal to the specified threshold distance.*

Measuring the degree of habitat connectivity

In this paper, I consider a graph with a vertex set of n vertices and an edge set of m edges. The length of the edges w_{ij} between vertex v_i and v_j is measured in kilometres. Graphs can be analytically represented as matrices, in which the relationships between the vertices are recorded in the rows and the columns. Graph theory provides parameters to quantify the degree of connectivity of the elements in a network.

Van Langevelde *et al.* (chapter 3) derived matrix-based parameters for the degree of connectivity of the individual patches. These parameters deal with the distance to other patches and the size and spatial configuration of the subset to which the habitat patches are connected. I used the parameter derived from the matrix **S'**, **S'** = (s'_{ij}), that provides the shortest-weighted paths between pairs of vertices: s'_{ij} is the reciprocal of the cumulative edge length of the shortest path between v_i and v_j, $s'_{ij} = 1 / \Sigma w_{ij}$.

To measure the degree of connectivity of the vertices, the vector $\boldsymbol{s'}$ can be obtained by multiplying matrix **S'** with the vector $\boldsymbol{l}$

$$\boldsymbol{s'} = \mathbf{S'}\,\boldsymbol{l} \tag{1}$$

in which $l_i = 1$, $i = 1, 2,..., n$. The vector $\boldsymbol{s'}$ sums the elements of each row in the matrix. The elements s'_i of the vector $\boldsymbol{s'}$ give the degree of connectivity of patch i. High values of s'_i represent highly connected patches.

To account for potential dispersal sources, matrix **B**, **B** = (b_{ij}), was defined as $b_{ij} = p_{j,t} \times s'_{ij}$ where $p_{j,t}$ is the local population size of vertex v_j in year t. When patch j is unoccupied in year t, $p_{j,t} = 0$. This patch has thus no contribution to the degree of connectivity b_i of patch i. The degree of connectivity b_i of the elements in vector $\boldsymbol{b}$ can be calculated in the same way as shown in equation (1).

A measure for the dispersion or overall degree of connectivity of the network can be derived from matrix **S'**. The dispersion $\hat{s}'$ is the sum of the degree of connectivity of all individual elements in the network. The dispersion $\hat{s}'$ can be calculated by multiplying the transpose of $\boldsymbol{s'}$ with $\boldsymbol{l}$ (Van Langevelde *et al.* chapter 3)

$$\hat{s}' = \boldsymbol{s}'^{T}\,\boldsymbol{l} \tag{2}$$

The threshold distance to calculate s'_{ij} was varied from 0.4 to 10 km with steps of 0.2 km from 0.4 to 4 km and with steps of 0.5 from 4 to 10 km. The distances between pairs of patches w_{ij} were measured from the centre of each patch. However, this may overestimate the inter-patch distances, especially between large patches. For each threshold distance, the degree of connectivity of the patches based on matrix **S'** and **B** was calculated. Also, the dispersion $\hat{s}'$ of the networks based on matrix **S'** was calculated for each threshold distance.

Statistical analyses

With logistic regression, the presence or absence of a colonization of a in year t+1 was explained by its degree of connectivity b_i calculated with the population sizes $p_{j,t}$ in year t. This was conducted for the pooled data of the three regions. For Zuidwest Drenthe, the data of patch occupancy from 1982 until 1995 were used since in the period before 1982 only few patches were occupied. Since differences between the regions exist in population level and size of the region (which affect the connectivity parameter s'_i), the regions were added as binary factors in the regression analyses. The size A_i of the patches was also added as explanatory variable.

In the regression model, I first added the region factors. Then, the size of the patches A_i and the interactions between A_i and the region factors were included. Finally, the variables for the degree of connectivity b_i calculated for the different threshold distances were added one by one, plus the interactions between b_i and the region factors. The final models contain only variables with significant coefficients (based on a two-sided t-test).

To select the model that best explains the colonization patterns, I used the Akaike's Information Criterion (*AIC*) (Akaike 1973, White and Bennetts 1996). The *AIC* is computed as

$$AIC = -2\log(L) + 2p$$

in which L is the maximum likelihood for the model and p is the number of parameters in the model. The model with the lowest values for *AIC* will be selected (the most parsimonious model) and explains the colonization pattern best. The threshold distance for which the variable b_i in the selected model was calculated, gives an indication of the distances covered by dispersing nuthatches which led to successful colonizations.

3 Results

For each threshold distance, the dispersion $\hat{s}'$ was calculated based on the degrees of connectivity s'_i of the individual patches that were calculated for these distances. In figure 4, the dispersion $\hat{s}'$ is presented per study region. In the study regions, the amount and spatial configuration of the habitat is assumed to be constant, whereas the dispersal distance of the observed species is varied. The absolute value of $\hat{s}'$ depends upon the number of patches and the distances between them (Van Langevelde *et al.* chapter 3). If the dispersal distance of forest species is more than about 3.5 km, the dispersion $\hat{s}'$ is relatively constant. This may be partly explained by the lack of data about habitat and the occupation of nuthatches more than 3 km outside the study regions. On the other side, the contribution of habitat at large distances to the degree of connectivity of the patches within the study region is small (Van Langevelde *et al.* chapter 3). When a species of deciduous forest has a dispersal distance above this threshold of 3.5 km, the forests in Midden Brabant can be considered to be sufficiently connected directly or indirectly with each other. Below this threshold, the overall degree of connectivity decreases rapidly. Species with dispersal distances below this threshold may experience effects of constrained dispersal. In Zuidwest Drenthe, this critical threshold is approximately 4 km and in Noordoost Twente approximately 2.5 km. The latter region is less fragmented from the point of view of habitat connectivity. (This region has on average the smallest patches, see figure 2.)

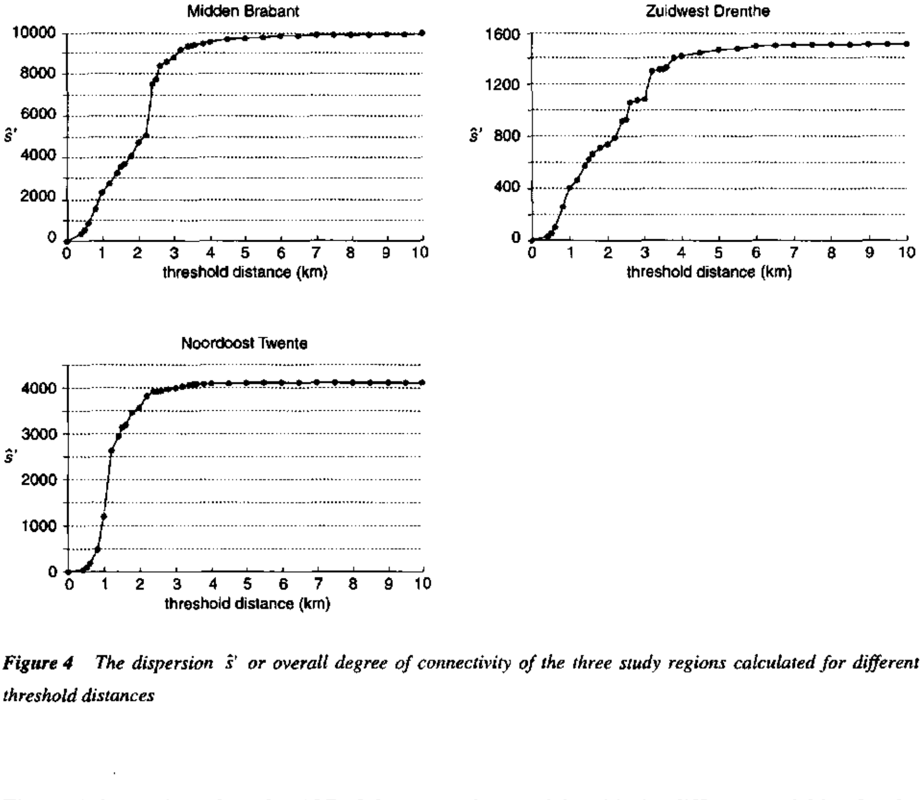

Figure 4 *The dispersion* $\hat{s}'$ *or overall degree of connectivity of the three study regions calculated for different threshold distances*

Figure 5 shows the values for *AIC* of the regression models with the different variables for the degree of connectivity b_i. The degree of connectivity could be significantly added to the models when it was calculated for threshold distances of 1.4 km or more. The significance of the degrees of connectivity b_i in the models for the range of threshold distances between 0.4 and 10 km is (two sided t-test: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns not significant): ns for b_i calculated for threshold distances less that 1.4 km; * for b_i calculated for threshold distances between 1.4 and 1.6 km; ** for b_i calculated for threshold distance of 1.8 km; *** for b_i calculated for threshold distances > 1.8 km.

The models with the degrees of connectivity b_i calculated for the threshold distances 2.4 to 3 km have low values for *AIC*. They best explain the colonization pattern. The model with b_i

calculated for 2.5 km has the lowest *AIC* value. In table 1, the regression model is given. In this model, colonization could be ascribed as a function of the natural logarithm of b_i, the region factors, the size of the patches A_i and the interaction of A_i with the region factor for Noordoost Twente (*NT*). The interactions of A_i and the other region factors and the interactions of b_i and the region factors were not significant.

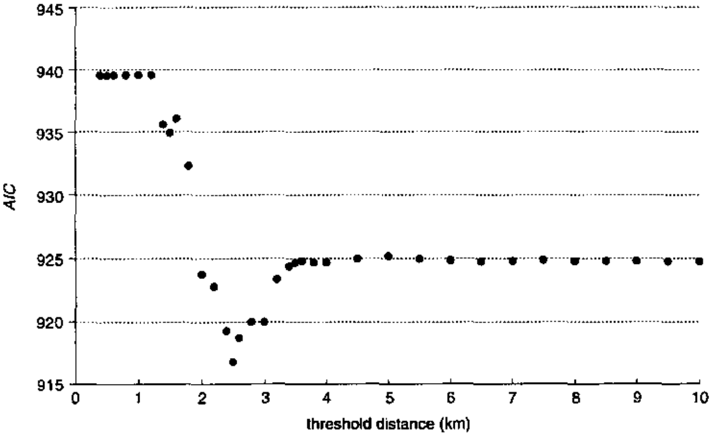

Figure 5 *The values for the Akaike's Information Criterion (AIC) of the regression models for colonization where the degrees of connectivity b_i calculated for the different threshold distances were added one by one. The minimum model to which b_i was added contained the size of the patches, the region factors for Noordoost Twente and Midden Brabant and the interaction between the patch size and the region factor for Noordoost Twente (table 1).*

Table 1 *The selected regression model for colonization of unoccupied patches in the three study regions Midden Brabant (MB), Zuidwest Drenthe (ZD) and Noordoost Twente (NT). The variable b_i is the degree of connectivity and A_i is the size of patch i. The estimates for the parameters, their standard deviation (between brackets) and significance are given (two sided t-test: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns not significant).*

Parameter	Estimate	
log(b_i)	0.844 (0.187)	***
NT	-1.853 (0.391)	***
MB	0.604 (0.275)	*
A_i	-0.0817 (0.0510)	ns
A_i×NT	0.582 (0.139)	***

4 Discussion

Effects of the degree of habitat connectivity on colonization

In this paper, I investigate the relationships between the degree of connectivity at different spatial scales and colonization of habitat patches by nuthatch populations. Several studies show that there are thresholds in the landscape for population persistence (*e.g.*, Andrén 1994, 1996, With and Crist 1995, Gustafson and Gardner 1996, Keitt *et al.* 1997, Metzger and Décamps 1997, With *et al.* 1997, Fahrig 1998). Mostly by theoretical studies, it is shown that there are critical thresholds of connectivity beyond which movement through the landscape suddenly becomes unlikely. When the degree of connectivity of the patches is calculated at different spatial scales, it can be expected that such critical thresholds will reveal for a certain species. As is shown in figure 4, critical thresholds for a species may appear when this overall degree of connectivity shows an abrupt shift for small changes in the dispersal distance. When dispersal distances of nuthatches is less than these thresholds, effects of constrained dispersal on colonization can be expected.

The results of the regression analyses indicate that the degree of connectivity of the patch, measured as b_i, can significantly explain colonization when it is determined with a threshold distance of about 1.4 km or more (figure 5). Regarding the values for *AIC*, the degrees of connectivity calculated for threshold distances between 2.4 and 3 km best explains the colonization patterns. I rejected the null hypothesis because the degree of connectivity explains the colonization of unoccupied patches by nuthatches.

The results agree with the study of Verboom *et al.* (1991). They found that the colonization probability of unoccupied patches depends on the number of occupied patches in a range of 2 km (with different weights for the effect of patches at a distance ≤ 1 km and 1-2 km). There are other studies in which the degree of connectivity is related to nuthatch data (Van Dorp and Opdam 1987, Schotman and Meeuwsen 1994, Enoksson *et al.* 1995, Van Langevelde and Schotman chapter 6). They also use the amount of habitat in a radius of several kilometres around the patch of observation.

Uncertainty exists about the dispersal behaviour of nuthatches in fragmented habitat. Dispersal distances of juveniles are measured in contiguous habitat (Enoksson 1987, Matthysen and Schmidt 1987) and in fragmented habitat (Matthysen *et al.* 1995). In contiguous habitat, the dispersal distances of juvenile nuthatches cover a few kilometres: the median distance was 1 km and distances longer than 4 km were rarely observed. In fragmented habitat, nuthatches seem to fly longer distances: 70% of the nestlings disperse at least 3 km from the natal territory. A lower tendency to disperse in fragmented habitat could also not be demonstrated (Matthysen *et al.* 1995). However, indirect evidence for limited dispersal in fragmented habitat is found: territories were taken up at a slower rate (Matthysen and Currie 1996) and more often by single birds (Matthysen and Currie 1996), habitat selection is limited (Van Langevelde and Schotman chapter 6) and, at population level, extinction of local populations is explained by patch size and colonization by the degree of connectivity (Verboom *et al.* 1991). One way to deal with the uncertainty about dispersal behaviour is to assume that an indication of the covered distances can be derived from colonization patterns obtained with long-term observations.

As can be expected, the degree of connectivity b_i calculated for threshold distances larger than 3 km also significantly explains colonization. The potential influx of individuals from nearby patches remains high, also when the patch can be reached from remote patches. The relative position measured by the parameter s'_i on which b_i is based, tend to be constant when the threshold distance increases (Van Langevelde *et al.* chapter 3). However, it should be noted that the influence of occupied habitat at large distances outside the regions could not be included.

The results also show that the colonization probability of large patches in Noordoost Twente is higher than of smaller ones (table 1). This indicates that nuthatches have a preference for large patches. The reason for the preference for large patches can be a higher level of resources than in smaller patches (available food, mates, nest holes), protection against weather by a stable microclimate, competition for holes and predation, or conspecific attraction. In Noordoost Twente, Schotman (in prep.) found a higher breeding success in larger patches (breeding success was negatively related to the relative edge length of the patch). In the two other regions, no effect of patch size on colonization was found. This can be explained by the relatively low degree of connectivity of the patches in these regions (figure 2 and 4): nuthatches are not able to locate and select territories in large patches better than in small patches. As can be expected, dependency exists between patch size and their connectivity (Fahrig 1992, Van Langevelde chapter 5).

Measuring the degree of connectivity

For such studies, information should be available about dispersal rate and distances, and about the behaviour of dispersing individuals in relation to landscape elements. In theoretical studies, dispersal success is often measured as the number of immigrants arriving in a patch each year (*e.g.*, Fahrig and Merriam 1985, Doak *et al.* 1992, Adler and Neurnberger 1994, Schippers *et al.* 1996, Schumaker 1996). The dispersal success rate provides a direct and independent measure for habitat connectivity. In empirical studies at landscape scale, such information is often lacking. In these studies, spatial determinants for the degree of connectivity are often related with population responses (*e.g.*, Verboom *et al.* 1991, Hanski 1994, Vos and Stumpel 1995).

Frequently used parameters for the degree of connectivity of patches concern (potential) influences of dispersal sources by measuring:

- the number or size of sources, or the area of habitat within a certain distance (Verboom *et al.* 1991, Vos and Stumpel 1995, Van Langevelde and Schotman chapter 6);
- the distance to the nearest occupied patch and its size or local population size (Gustafson and Gardner 1996);
- the distances to all occupied patches and their sizes or local population (Hanski 1994).

However, these parameters do not explicitly consider the size and spatial configuration of the subset to which the habitat patches are connected. The relevance to include these spatial determinants in the study to population dynamics is shown by Fahrig and Merriam (1985). The connectivity parameter s'_i measures these determinants. As is argued, this parameter provides the opportunity to measure the degree of connectivity at several spatial scales when the size of the subsets of connected patches varies.

In the definition of graphs, patches were represented as vertices, which may be either connected or not to other patches. Instead of distances (Euclidean distance or weighted by the permeability of the inter-patch distance due to corridors or barriers), the probability that organisms move between patches may be applied. To obtain such probabilities, relationships between distance and, for example, the number of individuals that can bridge this distance, should be known or assumed. Then, a matrix with edge probabilities can be used. Further research should investigate how the degree of connectivity of individual patches can be obtained based on this matrix.

As is argued, the approach with multiple spatial scales of fragmentation allows incorporating uncertainty in estimating the dispersal behaviour of particular species (Keitt *et al.* 1997). At community and ecosystem level, indications of the effect of patchiness can also be derived. One species may perceive a given landscape as highly fragmented (dispersal distance is less than the critical threshold in $\hat{s}'$) while it appears relatively connected to others that interact with the landscape at another spatial scale. Moreover, it allows the investigation of the relative importance of patches in the overall degree of connectivity by systematically removing and adding patches (Keitt *et al.* 1997).

Acknowledgements

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5 HABITAT SELECTION IN PATCHY LANDSCAPES

Submitted

Habitat selection in patchy landscapes

1 Introduction

The relationships between the patchiness of habitat and populations of species received a lot of attention in ecological research, especially in studies on effects of habitat fragmentation (*e.g.*, Kareiva 1990, Fahrig and Merriam 1994, Hanski and Gilpin 1997). For a species, habitat patchiness may affect dispersal abilities and influences processes at the scale of individuals and populations. When distances between patches are large relative to the distances individuals can bridge, negative effects on the selection of habitat can be expected. The main questions of this paper were: does habitat selection differ between landscapes with differently spaced habitat, and if so, what are the effects at population level? To address the main questions, three null hypotheses based on predictions for optimal habitat selection were tested. Therefore, I used a spatially explicit, stochastic and territory-based model to simulate the occupancy of breeding sites in patchy landscapes. In the simulations, the amount and spatial configuration of habitat in the model landscapes and the mobility of the model species were varied.

The occupancy of low quality breeding sites can occur in two different situations (Brown 1984, Pulliam and Danielson 1991, Pulliam 1996). First, individuals are forced to accept low quality breeding sites when population level is high and all high quality sites are occupied. Second, several low quality sites are occupied due to the insufficient degree of connectivity of high quality sites. Then, searching individuals should either be content with unoccupied habitat nearby which may be of low quality, or take a higher mortality risk during dispersal to distant unoccupied sites of high quality. Since habitat selection is affected, among others, by the population level, it should be first determined that the population level is low when dispersal is constrained. The first null hypothesis was that *there are no effects of patchiness of habitat on the population level.*

With patch selection measured as the occupation frequency of the patches, I tested the second null hypothesis that *there are no effects of patchiness on the selection of habitat patches*. The quality of the patches should largely determine the selection. As can be expected, the amount and spatial configuration of habitat also affect patch selection, especially when there is less habitat and the inter-patch distances are large related to the mobility of the species (Verboom *et al.* 1991, Adler and Neurnberger 1994, Andrén 1994, Venier and Fahrig 1996, Fahrig 1998).

The third null hypothesis was that *there are no effects of patchiness on habitat selection.* The habitat selection was measured as the proportion of occupied high quality breeding sites. To test this hypothesis, I compared simulated habitat selection with optimal selection. Habitat selection is considered optimal if individuals can spread freely according to the variation in quality of their habitat. The expectation was that the proportion of occupied sites of high quality habitat is low when the inter-patch distances are large related to the mobility of the species (Danielson 1992, Morris 1995, Pulliam 1996). Then, the simulated habitat selection deviates from the optimal selection.

2 Methods

Model structure

The simulation model uses the functionality of PCRaster (Van Deursen and Wesseling 1995, Wesseling *et al.* 1996). PCRaster is developed for spatially explicit dynamic modelling. The model landscapes for the simulations are rasters of 125 × 125 gridcells. These cells can be either breeding or non-breeding habitat. The size of the cells agrees with the territory size of the model species. The amount of breeding habitat (B in % of the total amount of cells) varies between the model landscapes. The breeding habitat contains high quality breeding habitat (O in number of sites) and low quality breeding habitat (M in number of sites). Each cell with breeding habitat provides a potential breeding site. The breeding habitat has a low resistance for movement of the model species. I also distinguished two types of non-breeding habitat with high and low resistance for movement.

The model simulates the occupancy of breeding sites by pairs. In a model landscape, the number and size of the breeding sites is constant, not depending upon population density or food availability. A site is occupied when a breeding pair is present, unpaired individuals are not considered. Each simulation starts with an initial population N_0 at year $t = 0$. The initially occupied territories are randomly selected. During the breeding season, each pair has a reproduction probability P_r that is a function of habitat quality. The size of the successful offspring J depends also upon habitat quality. The average offspring is $\beta = P_r\ J$. Adult pairs defend their sites, while juveniles search for unoccupied sites. Due to differences in the inter-patch distances and resistance for movement, the breeding sites are not equally accessible. The colonization probability of an unoccupied site depends upon the dispersal capacity of the species and the resistance of the landscape for movement. Individuals that do not find an unoccupied site are not explicitly followed further. They may die. The model landscapes were considered as closed systems, no immigration occurred. There is no correction for boundary effects at the border of a model landscape. This means that sites at the border of the model landscapes have lower occupation probability than sites in the middle. However, the size of the model landscapes is relatively large, so that boundary effects can be ignored.

When they occupy a territory, adults and juveniles have an independent survival probability, P_a and P_j, which depends upon habitat quality and the character of the winter (normal or severe). After the winter, the remaining population with size N_{t+1} can reproduce during the next year. If the spatial configuration of habitat do not affect population growth and the number of breeding sites is infinite, the population size at the beginning of the next year will be

$$N_{t+1} = P_a N_t + P_j \beta N_t = \lambda N_t$$

in which the rate of increase λ for the population is denoted as (Pulliam 1988)

$$\lambda = P_a + P_j \beta \qquad (1)$$

When $\lambda > 1$, reproduction exceeds mortality. Then, the habitat is a source for surrounding habitat. The habitat is a sink when mortality exceeds reproduction and $\lambda < 1$ (Pulliam 1988).

Parameters in the model can be divided into determinants of the spatial pattern of the model landscapes and of the demographics and movement of the model species (table 1).

Spatial pattern of the model landscapes

Patchiness of habitat increases when the size of the habitat patches and their degree of connectivity decrease (Harrison and Fahrig 1995). For variation in the patchiness of habitat, I distinguished two spatial scales at which the habitat was either clumped or randomly arranged. The spatial scales were hierarchically organized. Therefore, the model landscapes were divided into 25 square regions, which were each in turn divided into 25 square subregions. Each of these subregions contained 25 gridcells. In the model landscapes, I placed cells with either breeding or non-breeding habitat, based on a stratified assignment procedure. The available breeding habitat ($O + M$) varied from highly fragmented (2%) to not fragmented (20%). For the latter, no effects of the spacing of the habitat were found (Andrén 1994, Fahrig 1998).

The algorithm to generate the model landscapes is explained in the appendix. The habitat arrangement in the model landscapes is the product of two random processes (Diggle 1983). The initial process is a homogeneous Poisson process. The second process iteratively rearranges the initial Poisson distribution by randomly picking up and relocating habitat towards existing clusters of habitat.

Table 1 *Parameters and assumed values used for the simulation study*

Spatial pattern of the model landscapes		
landscape size 125 × 125 cells		
habitat arrangement at two spatial scales	varied (random versus clumped)	
proportion breeding habitat B	varied (2, 5, 10 or 20%)	
ratio high quality O / low quality M breeding habitat	1	
proportion non-breeding habitat	varied (20% - B)	
Demographics of the model species		
initial population size N_0	10% of the available breeding habitat	
probability of a severe winter	0.2	
	high quality O	low quality M
reproduction probability P_r	0.6	0.3
size of offspring J	3	2
survival probability of adults P_a		
in normal winters	0.8	0.6
in severe winters	0.7	0.45
survival probability of juveniles P_j		
in normal winters	0.6	0.4
in severe winters	0.3	0.2
Movement of the model species		
landscape resistance for movement		
breeding habitat	1	
non-breeding habitat with low resistance	1.25	
non-breeding habitat with high resistance	2	
	model species *SP1*	model species *SP2*
dispersal range of juveniles R_d	15 cells	50 cells
resettlement range of adults R_s	3 cells	15 cells

Patchy landscapes can be characterized by the size and the quality of the patches as well as by how these patches are spatially arranged. The patches were determined as clusters of contiguous breeding sites based on a king-neighbourhood relationship. The size S_i of patch i, representing its total carrying capacity for the model species, was calculated as

$$S_i = O_i + M_i \qquad (2)$$

where O_i is the number of sites with high quality breeding habitat and M_i the number of sites with low quality breeding habitat in patch i. The quality Q_i of patch i was calculated as the proportion of high quality breeding sites as

$$Q_i = \frac{O_i}{S_i} \qquad (3)$$

The connectivity C_i of patch i was obtained as the mean degree of connectivity c_j of all breeding sites j in patch i. The connectivity c_j for breeding site j in patch i was calculated as the reciprocal of the weighted distance W_{jk} from j to all other breeding sites k (Van Langevelde *et al.* chapter 3)

$$c_j = \sum_{k=1}^{B} \frac{1}{W_{jk}}$$

for $j \neq k$. The calculation of the weighted distance W_{jk} was based on a friction map with the differences in resistance for movement. The connectivity C_i of patch i was obtained by

$$C_i = \frac{1}{S_i} \sum_{j=1}^{S_i} c_j \tag{4}$$

The mean degree of connectivity $\overline{C}$ and the mean patch size $\overline{S}$ of a model landscape were also calculated, since in such theoretical studies the habitat amount, mean patch size and mean inter-patch distance cannot be varied independently. With a constant amount of habitat, larger patches in a landscape imply larger inter-patch distances (Fahrig 1992). The interpretation of the simulation results should consider this independence.

Demographics and movement of the model species

Two types of stochasticity were applied: demographic and environmental stochasticity. Demographic stochasticity resulted in an independent probability for each pair to reproduce (P_r) and for mortality of adults (P_a) and juveniles (P_j). The reproduction success differs between high and low quality breeding habitat and is density-independent. The probability of survival during one time step differs also between high and low quality habitat. Environmental stochasticity also affects the survival probability. During the winter (especially severe winters), low quality breeding habitat is assumed to provide insufficient food to ensure survival. Due to these differences, the high quality breeding habitat acts as a source ($\lambda = 1.88$ for years with normal winters, $\lambda = 1.24$ with severe winters) and the low quality breeding habitat as a sink ($\lambda = 0.84$ for years with normal winters, $\lambda = 0.57$ with severe winters).

After leaving their natal sites, juveniles search for unoccupied breeding sites. They will sample less potential breeding sites when distances between sites are relatively large. Each individual has a fixed amount of resources to be spent in finding a territory (Danielson 1992). Therefore, the probability PC_{jk} that site j is colonized by juveniles from site k is assumed to decline exponentially with the distance W_{jk} from j to k (in cells) according to (as in Wilcove *et al.* 1986)

$$PC_{jk} = 0.1^{\frac{W_{jk}}{R_d}} \tag{5}$$

in which R_d is the movement range of dispersing juveniles, *i.e.*, the distance at which $PC_{jk} = 0.1$. The distances to unoccupied sites thus indirectly determine the search direction. The individuals are also able to distinguish between high and low habitat quality, since the colonization probability was multiplied by 1 for high quality habitat and 0.5 for low quality habitat. When two juveniles choose the same site, the one with the highest colonization probability will occupy it. To reduce the time necessary to simulate, the behaviour of individuals of one sex is simulated during the dispersal phase. To form pairs, I assumed that when an individual occupies a site, the other sex will also find this site. In highly fragmented habitat, this assumption is not realistic (*e.g.*, Matthysen and Currie 1996).

The parameter R_d allows simulations for model species with a different dispersal capacity. I applied a distance sensitive *SP1* versus a less distance sensitive *SP2* model species. Therefore, two levels of R_d were used (table 1): 15 and 50 cells. The area covered by the distance of 15 cells encompasses 12% of the total landscape. For the distance of 50 cells, this is 40%.

Only juveniles disperse over relatively long distances after leaving their natal site. Once settled, adults are less likely to leave their territory. Those that leave for an unoccupied site of higher quality if it becomes available, move over short distances only. The probability for this resettlement S_{jk} from site *j* to site *k* is calculated conform equation (5). The resettlement radius R_s varies between the model species depending upon their dispersal capacity as juveniles (see table 1). This opportunistic shift to neighbour sites takes place before the winter by adult pairs of all ages.

Simulations and statistical analysis

The combination of the parameter values for the spatial pattern provides a set of model landscapes with varying degree of habitat patchiness at different scale levels. Examples of the model landscapes are presented in figure 1. Due to the stochastic character of the model, I conducted 10 simulations for each model landscape. Each simulation started with a randomly distributed N_0 and stopped after 100 time steps. Model species 1 was simulated in the model landscapes with B = 2, 5, 10 and 20%. Simulations with model species 2 were conducted in the model landscapes with B = 2 and 5%.

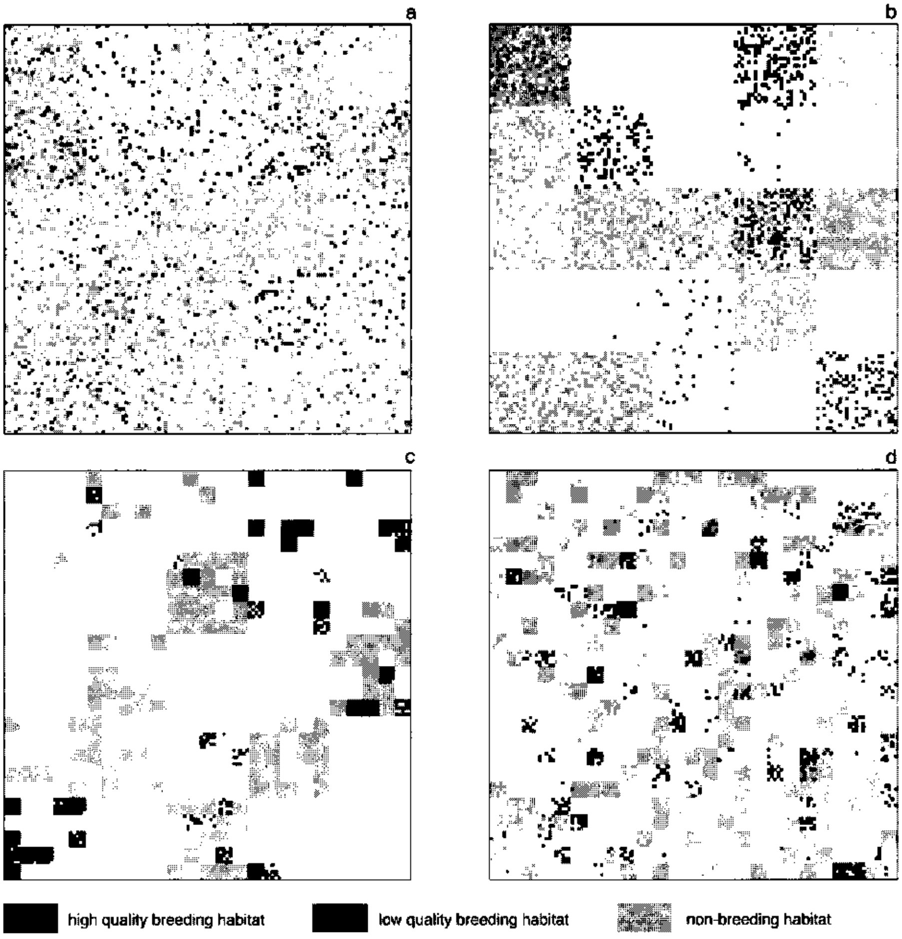

Figure 1 *Examples of model landscapes with varying degree of patchiness of the habitat. The amount of breeding habitat* $B = 5\%$*. The clustering of the breeding habitat is conducted at two spatial scales (see the appendix for algorithm): figure a is generated with* $l = 1$ *at the region level and* $l = 0$ *at the subregion level, figure b with* $l = 3$ *at the region level and* $l = 0$ *at the subregion level, figure c with* $l = 3$ *at the region level and* $l = 3$ *at the subregion level, figure d with* $l = 1$ *at the region level and* $l = 2$ *at the subregion level.*

To present the numerous simulation results in a convenient way and to test the hypotheses, statistical analyses were applied. In the statistical analyses of the results, the amount of breeding habitat B was treated as a quantitative variable, not as a factor, whereas the model species were included in the model as factors (*SP1* and *SP2*).

To test the *first null hypothesis*, the population level was measured as the proportion of occupied breeding sites PB_t per time step t

$$PB_t = \frac{N_t}{O+M} \times 100$$

For each simulation, the mean proportion of occupied breeding sites $\overline{PB}$ was calculated with PB_t for $t \geq 50$. For the period $t \geq 50$, the population reached a stochastic steady state and the population level is expected to be stable. Since $\overline{PB}$ concern data on proportions, I used multiple logistic regression (Crawley 1993) to test if $\overline{PB}$ differed with the amount of available breeding habitat B, the mean degree of connectivity $\overline{C}$ and the mean size $\overline{S}$ of the patches in the model landscapes, and differed among the two model species. Also, interactions between these variables were tested, especially interactions between the mean degree of connectivity and the other explanatory variables. These interactions indicate that the effect of the concerning explanatory variables on the population level depends upon the degree of connectivity.

To determine effects of the spatial arrangement and the amount of habitat on patch selection as predicted by the *second null hypothesis*, the frequency of occupation FO_i of each patch i by the model species were related to the measured landscape characteristics. The FO_i of each patch i in the period $t = 1$ until 100 was the output variable of the simulations at population scale. Due to the binary character of this variable, multiple logistic regression was performed (Jongman *et al.* 1995). The explanatory variables were: the amount of breeding habitat B in the model landscapes, the size S_i of patch i, its quality Q_i and its degree of connectivity C_i. To illustrate limited patch selection in patchy habitat, the effects of these explanatory variables and interactions between the degree of connectivity and the other variables were tested.

To test the *third null hypothesis*, I used the proportion of occupied high quality breeding sites SO_t and of low quality sites SM_t per timestep t. For each simulation, the mean $\overline{SO}$ and the mean $\overline{SM}$ were calculated for $t \geq 50$. They were compared with the expected proportions that were artificially drawn based on the optimal distribution of the present proportion. Since the model landscapes contain a fixed number of breeding sites per habitat patch, the optimal distribution of individuals can be described as preemptive (Pulliam and Danielson 1991, Pulliam 1996). Like the ideal distribution models of Fretwell and Lucas (1970), this model is ideal in the sense that individuals have complete knowledge of the breeding sites available to them. With differences in quality of the breeding sites, individuals have different probabilities of survival and reproduction success. Each individual chooses the best available unoccupied site. Once a site is occupied, it is no longer available to other individuals. However, when dispersal is constrained due to large inter-patch distances relative to the mobility of the species, the preemptive distribution may be biased. Then, individuals are not always able to select the unoccupied sites with the highest quality.

To calculate the expected proportions based on the preemptive distribution, the sites with high quality breeding habitat were occupied first. The remaining pairs occupied sites with low quality breeding habitat. Due to the environmental and demographic stochasticity, the mean occupation probability of a high quality site by adults is 0.78 [obtained by (4 × 0.8 + 0.7) / 5]. The expected mean proportions of occupied sites with high quality breeding habitat $\overline{EO}$ and with low quality breeding habitat $\overline{EM}$ were then calculated as

$$\overline{EO} = \frac{\overline{N}}{O} \times 100 \quad \wedge \quad \overline{EM} = 0 \quad \text{if} \quad \overline{N} \leq 0.78 \times O$$

$$\overline{EO} = 78 \quad \wedge \quad \overline{EM} = \frac{\overline{N} - O}{M} \quad \text{if} \quad \overline{N} > 0.78 \times O$$

in which $\overline{N}$ is the mean population size calculated for $t \geq 50$. For the comparison between the simulated proportions and the proportions based on the preemptive distribution, I used the space in which habitat selection can be found. Therefore, I also calculated the proportions based on a random selection RO_t and RM_t and the mean proportions $\overline{RO}$ and $\overline{RM}$ for $t \geq 50$. Random selection implies no preference for either high quality or low quality breeding habitat. In a graph, the space for habitat selection is bounded by three lines (figure 2a): (1) optimal selection $\overline{EO} = \overline{N}$ and $\overline{EM} = 0$ for $0 \leq \overline{N} \leq (0.78 \times O)$, (2) optimal selection $\overline{EO} = 0.78$ and $\overline{EM} = (\overline{N} - O)$ for $(O \times 0.78) \leq \overline{N} \leq (O+M)$, and (3) random selection when $\overline{RO} = \overline{RM}$ for $0 \leq \overline{N} \leq (O+M)$.

The simulated selection, the optimal selection and the random selection can be plotted in the graph using the proportion of occupied high quality sites and the proportion of occupied low quality sites as coordinates (see figure 2b for an example). The Euclidean distance between the simulated selection, with the coordinates ($\overline{SO}, \overline{SM}$), and the optimal selection, with coordinates ($\overline{EO}, \overline{EM}$), can be used as a measure of dissimilarity between the two (Jongman *et al.* 1995). Since this measure also depends upon the dissimilarity with the random selection, the ratio of the Euclidean distance between the simulated selection and the optimal selection and the Euclidean distance between the simulated selection and the random selection, provides a measure for the deviation of the simulated selection from the optimal selection. This deviation D was calculated as

$$D = \frac{\sqrt{(\overline{SO} - \overline{EO})^2 + (\overline{SM} - \overline{EM})^2}}{\sqrt{(\overline{RO} - \overline{EO})^2 + (\overline{RM} - \overline{EM})^2}} \tag{6}$$

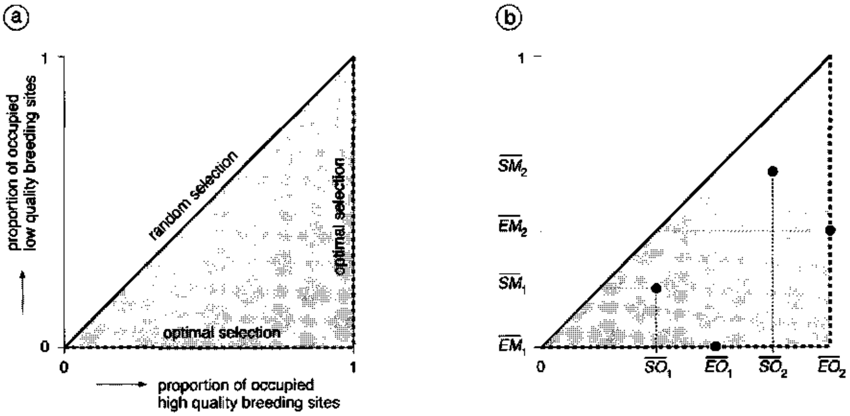

Figure 2 *Space in which habitat selection can be found (a), bounded by random selection where the proportions of occupied high and low quality sites are equal, and optimal selection where the high quality sites are filled up first and then the low quality sites. Examples of simulated and expected selection are given (b):* $\overline{SO}_1$ *as the proportion of occupied high quality sites and* $\overline{SM}_1$ *as the proportion of occupied low quality sites for simulation 1.* $\overline{EO}_1$ *and* $\overline{EM}_1$ *give the expected optimal selection for simulation 1.*

With logistic regression, I related the deviation D with the amount of available breeding habitat B, the mean degree of connectivity $\overline{C}$ and the mean size $\overline{S}$ of the patches in the model landscapes. Also, interactions between these explanatory variables were tested, especially interactions between the mean degree of connectivity and the other variables.

To test the three null hypotheses, I selected models with significant regression coefficients by systematically adding and dropping the explanatory variables. The significance was determined using the two-sided t-test. The resulting regression models are not intended to reveal the best possible. I used the regressions primarily to assess the effects of the degree of connectivity on habitat selection and population responses resulting from the simulations.

3 Results

In figure 3, the natural logarithm of the mean degree of connectivity $\overline{C}$ per landscape is plotted against the natural logarithm of the mean size $\overline{S}$ of the patches with breeding sites. As can be observed, these relationships differ with the amount of breeding habitat B.

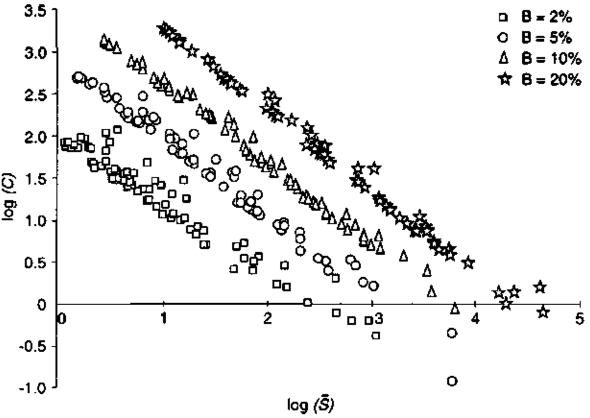

Figure 3 *Relationships between the mean degree of connectivity, log($\overline{C}$), and the mean size, log($\bar{S}$), of the patches in the model landscapes. B is the amount of breeding habitat in the model landscapes.*

Table 2 *Relationships between the population level $\overline{PB}$ resulting from the simulations with model species 1 (a) and with model species 1 (distance sensitive, SP1) and 2 (distance insensitive, SP2) (b) and the landscape characteristics. The sign of the coefficients and their significance are given (two-sided t-test: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).*

a. for model species 1			b. for model species 1 (*SP1*) and 2 (*SP2*)		
	model			*model*	
$\overline{PB}$	log($\bar{S}$)	+ ***	$\overline{PB}$	log($\bar{S}$)	+ ***
	log($\overline{C}$)	+ ***		log($\overline{C}$)	+ ***
	B	+ *		*B*	+ ***
	log($\bar{S}$)×*B*	- **		log($\bar{S}$)×*B*	- ***
	log($\overline{C}$)×*B*	- ***		log($\overline{C}$)×*B*	- ***
				SP2	+ ***
				log($\bar{S}$)×*SP2*	- ***
				log($\overline{C}$)×*SP2*	- ***
				B×*SP2*	- ***

The population level was measured as the mean proportion of occupied breeding sites $\overline{PB}$. For model species 1, relationships were found between $\overline{PB}$ and the natural logarithm of the mean patch size $\bar{S}$, the natural logarithm of the mean degree of connectivity $\overline{C}$, the amount of breeding habitat *B* and some interactions (table 2a). To give insight in the negative or positive effect of each variable and its significance in the regression model, table 2a includes the sign of the regression coefficients and the significance level. To illustrate the results of the effects of patchiness, predictions of the model for different mean degrees of connectivity of small patches are shown in figure 4. The effects of the landscape characteristics on population level were also tested for the pooled data of model species 1 (*SP1*) and 2 (*SP2*) in the model landscapes with $B = 2$ and 5%. The resulting model is given in table 2b. As can be expected, the population level of model species 2 is higher than of model species 1.

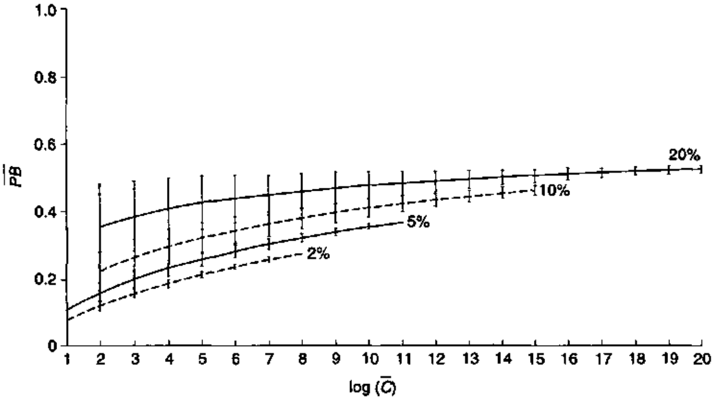

Figure 4 *Predictions and standard errors of the multiple logistic regression model for* $\overline{PB}$ *for different degrees of connectivity,* log($\overline{C}$), *and model species 1 in small patches (see table 2a)*

Table 3 *Relationships between the frequency of patch occupancy* FO_i *resulting from the simulations with model species 1 (a) and with model species 1 and 2 (b) and the landscape characteristics. In table b, the relationships are separately analyzed for* $B = 2$ *and* $B = 5\%$*. The sign of the coefficients and their significance are given (two-sided t-test:* *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, *ns not significant).*

a. for model species 1			b. for model species 1 (*SP1*) and 2 (*SP2*)			
	model			*model*	$B = 2\%$	$B = 5\%$
FO_i	$\log(S_i)$	+ ***	FO_i	$\log(S_i)$	+ ***	+ ***
	$\log(C_i)$	+ ***		$\log(C_i)$	+ ***	+ ***
	$\log(Q_i)$	+ ***		$\log(Q_i)$	+ ***	+ ***
	B	+ ***		$SP2$	+ ***	+ ***
	$\log(C_i)\times\log(S_i)$	ns		$\log(C_i)\times\log(S_i)$	+ *	ns
	$\log(C_i)\times\log(Q_i)$	+ ***		$\log(C_i)\times\log(Q_i)$	ns	ns
	$\log(C_i)\times B$	- ***		$\log(C_i)\times SP2$	- **	- ***
	$\log(Q_i)\times\log(S_i)$	+ ***		$\log(Q_i)\times\log(S_i)$	+ ***	+ ***
	$\log(C_i)\times\log(Q_i)\times\log(S_i)$	+ ***		$\log(Q_i)\times SP2$	+ ***	+ ***
				$\log(C_i)\times\log(Q_i)\times SP2$	+ ***	ns

For model species 1, the frequency of occupation FO_i of patch i could be written as a function of the natural logarithm of its size S_i, the natural logarithm of its degree of connectivity C_i, the natural logarithm of its quality Q_i, the amount of breeding habitat B and some interactions between these variables (table 3a). Predictions of the model for different degrees of connectivity of the patches are shown in figure 5. The same analysis was also conducted for the pooled data of model species 1 (*SP1*) and 2 (*SP2*) in the model landscapes with $B = 2$ and 5%. The results are presented in table 3b.

The effects of the landscape characteristics on habitat selection are enumerated in table 4a. The deviation D (equation 7) representing the dissimilarity between the simulated habitat selection and the optimal selection based on the preemptive distribution, showed a relationship with the amount of breeding habitat B, the mean degree of connectivity $\overline{C}$ and the mean size $\overline{S}$ of the patches and some interactions between these variables. The selected model is illustrated by predictions for different mean degrees of connectivity of the patches in figure 6. This analysis was also conducted for model species 1 (*SP1*) and 2 (*SP2*) in the model landscapes with $B = 2$ and 5%. The results are presented in table 4b.

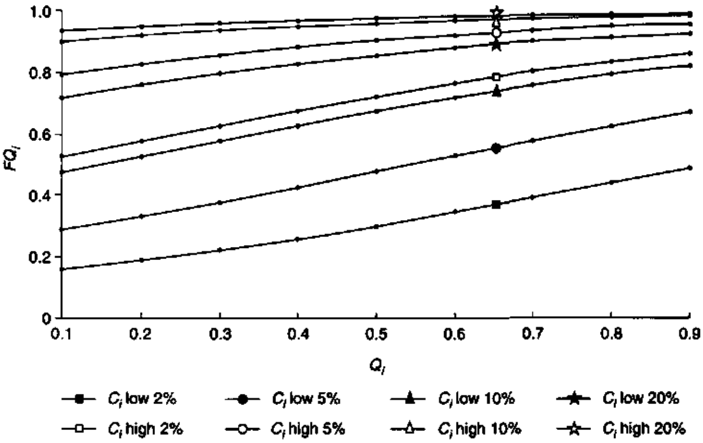

Figure 5 Predictions and standard errors of the multiple logistic regression model for FO_i for different values of quality Q_i and of connectivity C_i of small patches for model species 1 (see table 3a)

*Table 4 Relationships between the deviation D of the simulated habitat selection from the expected optimal selection for model species 1 (a) and for model species 1 and 2 (b) and the landscape characteristics. The sign of the coefficients and their significance are given (two-sided t-test: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$).*

a. for model species 1			b. for model species 1 (*SP1*) and 2 (*SP2*)		
	model			*model*	
D	$\log(\bar{S})$	- ***	*D*	$\log(\bar{S})$	ns
	$\log(\bar{C})$	- **		$\log(\bar{C})$	ns
	B	+ ***		B	+ **
	$\log(\bar{C})\times\log(\bar{S})$	- *		$SP2$	- ***
	$\log(\bar{S})\times B$	- ***		$\log(\bar{C})\times\log(\bar{S})$	ns
	$\log(\bar{C})\times B$	- ***		$\log(\bar{S})\times B$	- *
	$\log(\bar{C})\times\log(\bar{S})\times B$	+ *		$\log(\bar{C})\times B$	- *
				$\log(\bar{C})\times\log(\bar{S})\times B$	ns

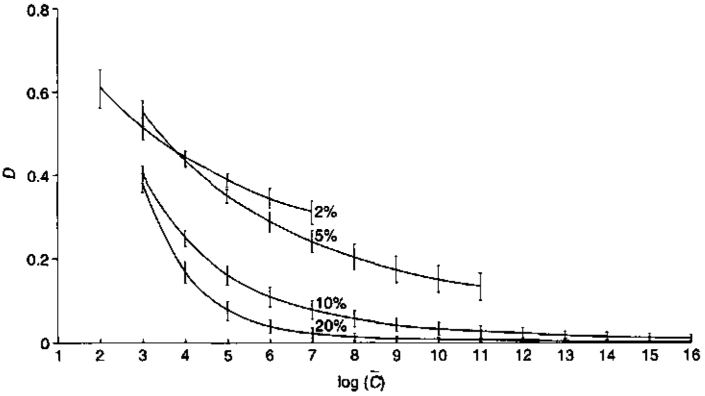

Figure 6 *Predictions and standard errors of the multiple logistic regression model for D for different degrees of connectivity, log($\bar{C}$), of small patches for model species 1 (see table 4a)*

4 Discussion

The understanding of the distribution of organisms in patchy landscapes depends not only upon habitat availability and quality (as advocated by the models that assume an ideal distribution), but also upon dispersal capacity of these organisms (Pulliam 1996). In these landscapes, the habitat connectivity is a fundamental component of the spatial pattern (Taylor *et al.* 1993, Andrén 1994, Hanski 1994, Fahrig and Merriam 1994). This paper deals with habitat selection in patchy landscapes by means of model simulations. The main questions were if habitat selection differs between landscapes with differently spaced habitat, and if so, what are the expected effects at population level. To address these questions, I tested three hypotheses. Therefore, model landscapes were generated containing breeding habitat with differences in the degree of connectivity and the size of the patches. The two model species differed in dispersal capacity. The results of the simulations were statistically analyzed. The statistical analyses should not be considered as a 'proof' of the merits of the simulation model. I solely used the analyses to show if the expected differences occur in the responses of the model species to the differences in the landscape characteristics.

The simulation model was designed with a minimum number of parameters that needed specification. Although this single-species model is not based on the life history of one species, its structure is suited to simulate the occupancy of sites by species that are sedentary the year round, habitat specific and have density dependent dispersal. For the sake of simplicity, there were no differences between pairs due to genetic or environmental influences. Moreover, I concerned only two types of breeding habitat. Other factors that influence habitat selection, such as a preference for large patches (Huhta *et al.* 1998), conspecific attraction (Smith and Peacock 1990), competition between species (Danielson 1992) and predation were also not considered.

Effects of patchiness on population level

Since a relationship can be expected between habitat selection and population level, the hypothesis about effects of patchiness on the population level was first tested. Effects of the mean patch size $\bar{S}$, the mean degree of connectivity $\bar{C}$ of the patches and the amount of habitat B on population level were found. The population level is lower in landscapes with less and more dispersed habitat. The interactions $\log(\bar{S})\times B$ and $\log(\bar{C})\times B$ imply that the influences of patch size $\bar{S}$ and connectivity $\bar{C}$ on population level decreases when the amount of habitat B increases, thus, the effects of patchiness on population level may disappear. The effects of the degree of connectivity and of the patch size on population level decreases when dispersal capacity is high. Based on these results, the first null hypothesis is rejected. These effects have also been demonstrated in other studies, both by theoretical (Fahrig and Paloheimo 1988, Andrén 1996, Venier and Fahrig 1996) and empirical (Andrén 1994) studies.

Effects of patchiness on patch selection

Patch selection, measured as the frequency of patch occupation FO_i, is determined by the degree of connectivity C_i of the patches, their size S_i, their quality Q_i and the amount of breeding habitat B. Patch occupancy is low when the amount of breeding habitat is low and the patches are small and isolated. This has also been demonstrated by other studies (Fahrig and Merriam 1985, Verboom *et* *al.* 1991, Hanski 1994). The positive interaction between the degree of connectivity and patch quality indicates that when the patch quality is low, the degree of connectivity has less effect on patch selection than it has for high quality patches. When the degree of connectivity is low, high quality and low quality patches have both a low occupation frequency. The occupation frequency is high when both the quality and the degree of connectivity of the patches is high, whereas the occupation frequency is lower for high quality patches with low degree of connectivity. This effect at low degree of connectivity can be interpreted as limited patch selection. Compared to model species 2 with large dispersal capacity, patch occupancy is lower for model species 1. For model species 2, higher quality means higher patch occupancy. The conclusion is that patch selection is affected by habitat patchiness. Therefore, I rejected the second null hypothesis.

Effects of patchiness on habitat selection

The rejection of the first and second hypothesis implies that effects of habitat patchiness for the model species with constrained dispersal capacity exists at population level. The results are consistent with patch models of metapopulation dynamics (Fahrig and Merriam 1985, Fahrig and Paloheimo 1988, Verboom *et al.* 1991, Andrén 1994, Hanski 1994), in which increasing isolation is assumed to decrease colonization rate and decreasing patch size increases extinction rate, and hence make occupancy less likely. Then, also effects on habitat selection can be expected.

Limited habitat selection means that low quality sites are more frequently occupied than can be expected when dispersal is not constrained and selection is optimal. The deviation D of the simulated habitat selection from optimal selection predicted based on the preemptive selection model was related to the landscape characteristics. High values of D can be interpreted as a large deviation of the simulated selection from the expected optimal selection. The deviation D shows negative relationships with the mean degree of connectivity $\overline{C}$ and the mean patch size $\overline{S}$. The simulated selection becomes equal to the optimal selection when the mean degree of connectivity and the mean size of the patch in landscapes increases. The negative interaction terms $\log(\overline{C})\times\log(\overline{S})$ and $\log(\overline{C})\times B$ imply that the effect of $\overline{S}$ and B on D is larger when $\overline{C}$ is higher, in other words, the selection becomes equal to the optimal selection when the amount of habitat B and/or the mean patch size $\overline{S}$ increases for high degree of connectivity. In the comparison between model species 1 and 2, the same relationships can be observed. The selection realized by model species 1 has a larger deviation from the expected optimal selection than the one realized by model species 2. Therefore, I also rejected the third null hypothesis.

Conclusion

When habitat patchiness increases, habitat selection increasingly deviates from the expected optimal selection as predicted by the preemptive selection model. This effect becomes smaller when more habitat is available, patchiness will then decrease (figure 2, Harrison and Fahrig 1995), or the species dispersal capacity evolves so that it can deal with the patchiness. Thus when the habitat of a species is fragmented, limited habitat selection can be expected when dispersal capacity is not adapted. This results in a lower density in optimal habitat than can be expected in contiguous habitat (Morris 1995, 1996). Patches with high quality breeding habitat will remain unoccupied. This effect is explained by the metapopulation theory (Verboom *et al.* 1991, Hanski and Gilpin 1997). However, whereas the theory of metapopulation dynamics legitimize the notion that suitable habitat is often unoccupied, the theory of source-sink dynamics explain that organisms often occur in unsuitable habitat (Pulliam 1988, Pulliam and Danielson 1991, Pulliam 1996). When individuals are forced to stay in sites of low quality, due to high costs of movement and/or low dispersal capacity, metapopulations in patchy landscapes with sink habitat are source-sink populations (Harrison 1991, Pulliam 1996). However, variation in patch quality and its influence on patch selection is rarely considered at the metapopulation scale (Lima and Zollner 1996). Metapopulation models that describe discrete populations in patchy landscapes connected by dispersal should consider source-sink dynamics: occupancy of low quality patches by populations in patch models (Gyllenberg and Hanski 1997) and effects population density in high and low quality habitat in individual-based models. This can be argued because when habitat selection is not optimal, negative effects on reproduction success and survival can be expected. Besides other effects of habitat fragmentation, such as increased sensitivity for environmental and demographic stochasticity (Harrison 1991), this may lead to an increase in extinction probability of populations when a greater proportion of the individuals occurs in low quality habitat.

This study was not designed to address questions about critical thresholds in species' response to landscape structure (With and Crist 1995, Andrén 1996, Fahrig 1998). It would be interesting to investigate under what conditions the effects of patchiness on habitat selection at individual level have a minor effect on population dynamics.

The modelling approach presented in this paper can provide knowledge about phenomena that can be observed in real landscapes with real species. This study resulted in predictions about habitat selection in patchy landscapes. The following hypotheses are worth to investigate: ideal distribution models, in this case the ideal preemptive distribution model for territorial species, cannot be applied when the degree of connectivity affects habitat selection. Then, habitat selection may be limited, and therefore, the mean reproductive success and survival will be lower than can be found in populations of the same density in contiguous habitat. Differences in population level between landscapes with fragmented habitat and contiguous habitat can also be expected. These predictions were tested with empirical data about the European nuthatch *Sitta europaea* in four regions in the Netherlands: one region with contiguous nuthatch habitat and three regions with fragmented habitat (Van Langevelde and Schotman chapter 6).

Acknowledgements

The author likes to thank the team of PCRaster consisting of Derk-Jan Karssenberg and Cees Wesseling for developing the colonization function in PCRaster, Cees Wiersum for his contribution to the analysis of the simulation results, and Rob Alkemade for the advice on the statistical analyses.

Appendix Algorithm to generate the model landscapes (cf. Doak *et al.* 1992)

The algorithm to generate the model landscapes contains two stages. First, the available habitat (breeding and non-breeding) was randomly distributed over the regions. Second, an iterative procedure of rearranging the initial random distribution was used to obtain a clumped distribution at the region level. Habitat cells were randomly selected one by one, and assigned to a region based on a probability distribution. This probability distribution was based on the distribution of the habitat amount in each region. Regions that received a relatively high amount of habitat cells in the initial random distribution have high probability to receive more habitat cells in the second stage. Each time a habitat cell is picked up and relocated, the distribution of habitat amount over the regions changes, and therefore, the probability to receive more habitat cells. In the two stages, the high quality breeding habitat O was first randomly distributed and iteratively rearranged. Then the low quality breeding habitat M was treated, followed by the non-breeding habitat with low resistance for movement. The iterative procedure was conducted l times, for $l = 0$, 1, 2 and 3. For $l = 0$, the initial random distribution was taken. For high values of l, the procedure results in a more clumped pattern.

At the subregion level, the same procedure was used. For each l, the assigned amount of habitat in a region was used as starting point for the distribution of habitat cells over the subregions in this region. Exchange of habitat cells between the regions was not permitted. The iterative procedure was also conducted l times, for $l = 0$, 1, 2 and 3. Within a subregion, the assigned habitat cells were randomly distributed.

The variables for habitat arrangement at the two spatial scales allowed 16 combinations. For each combination, 5 replicate model landscapes were generated.

6 REGIONAL AND TEMPORAL DIFFERENCES IN HABITAT SELECTION IN FRAGMENTED AND CONTIGUOUS NUTHATCH POPULATIONS

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Regional and temporal differences in habitat selection in fragmented and contiguous nuthatch populations

1 Introduction

In human-dominated landscapes, effects of habitat fragmentation on populations have been demonstrated (*e.g.*, Van Dorp and Opdam 1987, Verboom *et al.* 1991, Andrén 1994, Wahlberg *et al.* 1996). These effects are often explained with the theory of metapopulation dynamics (Levins 1970, Hanski and Gilpin 1997). In metapopulations, dispersal is the key process for population survival. Constrained dispersal leads, among others, to increased extinction of local populations and reduced colonization of empty patches, and to limited habitat selection on individual level. It can explain that in landscapes with fragmented habitat vacant patches with apparently high quality habitat were found, while nuthatches elsewhere occupied low quality patches (Verboom *et al.* 1991, Bellamy *et al.* 1997, 1998, Wiggins and Møller 1997). However, the simplest explanation for the absence in small patches is the random sample hypothesis (Connor and McCoy 1979, Haila 1983). The random sample hypothesis argues that small patches can be considered as random samples from large areas. It ascribes the effects of habitat fragmentation as solely due to habitat loss. Although the random sample hypothesis could be rejected on the population level (Verboom *et al.* 1991, Andrén 1996), we tried to reject this hypothesis on the individual level by focusing on habitat selection. When dispersal is not constrained, the distribution of individuals is ideal and habitat selection is optimal.

Habitat selection was measured as the quality of the occupied territories. We studied habitat selection in European nuthatch *Sitta europaea* populations. Our main question was if habitat selection in nuthatch populations in fragmented habitat is optimal or not. The nuthatch is a songbird of mature deciduous forests that lives in territories throughout the year. In the agricultural landscapes of Northwest Europe, effects of habitat fragmentation on nuthatch populations have been found (Opdam *et al.* 1985, Van Dorp and Opdam 1987, Verboom *et al.* 1991, Enoksson *et al.* 1995, Verboom and Schotman 1994, Matthysen and Currie 1996, Bellamy *et al.* 1997, 1998). Nevertheless, a lower tendency to disperse or a reduction in dispersal distance in fragmented habitat could not be demonstrated (Matthysen *et al.* 1995).

We compared habitat selection in nuthatch territories in four regions of the Netherlands: Midden Brabant, Zuidwest Drenthe, Noordoost Twente and Veluwezoom. The degree of fragmentation and the population level in the regions differ. The first three regions contain fragmented habitat. The latter can be considered as a reference region with contiguous habitat.

2 Hypotheses

Several models describe habitat selection in birds (*e.g.*, Fretwell and Lucas 1970, Cody 1985). For territorial species, the preemptive selection model (Pulliam and Danielson 1991, Pulliam 1996) is an alternative for the ideal free distribution (Fretwell and Lucas 1970). Moreover, the ideal free and ideal despotic distributions assume one type of habitat (Fretwell and Lucas 1970). We used the preemptive selection model for predictions about optimal habitat selection in nuthatches. Since nuthatches have strong territorial and opportunistic behaviour, nuthatches first occupy and defend the best quality territories regarding survival and breeding success, and then the suboptimal ones when population level increases (Matthysen 1990, Burkhardt *et al.* 1998). Once a site is occupied, it is preempted and thus not available for other individuals. To test if habitat selection is optimal in the reference region, we first correlated the occupation frequency of territories with breeding success.

When nuthatches are ideally distributed, the frequency that territories are occupied may reflect differences in habitat quality. In habitat selection studies, evidence at appropriate spatial scale must be provided that individuals recognize and respond to certain cues of habitat quality (Wiens 1989, Burkhardt *et al.* 1998, Pribil and Picman 1997). For nuthatches, vegetation characteristics such as the presence of deciduous trees and their age, may act as cues of habitat quality. We identified cues of habitat quality by the correlation of the occupation frequency and breeding success with some habitat characteristics.

Our first null hypothesis was that *the influence of the degree of regional connectivity on habitat selection is the same in contiguous and fragmented habitat.* When the occupation patterns in fragmented habitat does not solely reflect habitat quality but can also be explained by habitat connectivity on regional scale, we reject the first null hypothesis.

Since the population level among others, determines habitat selection, we tested the second null hypothesis that *there are no differences in the effects of population level on habitat selection due to the degree of connectivity.* In contiguous habitat, it can be expected that the mean quality of occupied territories is higher than the mean quality of all territories, especially at low population level. However, this will not be true in fragmented habitat. We will reject the second null hypothesis when the mean quality of the occupied territories related to the mean quality of all territories cannot solely be explained by population level, but also by the degree of connectivity.

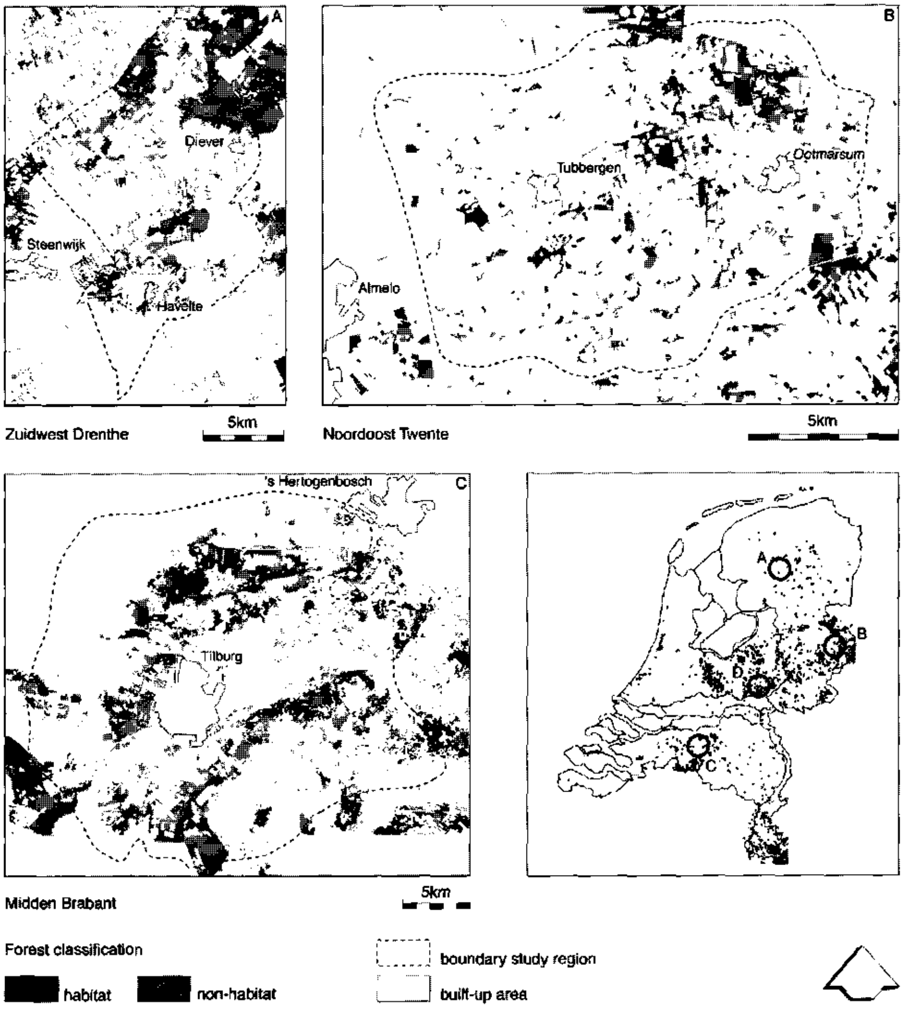

Figure 1 *The three study regions, Zuidwest Drenthe (A), Noordoost Twente (B), and Midden Brabant (C), with fragmented habitat for the nuthatch. The location of these regions and the region with contiguous habitat, Veluwezoom (D), is indicated on the map with deciduous forests in the Netherlands.*

Yet, it is unlikely that the population level in fragmented habitat is high. Rejecting the first and second hypothesis indicates that habitat selection is not optimal in fragmented habitat due to constrained dispersal. We can then expect effects on the population level (Fahrig and Paloheimo 1988, Andrén 1994, Venier and Fahrig 1996). Our third null hypothesis was that *there are no* *differences in population density between regions with fragmented habitat and regions with contiguous habitat.* We reject the third null hypothesis when the population density is different (*i.e.*, lower) due to the degree of connectivity.

3 Methods

Study regions with time series

Some features of the study regions are enumerated in table 1. Midden Brabant, Zuidwest Drenthe and Noordoost Twente have forested patches in a matrix of farmland, predominantly grassland and maize (figure 1). In these regions, the area of suitable habitat is less than 5% of the total study area (table 1). The majority of the suitable habitat is located within 100 m from a forest edge. The Veluwezoom region is part of a large contiguous forest in the central part of the Netherlands containing both coniferous and deciduous forests. Within this region, we studied two areas: Hoekelum and Hagenau.

Table 1 *Some features of the study regions*

	Midden Brabant	*Zuidwest Drenthe*	*Noordoost Twente*	*Veluwezoom**	
				HO	*HA*
total area (km^2)	648	193	145	1.2	0.75
% forest of total	17	21	10	83	100
% optimal habitat of total	2	2	4	33	18
% marginal habitat of total	1	1	1	3	13
% habitat within 100 m of a forest edge	76	78	94	52	0
number of patches	178	66	123	-	-
number of permanent territories	271	151	193	58	30
number of selected territories	88	75	92	58	30
% selected territories within 100 m from forest edge	83	85	96	52	0
years of survey	1990-1992, 1996	1966-1996	1986-1994, 1996	1981-1996	1990-1996

* This region contains contiguous habitat in which Hoekelum (HO) and Hagenau (HA) are located.

Time series of territory occupancy by nuthatches in the breeding season were available for the four regions. The data of the Veluwezoom (Hoekelum: S. Ens *et al.* unpubl., Hagenau: R. Vogel unpubl.), Zuidwest Drenthe (A. van Dijk unpubl.) and Midden Brabant (F. Post *et al.* unpubl.) were collected by local bird watchers working with high territory mapping standards (Hustings *et* *al.* 1985). In Hoekelum, breeding success was also recorded. Based on these time series, we delineated 725 permanent breeding territories (cf. Matthysen 1988). The territorial boundaries were drawn on the basis of the location of the nuthatches during the census periods. For each territory, we measured several habitat and connectivity characteristics.

Habitat quality of the territories

Since nuthatches prefer mature oaks *Quercus robur*, *Q. petraea*, *Q. rubra* and beeches *Fagus sylvatica* (Löhrl 1957), we measured the mean trunk diameter (*DIA*) of these trees. The majority of the territories contained oaks. We also used the presence of beech (*BEECH*) in the analysis (Nilsson 1976, Enoksson 1990, Burkhardt *et al.* 1998). The mean trunk diameter (in cm) was measured at breast height of a minimum of 15 trees, which diameters were at least 20 cm, along two different transects in the centre of each territory. The mean trunk diameter is assumed to represent food availability, the amount of nest holes and protection from predators and extreme weather (Löhrl 1957, Matthysen 1990). Since food supply during winter affects survival and breeding success (Nilsson 1987), its presence (*WINT*) was noted when houses or farmsteads were adjacent to the territory.

Connectivity of the territories

We measured connectivity of the territories at three spatial scales: local, regional and interregional level. Therefore, we made habitat maps for each region with gridcells of 500 × 500m. At the local scale, the connectivity of a territory (*LC*) was obtained by the amount of habitat (in ha) in the gridcell in which the territory was located. We used the local degree of connectivity as a measure for the size of the habitat patch, in which the territories are located, because there is a practical problem in delineating patch size for extensive and contiguous habitat.

The amount of habitat (in ha) in a range of 0.5-3 km was used as a measure for connectivity at regional scale (*RC*). This range appears to be a good estimate for within-region dispersal (Van Dorp and Opdam 1987, Verboom *et al.* 1991, Schotman in prep.). The amount of habitat (in ha) in a range of 10 to 15 km represented the connectivity at interregional level (*IC*). We expected that the regional and interregional connectivity would differentiate between the reference region and the regions with fragmented habitat. We also measured the amount of habitat in the range from 3 to 10 km, but this variable could not be used due to the high correlation with the amount of habitat in the range 10-15 km ($r = 0.59$).

For the habitat maps, we used data of the Dutch national forest statistics (CBS 1984). These statistics provided detailed information about the location of the forests (the minimum-mapping unit is 0.2 ha), the dominant tree species and some vegetation characteristics, among which the mean trunk diameter of the dominant tree species. The four regions were mapped between 1981 and 1983. Comparisons between the actual situation and the forest statistics showed that the amount and distribution of the forests were hardly changed. However, for a proper description of the vegetation, these statistics are relatively old. We measured the mean trunk diameter of deciduous trees to obtain a correction factor to estimate the current trunk size. Therefore, we used data of the mean trunk diameter measured in the territories and at other randomly selected locations in the four regions in 1995-1996. These data were related with the mean trunk diameter DIA_f measured at the same locations as in the forest statistics. We estimated the actual trunk diameter of oaks and beeches DIA as a linear relationship: $DIA = 9.676 + 0.8696 \times DIA_f$ (t-test: $P < 0.001$, $n = 244$).

Selection and census of territories

We selected a priori 343 territories in the four regions based on habitat quality and connectivity. These territories were considered suitable for nuthatches due to the presence of a territorial nuthatch pair in at least one breeding season in the preceding years. In each region, we selected about 48 territories evenly distributed over 8 classes that were determined for the mean trunk diameter of oaks and beeches (*DIA*), the degree of local (*LC*) and regional (*RC*) connectivity: each of the three variables were split into low and high values (see table 2). The mean trunk diameter *DIA* was used to select low and high quality territories. The values of these three variables for each class do not differ much between the regions. The selection provided us a balanced sample for studying territory occupancy and breeding success. This was needed, because we noticed relative high numbers of territories with high quality and low connectivity in the regions with fragmented habitat, especially in Noordoost Twente (De Heer 1995, Schotman in prep., see figure 1). We censused the selected territories in 1996. The censuses were conducted between 1 March and the end of April. Presence or absence of nuthatches was recorded after a minimum of 4 visits in this period, breeding success after 2 additional visits by the end of May and in June. We distinguished unpaired and paired nuthatches that occupied the territories. Breeding success was recorded if parents were feeding nestlings or fledged youngs. The census of breeding success in 1996 was limited to the three regions with fragmented habitat.

Table 2 *Number of selected territories per region and the mean (and standard deviation) of some habitat and connectivity variables measured in these territories (MB Midden Brabant, ZD Zuidwest Drenthe, NT Noordoost Twente and VZ Veluwezoom). The selection was made based on the degree of regional connectivity of the territories (RC in ha), the size of the patches in which the territories were located (LC in ha) and the habitat quality of the territories (the mean trunk diameter of oaks and beeches DIA in cm).*

		RC low		*RC high*	
		DIA low	*DIA high*	*DIA low*	*DIA high*
LC low	MB	12	12	12	8
	ZD	8	12	6	11
	NT	12	11	12	13
	LC	2 (1.2)	2.4 (1.4)	4.3 (4.4)	3.0 (2.0)
	RC	337 (171)	339 (172)	803 (392)	759 (354)
	DIA	31.8 (4.7)	47.9 (5.3)	31.2 (3.8)	46.0 (5.3)
LC high	MB	12	12	9	11
	ZD	12	12	8	6
	NT	8	11	13	12
	LC	7.3 (3.3)	8.5 (4.0)	9.0 (5.5)	7.4 (4.6)
	RC	634 (357)	567 (221)	909 (410)	1036 (315)
	DIA	31.9 (3.8)	44.5 (3.8)	34.0 (6.2)	46.3 (5.4)
	VZ			42	46
	LC			8.0 (2.1)	7.2 (2.7)
	RC			2753 (918)	1618 (490)
	DIA			32.0 (3.0)	47.5 (6.4)

Statistical analyses

As predicted by the preemptive selection model for optimal selection, we first tested in the reference region if breeding success is related to the frequency of territory occupancy. Therefore, we conducted linear regression with the frequency of successful breeding as response variable and the frequency of territory occupancy as explanatory variable for the data of Hoekelum, an area in the reference region Veluwezoom. The territory occupation frequency (*TOF*) was calculated as the ratio of the number of times a territory was found occupied and the number of times it was surveyed. We obtained the frequency of successful breeding (*BSF*) as the ratio of the number of times a successful breeding attempt was found and the number of times it was occupied.

Second, we analysed the relationships between the territory occupancy per year (*TO*) and the breeding success per year (*BS*) and the measured habitat characteristics in the reference region. This analysis provided variables to measure habitat quality. The response variables were *TO* and *BS* in a multiple logistic regression model (Jongman *et al.* 1995). Population level (*PL*), measured as the number of nuthatches per year, was included in the model since it also determines the probability of territory occupancy.

We tested the *first null hypothesis* by the analysis of the effects of habitat quality and connectivity on the occupancy of the selected territories (*TO96*) and the breeding success of the paired nuthatches (*BS96*). Because the regions differ in, among others, the population level and the degree of interregional connectivity, we first treated each region as a binary factor in the model for territory occupancy. These binary factors allowed us to differentiate in the relationships between territory occupancy and habitat quality and connectivity. We tested the interactions between the region Veluwezoom and habitat quality and between regional connectivity and the factors for the regions with fragmented habitat. To test if the degree of connectivity at interregional scale affects the selection of territories, we replaced the region factors by the connectivity at interregional scale (*IC*).

To test the *second null hypothesis*, we analyzed time series of territory occupancy for the period 1987-1996 of territory occupancy in the three regions with fragmented habitat. For the selected territories with low and high degree of regional connectivity, we calculated the mean trunk diameter of the occupied territories (DIA_{occ}) and the mean trunk diameter of all territories (DIA_{av}) per region and per year. Based on these values, we calculated the standardized difference between the habitat quality of occupied territories and the habitat quality of all territories ΔDIA as

$$\Delta DIA = \frac{DIA_{occ} - DIA_{av}}{DIA_{av}}$$

We also calculated per year and per region the proportion of territories that was occupied (*PO*) as a measure for the population level: for territories with low degree of regional connectivity and for the ones with high degree (n = 72). The degree of regional connectivity was applied as a binary factor. We conducted linear regression with ΔDIA as response variable and the proportion of territories *PO* and the factors for the degree of regional connectivity as explanatory variables. All possible dependencies in the data of territory occupancy were neglected.

We tested the *third null hypothesis* by the analysis of the effect of connectivity on population density. For the population density (*PD* in pairs per ha), we used the overall population size per year and per region. Based on the estimated relationship between the mean trunk diameter of oaks and beeches in the forest statistics and the actual mean trunk diameter, we could reconstruct the available amount of habitat per year. This was done for the years 1981-1996, *i.e.*, the period between the forest statistics and our census. With these data, we could obtain the mean degree of local (*MLC*), regional (*MRC*) and interregional (*MIC*) connectivity per year for each region. We also made a rough distinction in habitat quality: low quality habitat contains oaks and beeches with the mean trunk diameter greater than 25 cm and less than 32 cm. The ratio between the amount of high quality habitat and low quality habitat (*Q*) provided us an indication of the changes in the overall suitability of the forests. Although nuthatches occupy more or less permanent territories, we did not treat *PD* as data on proportions with a fixed maximum for nuthatch density. Linear regression was used to relate *PD* and the mean degree of local (*MLC*), regional (*MRC*) and interregional (*MIC*) connectivity and the suitability of the forests (*Q*). Again, all possible dependencies in the data of territory occupancy were neglected.

We selected models with significant regression coefficients by systematically adding and dropping habitat variables. The presented regression models are not necessarily the best possible for territory occupancy or breeding success. We used the models primarily to assess habitat selection in nuthatch populations by focusing at effects of the territory characteristics on territory occupancy and breeding success.

4 Results

Preemptive selection model in the reference region

In the reference region, we found that the frequency of breeding success (*BSF*) is positively correlated with territory occupancy frequency (*TOF*) (table 3). Territories that are frequently occupied have generally a higher breeding success then less frequently occupied territories. We also found that the probability of territory occupancy per year (*TO*) can be ascribed as a function of the variables: the mean trunk diameter of oaks and beeches in the territories (*DIA*), the degree of local connectivity (*LC*) and the population level (*PL*) (table 3). Breeding success was a function of the variable *DIA* (table 3). Addition of the variable for connectivity at local scale (*LC*) was not significant. Based on these analyses, we used the mean trunk diameter as the main characteristic to describe the quality of breeding habitat.

Effects of connectivity on habitat selection

A summary of some habitat and connectivity variables measured in the selected territories is given in table 2. In 1996, 171 territories out of 343 were found occupied. In the subset of 255 territories in the three regions with fragmented habitat, we found 91 pairs, 18 unpaired individuals and breeding success in 60 pairs. For each class of connectivity at regional scale (*RC*) and habitat quality (*DIA*), the fraction of occupied territories is presented in table 4. Also, the population level per region measured as the fraction of occupied territories of the total set of selected territories is given. In table 4, the fraction of successful pairs in the three regions with fragmented habitat is also presented for the territories with high and low habitat quality.

Table 3 *Relationships between the frequency of breeding success (BSF) and the territory occupation frequency (TOF), and between territory occupancy per year (TO), breeding success per year (BS) and the habitat and connectivity variables in Hoekelum, an area in the reference region Veluwezoom (two-sided t-test: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns not significant). The variables are: DIA is the mean trunk diameter of oaks and beeches of a territory, LC is the degree of local connectivity, WINT is the presence of food supply during winter and BEECH is the presence of beech in a territory.*

	Model			Model	
BSF	*TOF*	***	*BS*	*DIA*	***
				WINT	ns
TO	*DIA*	***		*BEECH*	ns
	LC	***		*LC*	ns
	PL	***			
	WINT	ns			
	BEECH	ns			

Table 4 *Fraction occupied territories and breeding success per pair distinguished over the two habitat quality classes (measured as the mean trunk diameter of oaks and beeches, DIA low and DIA high) in the selected territories (see table 2). The fraction occupied territories is also distinguished over the two connectivity classes (the degree of regional connectivity, RC low and RC high) and combined (overall) per region. Presented are the regions with fragmented habitat (MB Midden Brabant, ZD Zuidwest Drenthe, NT Noordoost Twente and FRAG for the three regions combined) and the reference region (VZ Veluwezoom). The population level, calculated as the fraction of occupied territories, is also given.*

	DIA low				*DIA high*				pop.
	fraction occupied territories			breed. suc.	fraction occupied territories			breed. suc.	level
region	*RC low*	*RC high*	*overall*		*RC low*	*RC high*	*overall*		
MB	0.25	0.19	0.22	0.57	0.42	0.53	0.47	0.69	0.34
ZD	0.15	0.00	0.09	0.50	0.42	0.18	0.32	0.92	0.21
NT	0.25	0.84	0.58	0.43	0.64	0.80	0.72	0.72	0.65
FRAG	0.22	0.42	0.31	0.47	0.49	0.54	0.51	0.75	0.47
VZ			0.54				0.84		0.70

In the selected territories, the occupancy (*OC96*) can be denoted as a function of: the mean trunk diameter (*DIA*), the presence of winter food (*WINT*), the degree of connectivity at both local and regional scale (*LC* and *RC*), the region factors and some interaction terms (table 5a). Addition of the presence of beeches (*BEECH*) significantly increased the deviance of the model. However, the effects of the other variables decreased. Therefore, we excluded *BEECH* from the model. Based on this regression model, we made predictions for differences in the variables *DIA* and *RC* to illustrate the results (figure 2). The interactions between the region Veluwezoom (*VZ*) and the mean trunk diameter (*DIA*) may indicate that the occupation frequency of low and high quality territories differs between the reference region and the regions with fragmented habitat. This can be interpreted as a difference between habitat selection in contiguous and fragmented habitat. The interactions between regional connectivity (*RC*) and the factor for Noordoost Twente (*NT*) with fragmented habitat may account for differences in the occupation frequency of highly connected territories due to the population level: most of these territories may be occupied when population level is high, and not if population level is low.

Table 5 *Relationships between the occupation (OC96, in model a and b), and breeding success (BS96 in model c) of the selected territories and the habitat and connectivity characteristics (one-sided t-test: *** P < 0.001, ** P < 0.01, * P < 0.05, ns not significant). The variables are: DIA is the mean trunk diameter of oaks and beeches of a territory, LC is the degree of local connectivity, RC is the degree of regional connectivity, WINT is the presence of food supply during winter and BEECH is the presence of beech in a territory, NT is a binary factor for the region Noordoost Twente and VZ for the region Veluwezoom. In model b, the territory occupancy is explained by a composite variable (CON) of the degree of regional and interregional connectivity (IC) (see text for explanation). The parameter estimates of the final models are given.*

	Model	Parameter estimate			Model	Parameter estimate	
a. *OC96*	Constant	-14.78		b. *OC96*	Constant	-9.60	
	log(*LC*)	1.052	***		log(*LC*)	1.116	***
	log(*DIA*)	3.031	***		log(*DIA*)	1.64	ns
	VZ	-13.21	*		*WINT*	0.638	*
	log(*DIA*)×*VZ*	3.74	**		*CON*	-5.77	*
	WINT	3.031	*		log(*DIA*)×*CON*	1.933	*
	RC	9.98	***				
	NT	0.030	ns				
	RC.NT	29.3	**				

c. *BS96*	Constant	-8.70	
	log(*DIA*)	2.57	***
	WINT	-	ns
	BEECH	-	ns
	LC	-	ns
	RC	-	ns
	IC	-	ns

After replacing the region factors by the connectivity at interregional scale (*IC*), we found that the occupancy of the selected territories (*OC96*) was a function of the following variables: the mean trunk diameter (*DIA*), the presence of winter food (*WINT*) and the connectivity at local (*LC*), regional (*RC*) and interregional scale (*IC*) (not presented). To test the interaction between the degree of regional and interregional connectivity and habitat quality, we constructed a composite variable (*CON*), calculated based on the estimated regression coefficients for *RC* and *LC* as $CON = (5.37 \times RC) + (0.873 \times IC)$. We also found an interaction between the composite variable *CON* and the mean trunk diameter (*DIA*) (table 5b). This can be interpreted as a difference between habitat selection in contiguous and fragmented habitat. Again, addition of *BEECH* significantly increased the deviance of the model, but decreased the effects of the other variables.

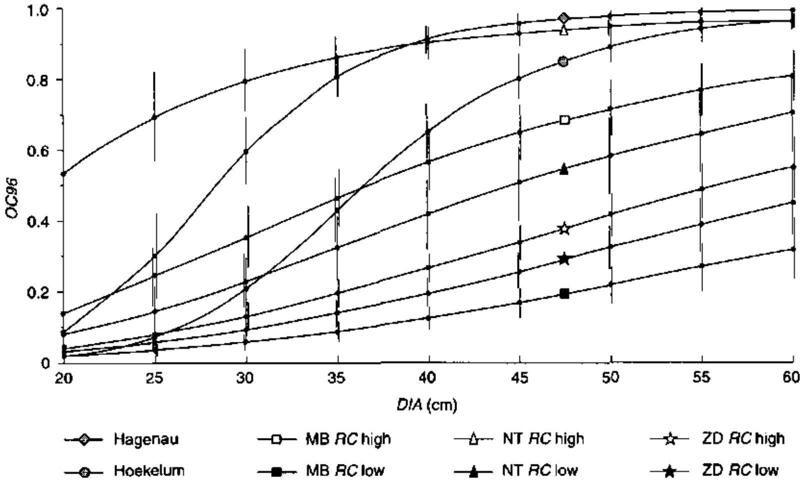

Figure 2 *Predictions with standard errors from the multiple logistic regression model for territory occupancy OC96 (see table 5a) for differences in habitat quality, measured as the mean trunk diameter of oaks and beeches (DIA), and the degree of regional connectivity (RC high and low). The predictions for the Veluwezoom are distinguished for Hagenau and Hoekelum (MB Midden Brabant, ZD Zuidwest Drenthe, NT Noordoost Twente).*

For the regions with fragmented habitat, we found that breeding success (*BS96*) was positively related with the mean trunk diameter (*DIA*) (table 5c). The variables for degree of connectivity at local, regional and interregional scale could not be significantly added to the model for breeding success.

Effects of population level on habitat selection

For the time series of territory occupation in the three regions with fragmented habitat, we found that the mean quality of occupied territories (*ΔDIA*) in both highly and badly connected habitat is a function of the proportion of occupied territories (*PO*) and the degree of regional connectivity (*RC*) (table 6). The interaction between *PO* and *RC* implies that the effect of population level on the mean quality of occupied territories differs with the degree of connectivity. This is illustrated in figure 3.

Table 6 *Relationships between the mean quality of the occupied territories (ΔDIA) and the population level (proportion of occupied territories, PO) and the degree of regional connectivity (RC). The sign and significance of the regression coefficients are given (two-sided t-test: *** P < 0.001, ** P < 0.01, * P < 0.05, ns not significant)*

	Model	
ΔDIA	log(*PO*)	- *
	RC	+***
	log(*PO*)×*RC*	- ***

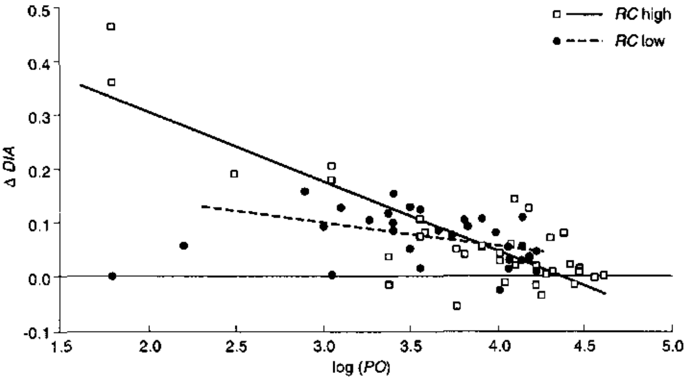

Figure 3 *Predictions for the mean quality of the occupied territories (ΔDIA) for differences in the proportion level [proportion of occupied territories, log(PO)] and the degree of regional connectivity (RC high and low) (see table 6).*

Differences in population density between the regions

The estimated amount of habitat (as proportional increase) and the mean degree of local (*MLC*), regional (*MRC*) and interregional (*MIC*) connectivity per year for the period 1981-96 are presented in figure 4. The mean degree of local connectivity (*MLC*) calculated over all gridcells with habitat may decrease when gridcells with new habitat 'appeared'. As shown in figure 5, the population density in fragmented habitat is much than in contiguous habitat. In the three regions with fragmented habitat, a considerable proportion of habitat was unoccupied. We found that the differences in population density (*PD*) could be explained by the overall quality of the habitat (*Q*), the mean degree of regional (*MRC*) and interregional (*MIC*) connectivity (table 7). The interaction between *Q* and *MRC* may be interpreted as a higher population density in highly connected habitat than in badly connected habitat when the habitat quality is higher. The mean degree of local (*MLC*) could not be significantly added to the model.

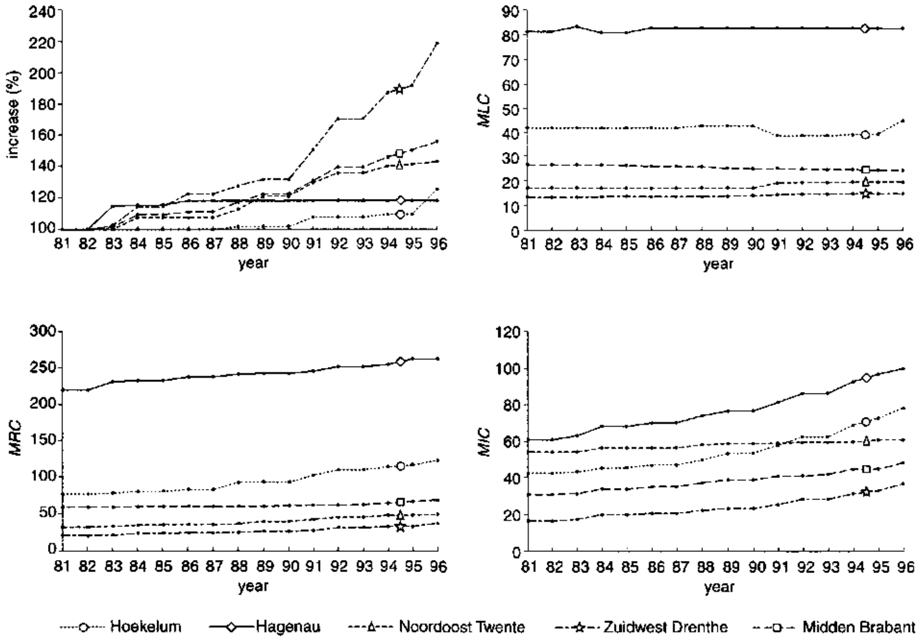

Figure 4 *Estimated development in the amount of habitat (the proportional increase with the year 1981 as 100%, see table 1 for the amount of habitat in 1996), the mean degree of local (MLC), regional (MRC) and interregional (MIC) connectivity per year for the period from 1981 to 1996 per study region. The two areas Hagenau and Hoekelum are distinguished in the region Veluwezoom.*

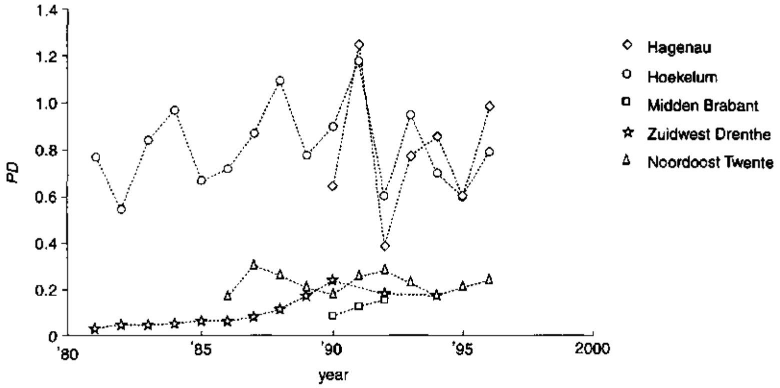

Figure 5 *Population density (PD in pairs per ha) in the study regions. The population density for the Veluwezoom is distinguished for Hagenau and Hoekelum*

Table 7 *Relationships between the population density PD of the four regions in the period 1981-96 and the mean habitat and connectivity characteristics of these regions (two-sided t-test with df = 44: *** P < 0.001, ** P < 0.01, * P < 0.05, ns not significant). The variables are: Q is the overall quality of the habitat, MRC is the mean degree of regional connectivity and MIC the mean degree of interregional connectivity. The parameter estimates of the final model are given.*

	Model	Parameter estimate	
PD	Constant	0.0235	
	Q	-0.0346	ns
	MRC	-0.000796	ns
	Q×*MRC*	0.002087	**
	MIC	0.00481	**

5 Discussion

We compared habitat selection in nuthatch fragmented and contiguous populations to determine if habitat selection in fragmented habitat is optimal or not. In the regions with fragmented habitat, effects of connectivity on patch occupancy and colonization are found (Verboom *et al.* 1991, De Heer 1995, Wiecherink 1996, Van Langevelde chapter 4). This may indicate that the set of local populations in these regions act as metapopulations. Then, effects on habitat selection can be expected.

Among others, several factors may influence habitat selection in fragmented habitat: (1) limited dispersal capacity, (2) preference for large habitat patches and (3) costs of searching. Regardless these factors, it may be possible that individuals have different strategies (*e.g.*, in oystercatchers, Ens 1992).

ad. (1) Limited dispersal capacity: The three regions with fragmented habitat have low amount of habitat, which is located in relatively small patches (tables 1 and 2). Due to isolation effects on patch occupancy and colonization, it was assumed that nuthatches have a limited dispersal capacity related to the distances between the forest fragments (Opdam *et al.* 1985, Van Dorp and Opdam 1987, Verboom *et al.* 1991, Bellamy *et al.* 1997, 1998, Schotman in prep.). However, Matthysen *et al.* (1995) found that fragmentation causes an increase in natal dispersal distance compared to juveniles dispersing in contiguous habitat. This may indicate that dispersal capacity is not limited related to the distances between the forest fragments in the three regions.

ad. 2) Preference for large habitat patches: Strong effects of patch area on presence and persistence of local populations of nuthatches are found (Opdam *et al.* 1985, Van Dorp and Opdam 1987, Verboom *et al.* 1991). This may indicate that nuthatches prefer large habitat patches. The reasons for such preference can be a higher level of resources than in small patches (available food, mates, nest holes), protection against weather by a stable microclimate, and less competition for holes and predation. Another reason for the preference for large habitat patches can be that nuthatches prefer to settle close to each other (as advocated by Stamps 1988, Smith and Peacock 1990). Individuals may use the presence of resident conspecifics as a positive cue when selecting territories. However, the latter is not demonstrated in nuthatches. Preference for occupying large patches was included in our analyses by patch size, measured as the degree of local connectivity (*LC*). We considered *LC* was a proper measure for patch size since we found a strong correlation between the size of the patch in which each territory was located and *LC* ($r = 0.69$, $n = 255$).

ad. (3) Costs of searching: In contiguous habitat, the benefits of selecting a good territory may be higher than the costs of searching. Increased distance between habitat patches is likely to elevate the cost/benefit ratio of habitat selection, which may result in lower dispersal success and/or a reduced tendency to dispersal (Danielson 1992, Matthysen and Currie 1996). Nuthatches are then not able to monitor territories, which forces nuthatches to be less choosy in accepting a vacant territory. High costs of searching may explain that once settled, nuthatches are less likely to leave their territory in fragmented habitat than in contiguous habitat (Matthysen *et al.* 1995). Matthysen and Currie (1996) suggest that the most plausible explanation for the higher costs is a higher mortality risk during movements. If so, dispersal can be expected to be constrained to patches with low degree of connectivity at regional and interregional level. This may explain limited habitat selection in fragmented habitat.

In other analyses of nuthatch data from a fragmented population (Schotman in prep.), habitat selection seemed to be not optimal. However, it could not be demonstrated whether nuthatches really did not select the best territories on the basis of vegetation characteristics, or that successful selection was hidden by a random factor (*i.e.* competition for holes). Moreover, habitat selection in fragmented habitat could not be compared with selection in contiguous habitat. Our study overcomes these problems.

Preemptive selection model in the reference region

Although we did not consider the settling order of the territories, our findings demonstrated that nuthatches could select territories where breeding success is higher than in the alternative ones. When population level increase, the best unoccupied territories becomes also occupied. This agrees with the findings of Nilsson (1987) and Matthysen (1990). The effect of the degree of local connectivity (*LC*) on territory occupancy in contiguous habitat indicates the relevance of a certain amount of habitat in the surroundings of the territory, not that dispersal is constrained on this scale level (see also Matthysen and Schmidt 1987).

Our findings indicate that the selection of territories is optimal in contiguous habitat. Other authors also found non-random selection of territories in nuthatches. The quality of the territories is found also to determine the laying date and clutch size (Schmidt *et al.* 1992), the order of settling by juveniles in summer, the order of settling by immigrant females in spring and the direction of post-settling movement between territories by adults (Matthysen 1990, Häupt 1992). The optimal selection is consistent with the predictions from the preemptive selection model. However, there are limitations of explaining habitat selection in nuthatches by this model. Although nuthatches occupy permanent territories, the size of the territories gets smaller when population level increases (Nilsson 1976, Enoksson 1990). In contrast to the assumption of the preemptive model that the occupancy of territories does not affect breeding success and survival in other territories, the decrease in territory size may have consequences for the breeding success since it is found to be dependent upon the amount of habitat in a territory (Löhrl 1957). In our analysis, we could not apply territory size since we were not able to measure it in the same way in each region.

Based on the found relationships between territory occupancy and breeding success, we used the mean trunk diameter of oaks and beeches as the main characteristic for habitat quality at the scale of territories. Also in other studies, the mean trunk diameter of oaks and beeches was used to measure habitat quality for nuthatches (Burkhardt *et al.* 1998, Matthysen and Adriaensen 1998). We acknowledge that this measure can only partly represent habitat quality. We could not measure factors such as food availability or predation. Also, weather factors such as severe winters and wet, cool summers may have negative impacts on territory occupancy and breeding success of nuthatches (Matthysen 1990).

Effects of connectivity on habitat selection

The patterns of territory occupancy indicate that habitat selection is not optimal in fragmented habitat compared to contiguous habitat. The occupation frequency of low quality territories with a low degree of connectivity is relative high compared to the occupation frequency of territories of the same quality in contiguous habitat. The effect of the degree of regional connectivity in the regression models for territory occupancy is highly significant (table 5a). This can only be interpreted as an effect of constrained dispersal. We can conclude that the influence of the degree of regional connectivity on habitat selection differs between contiguous and fragmented habitat. Thus, we rejected the first null hypothesis. A distinction appeared between the regions Midden Brabant and Zuidwest Drenthe and the region Noordoost Twente. In the latter region, highly connected territories have a high occupation probability. This may be due to the higher population level that can be (partly) explained by the high degree of interregional connectivity (see *Differences in population density between the regions* for further discussion).

The effects of the degree of local connectivity (*LC*) on territory occupancy may indicate that nuthatches prefer large habitat patches. However, we could not find a preference for large patches regardless their degree of regional connectivity: the inclusion of the interaction between the degree of local and regional connectivity (*LC×RC*) was only suggestive (t-value: -1.69). Although, the occupation probability in large patches may be higher than in smaller ones, higher breeding success could also not be demonstrated: the degree of local connectivity (*LC*) is not significant in the model for breeding success *BS96* (table 5c). In Noordoost Twente, Schotman (in prep.) found that breeding success is negatively related to the relative edge length of the patch in which the territory is located, as result of higher competition for nest holes. Since larger patches have generally smaller relative edge length than smaller patches, this may indicate that breeding success is higher in large patches. A possible explanation why in our study the size of the patch is not related to breeding success may be that the majority of the selected territories is located within 100 m of a forest edge (table 1).

There is other empirical evidence for limited habitat selection of nuthatches in fragmented habitat. Matthysen and Currie (1996) found that vacant territories were taken up at a slower rate, more often by single birds, and several territories were never settled in fragmented habitat. In contrast to contiguous habitat, where settlement was swift and accompanied by rapid pair formation, and almost no vacancies remained. In the large forests, there was a significant correlation between settling rank and territory quality, but not so in the fragments (Matthysen and Currie 1996).

An alternative explanation for constrained dispersal is that the quality of territories in fragmented habitat is less than in contiguous habitat (Huhta *et al.* 1998). However, beside edge effects such as increased competition and nest predation, there is no reason to assume a lower habitat quality (Matthysen and Currie 1996, Nour *et al.* 1997, Matthysen and Adriaensen 1998). Competition measured as the presence of other species, however, could not explain the absence of nuthatches in small patches (Wiggins and Møller 1997). Schotman (in prep.) found increased hole take over probability in small patches that may lead to a lower occupancy of these patches. As argued above, the probability of hole take over may be equal for the selected territories. The explanation of a lower habitat quality of small patches cannot be applied as alternative for constrained dispersal since we found no relationship between breeding success and the degree of connectivity: breeding success increases with increasing habitat quality (*DIA*) and not with connectivity at local (*LC*), regional (*RC*) or interregional (*IC*) level (table 3, 4 and 5). This agrees with Matthysen and Currie (1996) and Matthysen and Adriaensen (1998): they found no lower breeding success of nuthatches in the fragments than in the contiguous forests. For the blue tit and great tit (Nour *et al.* 1998) and pied flycatcher (Huhta *et al.* 1998), effects on breeding success in small fragments were also not found.

Another alternative explanation is that territories in the fragmented habitat are less variable in quality. Then, the benefits of monitoring are smaller. If so, the occurrence of unoccupied good territories does not necessarily mean that habitat selection is not optimal, because there may be maximum or equal chance to survive and reproduce for all the birds. Matthysen and Currie (1996) and Matthysen and Adriaensen (1998) could not demonstrate effects of fragmentation on breeding success of nuthatches. A possible explanation for this might be that in their study, the average habitat quality of the territories in the fragments is high enough for successful breeding. This can be supported by the mean trunk diameters reported in Matthysen and Adriaensen (1998). The mean trunk diameter varies from 37 to 60 cm in the fragments (mean: 46 cm) and 53 and 58 cm in the large forests (mean: 55 cm). In our study, we considered a larger range of trunk diameter that nuthatches are likely to assess: from 21 to 65 cm in the fragments and from 26 to 60 cm in the Veluwezoom (see table 2 for mean values). We showed that the variation in habitat quality could be related to the frequency of territory occupancy and breeding success (table 3 and 5). Therefore, it is not likely that this explanation can be applied for the territories in fragmented habitat.

Effects of population level on habitat selection

For nuthatches in contiguous forest, Nilsson (1987) and Schmidt *et al.* (1992) found density-related variation in the quality of occupied territories since breeding success was negatively correlated with population level which was explained by a decrease in the mean territory quality. We also found this, but also differences in the mean quality of occupied territories depending upon the degree of regional connectivity. The different relationships between population level and the mean quality of occupied territories (*ΔDIA*) with high and low degree of connectivity (table 6) also indicate that habitat selection in fragmented habitat is not optimal. The average quality of occupied territories with low degree of connectivity is lower than in highly connected territories at low population level. As population level increases, the average habitat quality of occupied territories with high and low degree of connectivity becomes equal. So, there are differences in the effects of population level on habitat quality in territories related to the degree of connectivity. Thus, we rejected the second null hypothesis.

Differences in population density between the regions

The results showed that the amount of habitat in the regions with fragmented habitat over the last 10 to 15 years has increased (figure 4). Also the mean degree of local, regional and interregional connectivity have a slight positive trend. Figure 4 provides only indications of these developments. It appears that despite a relatively fast population growth in the last decade, the population densities in Midden Brabant, Zuidwest Drenthe and Noordoost Twente are still lower than can be expected from the available amount of habitat (figure 5). An alternative explanation for the effects of fragmentation, among which reduced breeding success due to limited habitat selection and increased environmental and demographic stochasticity, is that differences in population density can be explained by population history, *e.g.*, as result of changes in the suitability of the habitat (Opdam *et al.* 1993). When this is true, the low population density can be expected to increase to the same level as found in contiguous habitat.

As could be expected, the population density could on the one hand be explained by the quality of the habitat (table 7). The increase of the suitability of the habitat resulted in a higher population density. On the other hand, the population density could be related to the degree of regional and interregional connectivity. It appeared that the effect of quality depends on the degree of connectivity: the increase in population density is lower in fragmented habitat than in contiguous habitat due to the low degree of regional and interregional connectivity. Therefore, we rejected the third hypothesis.

The population in Midden Brabant has grown exponentially in the second half of the 80's (Post and Ongenae 1990, Poelmans *et al.* 1997). For this region, more data about population development were not available. Regarding the population density *PD*, it is possible that the number of nuthatches will increase in the future and that effects of fragmentation will diminish. On the other side, literature, local bird watchers and our data acknowledge that in the period before the increase in population growth, sufficient suitable habitat was available. Moreover, several local populations were present in the surroundings of the region from the 50's (Braaksma *et al.* 1958, Moller Pilot pers. com.).

For the region Zuidwest Drenthe, data about the population size per year were available from population start. This population has also exponentially grown in the second half of the 80's (Van Dijk unpubl. data, Van den Brink *et al.* 1996). It appears that this fast increase stabilizes at the moment. The population density of Zuidwest Drenthe is far below the one found in the regions with contiguous habitat.

The population density in Noordoost Twente is higher than in the two other regions with fragmented habitat probably due to the high degree of interregional connectivity. In the beginning of the 1980s, the population started to increase. Few data are available for this period.

It appears that nuthatches were able to colonize the regions with fragmented habitat due to the increase in the amount and quality of habitat and in the degree of interregional connectivity. However, we found that habitat selection in the regions with fragmented habitat is limited compared with contiguous habitat. This is even the case in Noordoost Twente, where the population level is relatively high. The degree of local, regional and interregional connectivity may still be too low to overcome such fragmentation effects. Based on our results, we expect that fragmentation effects will continue to cause a lower population density in the regions with fragmented habitat compared to the regions with contiguous habitat.

Is habitat selection optimal or not in fragmented habitat?

In this paper, we directly compared habitat selection in fragmented and contiguous habitat and could relate this to habitat characteristics, *i.e.*, the mean trunk diameter of oaks and beeches. We can conclude that habitat selection is not optimal in fragmented habitat compared to selection in contiguous habitat, especially when the population level is low. We showed that the limited habitat selection leads to reduced breeding success in fragmented habitat. Our findings provide evidence that the effects of fragmentation will especially be manifest when the population level is low. Compared to contiguous habitat, there is no negative feedback between population level and the quality of occupied territories, and therefore, the mean breeding success. This may increase the extinction probability of local populations in fragmented habitat. Therefore, we can support the assumption that populations at a low level are sensitive for habitat fragmentation. Effects at landscape level are then evident since it may result in a lower growth rate and population level.

So, effects at the individual level may reinforce metapopulation dynamics of nuthatches in fragmented habitat.

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7 COMPETING LAND USE IN THE RESERVE SITE SELECTION PROBLEM

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Competing land use in the reserve site selection problem

1 Introduction

Developments in land use, especially in agriculture, transportation and urbanization, have led to a continuous decline in biodiversity due to habitat alteration, loss and isolation. Many species were not able to adapt to these changes and their numbers declined or they disappeared (Saunders *et al.* 1991, Opdam *et al.* 1993, Andrén 1994). The need for preserving biodiversity through the selection and management of reserves has generally been recognized (Noss *et al.* 1997). However, the number and size of the remaining reserves have often become small and spatial claims of competing land use are high. Spatial planning can play a role in the preservation of biodiversity by selecting reserve networks and through optimization of land use allocation. The effectiveness of selecting reserve networks in human-dominated landscapes depends on the extent to which the spatial claims and suitability of the land for competing land use are included (Van Buuren and Kerkstra 1993, Cook and Van Lier 1994, Nantel *et al.* 1998).

The reserve site selection problem (RSSP) has drawn increasing interest in conservation planning. A number of approaches has been applied to the problem of selecting sites that should be included in a reserve network (*e.g.*, Margules *et al.* 1988, Bedward *et al.* 1992, Arthur *et al.* 1997, Csuti *et al.* 1997). These approaches focus on the selection of reserves based on the present distribution of species. However, the presence of a species in an existing site may depend upon stochastic processes. Especially in small and isolated sites, extinction may exceed colonization. When metapopulation dynamics are operating, only a fraction of the sites that contain suitable habitat is often occupied (Opdam *et al.* 1993, Hanski 1994). Moreover, it appears that the present distribution of a species may deviate from the expected one due to fragmentation effects (Van Langevelde and Schotman chapter 6). It has been argued that empty sites that contain suitable habitat (where the species is not currently present) should also be explicitly considered in the RSSP (Opdam *et al.* 1993, Hanski *et al.* 1996). Enlargement of existing sites or addition of new sites may enhance biodiversity by diminishing fragmentation effects. Then, spatial claims of competing land use should also be considered. However, the current approaches for the RSSP do not deal with spatial claims of other land uses. We defined the RSSP as a problem of selecting sites that both enhances biodiversity and minimizes the disadvantages for the competing land uses. Our objective is to present an approach that addresses these omissions in the RSSP. This approach is worked out in a spatial optimization model for conservation planning in human-dominated landscapes: MENTOR (*Model for Ecological Networks as Tool for Optimization of land use*

Reallocation). First, we discuss the outline of MENTOR. We illustrate the model using a case with competition for space between nature and agriculture as it occurs in the Netherlands. Some results of the model are discussed for the De Leijen region in the southern Netherlands. The approach can be applied in situations where the RSSP deals with competing land uses, either in rural areas or in urban areas.

2 Outline of MENTOR

2.1 Objective

In many situations, it appears that the actual reserves do not guarantee stable populations over time of some species since they are often too small and isolated (Kalkhoven *et al.* 1995, Hanski *et al.* 1996). When populations of certain species are small, exchange of individuals is hampered and local extinction frequently occurs. Although there is a general acceptance that actual reserves should be large or at least close together to address effects of environmental stress and habitat fragmentation (Frankel and Soulé 1981, Forman 1995), it is often not possible to plan large reserves in human-dominated landscapes. The intensity of the use, the availability and price of the land appears to be limiting factors. In these landscapes, networks of reserves may benefit biodiversity by facilitating exchange of individuals by "stepping stones" or corridors between the reserves (Opdam *et al.* 1993, Forman 1995, Hanski *et al.* 1996). The concept of networks received a lot of attention in conservation planning (Smith and Hellmund 1993, Cook and Van Lier 1994, Arts *et al.* 1995). Possible interventions can either enhance the quality of habitat, enlarge the reserves or increase the connectivity between the reserves. Enlargement of existing reserves and addition of new sites to enhance the connectivity between the reserves implies a change of use and vegetation cover of areas that are currently in use by other land use. Thus, there will be competition between these other land uses and the need for preserving biodiversity. This competition becomes stronger when the suitability of the land for the competing uses is high and can often be understood in basic economic terms of supply and demand (Van Lier 1994). Optimization of land use allocation aims to maximize the societal profits through the selection of the optimal configuration of a reserve network with minimum disadvantages for the other land uses. The maximum area to be assigned to a reserve network is often restricted, *e.g.*, due to economic, legal or political constraints.

The research and literature on the RSSP has been concentrated on procedures to select sites that represent all species or each habitat type in the smallest number of sites (*e.g*, Margules *et al.* 1988, Bedward *et al.* 1992, Arthur *et al.* 1997). The selected set of sites can be considered as a nominal core reserve network that should be preserved (Nicholls and Margules 1993). The objective of MENTOR is to assign locations for stepping stones between existing sites. The assignment of the stepping stones is based on ecological guidelines derived from knowledge about population dynamics of the species concerned. The model accommodates the suitability of the land for habitat and for other land uses. We focused on the problem of selecting reserve sites with agriculture as competing land use. The problem of selecting reserve sites concerning more types of land use is principally the same. However, this may require more computational effort.

2.2 Spatial aspects of population dynamics

Many RSSP approaches are conducted as a multi-species approach (Margules *et al.*, 1988, Bedward *et al.* 1992, Arthur *et al.* 1997, Csuti *et al.* 1997). Our model is based on a single-species approach, since species differ greatly in the space they need to complete their life cycles (see also Murphy and Noon 1992, Nevo and Garcia 1996, Hof and Raphael 1997). We used an umbrella species (*sensu* Simberloff 1998) that has such spatial requirements that many other species are assumed to benefit from the reserve network. The presented application of MENTOR is based on the European nuthatch *Sitta europaea*. The nuthatch is a songbird of mature deciduous forests. Deciduous woodlots form the majority of small reserves in the agricultural landscapes on the Pleistocene sandy soils in the Netherlands. The assemblages of forest bird species and the dynamics of the local populations of many bird species in forest fragments are affected by the size of the fragments and the distance to other forest fragments (Opdam *et al.* 1985, Van Dorp and Opdam 1987, McCollin 1993, Enoksson *et al.* 1995, Bellamy *et al.* 1996). Research indicates that populations of nuthatches are affected by fragmentation (Van Dorp and Opdam 1987, Verboom *et al.* 1991, Enoksson *et al.* 1995, Matthysen and Currie 1996, Bellamy *et al.* 1997, 1998). From the group of birds related to mature deciduous forests, the nuthatch shows strong effects of area and connectivity on presence. If the landscape provides conditions for sustainable nuthatch populations, we can then also expect that most other forest birds are present.

To derive spatial guidelines for the habitat network of the nuthatch, we examined if two generally accepted principles for reserve design, about area and connectivity, could be applied for the habitat of the nuthatch at the observed spatial scale in the study region De Leijen:

1) Large habitat patches that support large populations of the species will support this species for longer periods of time than small patches that support fewer individuals.

Previous research has shown that the nuthatch occupation probability is higher and local extinction rate lower in large patches than in smaller patches (Van Dorp and Opdam 1987, Verboom *et al.* 1991, Bellamy *et al.* 1997, 1998). In De Leijen and surroundings, we also found an effect of habitat area on territory occupancy by nuthatches (Van Langevelde and Schotman chapter 6). The relationship between the size of a habitat patch and population survival is also supported by Verboom *et al.* (1993). They simulated population survival in different arrangements of habitat. The results showed that the average proportion of occupied habitat by nuthatches increases when a given amount of habitat is distributed in larger patches. Also, the average time to extinction of the population is larger in large habitat patches than in small patches. Moreover, they found that large areas with large populations have a stabilizing role for the populations found in the surrounding fragments.

2) Habitat patches that are sufficiently connected to allow dispersal support populations for longer periods than habitat patches that are less connected.

The distance between the patches mainly determines the connectivity of habitat patches for nuthatches. We could not find any evidence that nuthatches use physical corridors between habitat patches. In regions with fragmented habitat, the connectivity of patches affects nuthatch occupation and colonization (Van Dorp and Opdam 1987, Verboom *et al.* 1991, Bellamy *et al.* 1997, 1998). This can be explained by problematic dispersal of nuthatches in fragmented habitat (Matthysen and Currie 1996, Van Langevelde chapter 4, Van Langevelde and Schotman chapter 6, Schotman in prep.).

Verboom *et al.* (1993) found that small nuthatch populations buffered the fluctuations in large populations and served as stepping stones between these large populations. In such situations, the frequency of colonization may be sufficient to minimize regional extinction. The effects of large populations on the colonization of the fragments (see above) and the effects of the populations in the fragments on the large populations diminish with distances between the patches.

2.3 Guidelines and strategy of the model

We used the following guidelines for the habitat network of the nuthatch, which were derived from the literature as reviewed above (table 1). In the Netherlands, breeding pairs of nuthatches are found in fragments of 1 ha with high quality habitat. However, the occupation probability of these fragments is low (Van Dorp and Opdam 1987, Opdam *et al.* 1994). We assumed that habitat patches of at least 1 ha could act as stepping stones, since this is considered as the minimum territory size of nuthatches. Nevertheless, a size of 3 ha is preferred, since for which the estimated occupation probability exceeds 0.6 (Van Dorp and Opdam 1987). The distance between patches may not exceed certain thresholds because of the necessary exchange of individuals. Empirical studies showed that the amount of habitat within a range of 3 km from the observed patch can significantly explain the patch occupancy and colonization by nuthatches (Verboom *et al.* 1991, Schotman in prep., Van Langevelde chapter 4, Van Langevelde and Schotman chapter 6). We applied 3 km as threshold distance for patches larger than 3 ha. For smaller patches that act as stepping stone (1-3 ha), the inter-patch distance should be at most 1 km since the occupation of these patches is highly dependent on dispersal from surrounding habitat.

We considered two classes of habitat quality, high and low quality habitat. This distinction is made based on vegetation characteristics, especially the trunk diameter of the deciduous trees (Van Langevelde and Schotman chapter 6). We assumed that breeding pairs in low quality habitat need twice the amount of area than in high quality habitat based on the nuthatch density in low and high quality habitat, see the densities of breeding pairs as given in Nilsson (1976) and Bellamy *et al.* (1998).

Table 1 *Threshold distances for an acceptable probability on successful dispersal of nuthatches between the distinguished size classes of habitat patches*

	To:	
From:	1-3 ha	> 3 ha
1-3 ha	1 km	3 km
> 3 ha	3 km	3 km

As shown by Verboom *et al.* (1993), there should be some large populations in the network that act as a source for dispersing individuals. We assumed that populations of at least 20 reproductive females could be source populations, provided there is an exchange of at least a few individuals per generation with other populations (Quinn and Hastings 1988, Kalkhoven *et al.* 1995). From the literature, source populations can be found in areas of 30-50 ha mature deciduous forest or 40-200 ha mixed forest (Kalkhoven *et al.* 1995).

As is argued, the available space in human-dominated landscapes to enlarge habitat patches and add new habitat close to existing habitat is often limited due to competing land uses. To obtain a reserve network that supports viable populations, the model allocates a path of habitat patches and stepping stones between pairs of selected patches. These selected patches are the "pegs" on which the network hangs. We selected patches, called sources areas, that may support source populations and act as a dispersal source for surrounding patches. When the existing reserves are separated by a distance that exceeds the threshold, adding new sites then connected the reserves. The location of these new sites should be near the existing sites, preferably adjacent to existing sites, but within the threshold distance to existing sites. The final paths contain sets of habitat patches, among which stepping stones are included, that are located within the threshold distances and connect each pair of source populations. The spatial guidelines and this strategy were implemented in the search module of MENTOR. In Van Langevelde *et al.* (chapter 8), we discuss the search module.

2.4 Minimizing competition with other land uses

The problem of competition between the allocation of land for a reserve network and for other land uses can be understood as an optimization problem. Sites with high suitability for habitat, in our case deciduous forest, should be part of the reserve network. However, they can also have a high suitability for other land uses, in our case agriculture. What should be preferred in these sites: agriculture or wildlife habitat? To address this question, sites with high suitability for habitat and low suitability for agriculture should be included in the reserve network, whereas sites with low suitability for habitat and high suitability for agriculture would remain agriculture. The final decision about the size and configuration of the reserve network depends on the ecological guidelines and the maximum amount of farmland to be transformed to deciduous forest.

We constructed suitability maps for deciduous forest and agriculture. These were the input for MENTOR. Therefore, we divided the landscape into gridcells of 1 ha. The size of the gridcells refers to the minimum area of a nuthatch territory. For each gridcell, the suitability for agriculture and habitat should be known. The position of each gridcell g_{ij} is represented by its coordinates (i,j) in which $i = \{1, \ldots, m\}$ and $j = \{1, \ldots, n\}$. The set of gridcells G is defined as $G := \{g_{11}, \ldots, g_{mn}\}$.

We defined the following coefficients:

Sh_{ij} ~ the suitability of gridcell g_{ij} for habitat

Sa_{ij} ~ the suitability of gridcell g_{ij} for agriculture

To balance the interest between habitat and agriculture, the suitability of both can be weighted by coefficients. These weights can be interpreted as the priority given by society to agriculture and nature conservation. We used the parameters *Wh* and *Wa* as weighting coefficients

Wh ~ the interest of nature conservation

Wa ~ the interest of agriculture

The decision variables are defined as:

x_{ij} ~ a binary variable indicating whether gridcell g_{ij} is assigned as reserve site (x_{ij} = 1) or not ($x_{ij} = 0$)

Now, the allocation problem can be formulated as

$$Max\{Z = \sum_{(i,j)\in G_h} (Wh \cdot Sh_{ij} \cdot x_{ij} + Wa \cdot Sa_{ij} \cdot (1 - x_{ij}))\} \qquad (1)$$

subject to

$$\sum_{(i,j)\in G_b} x_{ij} \le T \tag{2}$$

$$x_{ij} \in \{0,1\} \qquad \forall\, i, j \tag{3}$$

in which T is the available area (*i.e.*, the number of gridcells) of farmland for new habitat

$Wh,\ Wa > 0$

$Wh + Wa = 1$

the subset $G_b \subset G$ denotes the set of gridcells from which the final configuration of reserve sites will be selected

An integer programming problem like equation (1) to (3) with a single constraint (2) is well known as a knapsack problem (Williams 1990, 1993, Hillier and Lieberman 1995). However, our description of the problem for the stepping-stone strategy needs an additional constraint:

Distances between the stepping stones connecting existing reserve sites may not exceed the threshold distances (see table 1) (4)

Without the constant $\Sigma\,(Wa \bullet Sa_{ij})$, the objective function of equation (1) can be rewritten as

$$Max\{Z' = \sum_{(i,j)\in G_b} (Wh \cdot Sh_{ij} - Wa \cdot Sa_{ij}) \cdot x_{ij}\} \tag{5}$$

For each gridcell g_{ij}, the term $(Wh \bullet Sh_{ij} - Wa \bullet Sa_{ij})$ in equation (5) can be calculated in advance and is called the subtracted value SV_{ij} of gridcell g_{ij}. In MENTOR, the SV_{ij} is used as the optimization criterion for minimizing the competition between allocating new habitat and agriculture. The weighting coefficients can have a strong influence on SV_{ij}. However, the influence largely depends upon the input data, *i.e.*, the values for Sh_{ij} and Sa_{ij}. For example, a high preference for agriculture with high value for Wa will consolidate the value of agriculture in the calculation of SV_{ij}. Table 2 illustrates the impact of the weighting coefficients Wh and Wa on SV_{ij}. The SV_{ij} values of 4 gridcells were calculated with constant Sh_{ij} and Sa_{ij} and different sets of Wh and Wa. For each set of Wh and Wa, the ranking order of the gridcells was determined from the highest SV_{ij} to the lowest SV_{ij}. Due to the weighting coefficients, SV_{ij} and the ranking order of the cells change. We approached the maximization of SV_{ij} in an heuristic algorithm (see Van Langevelde *et al.* chapter 8).

Table 2 *The impact of the weighting coefficients Wh and Wa on* $SV_{ij} = (Wh \bullet Sh_{ij} - Wa \bullet Sa_{ij})$ *[see equation (2)].* SV_{ij} *is used as the optimization criterion for minimizing the competition between allocating new habitat and agriculture.* SV_{ij} *values for 4 gridcells were calculated with constant* Sh_{ij} *(the suitability of gridcell* g_{ij} *for habitat) and* Sa_{ij} *(the suitability of gridcell* g_{ij} *for agriculture) and different sets of Wh and Wa (Wh + Wa = 1). Wh and Wa represent the interest for nature conservation and agriculture respectively. For each set of Wh and Wa, the ranking order of the gridcells was determined from the highest* SV_{ij} *to the lowest* SV_{ij} *(between brackets). The values for* Sa_{ij} *and* Sh_{ij} *are between 0 and 5, where 0 represents the lowest suitability value and 5 the highest.*

Wh	gridcell 1 $Sh_{ij} = 3$ $Sa_{ij} = 0.1$	gridcell 2 $Sh_{ij} = 4$ $Sa_{ij} = 2$	gridcell 3 $Sh_{ij} = 5$ $Sa_{ij} = 2$	gridcell 4 $Sh_{ij} = 5$ $Sa_{ij} = 3$
0.1	0.21 (1)	-1.4 (3)	-1.3 (2)	-2.2 (4)
0.4	1.14 (1)	0.4 (3)	0.8 (2)	0.2 (4)
0.5	1.45 (2)	1.0 (3.5)	1.5 (1)	1.0 (3.5)
0.6	1.76 (3)	1.6 (4)	2.2 (1)	1.8 (2)
0.9	2.69 (4)	3.4 (3)	4.3 (1)	4.2 (2)

Regarding the principle of calculating the difference between the suitability values, we can formulate some requirements for suitability mapping. First, the maps should reflect both the actual situation and potentials for wildlife habitat and for other land uses. Second, the suitability values should be at one scale in order to make them comparable (in fact, we compare apples and oranges). Given that the suitability of gridcells for both agriculture and habitat varies from high to low values, the highest values may represent the best possible conditions for either agriculture or habitat and gridcells with the lowest values are hardly suitable. However, the nature of the criteria to determine the suitability for both may be very different and they are expressed in different units and scales. One way to make these values comparable is to transform the values (figure 1). This procedure provides one scale for both the suitability of the land for habitat and agriculture with a fixed minimum and maximum value which represent respectively the lowest and highest suitability.

2.5 Estimation of population characteristics and bird species richness

To estimate the effect of the reserve design, we measured some population characteristics in the reserve network. Therefore, we used the spatially structured, stochastic population model METAPHOR (Verboom 1996). This model simulates year-to-year behaviour of individual nuthatches in patches. In the model, the mortality, recruitment and dispersal are density dependent. These life history parameters are derived from literature (see Verboom 1996). The spatial location (in terms of x- and y-coordinates) and the area of the habitat patches form the input for METAPHOR. Based on this information, METAPHOR calculates the maximum number of breeding pairs that can be found in the patches based on the amount of habitat, as well as the probability of dispersal success between pairs of patches based on the distances between patches. The output of the model is the probability of extinction and colonization and the final number of nuthatch pairs in each patch. We simulated the population dynamics of nuthatches for a period of 100 years to determine effects of the number, size and configuration of patches on local populations.

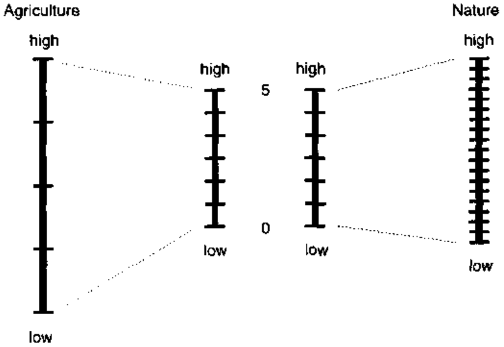

Figure 1 *Transformation of the suitability values for agriculture and nature*

We compared the differences in extinction and colonization probability of habitat patches in the present situation and the planned situations resulting from MENTOR. However, the patches in the present and planned situations cannot be compared since the size and number of the patches changed: patches may be added or enlarged, or several patches may be joined. Therefore, we overlaid the maps with the patches with a raster of 1 ha gridcells. The gridcells received its extinction and colonization probability of the underlying patches. To compare the extinction and colonization probability of the patches in the present and planned situations, we used the set of gridcells that were covered by habitat in the planned situation.

To predict the bird species richness in the sites of the reserve network, we used the regression model as presented in Hinsley *et al.* (1998)

$$N_s = 12.5 + 7.55 \cdot 10\log(A_s)$$

in which N_s is the expected number of forest bird species and A_s is the area (ha) of deciduous forest in patch s. This model is based on the data about forest birds by Van Dorp and Opdam (1987). For the bird species richness, we also compared the set of gridcells of the patches in the present situation with the same set in the planned situations. Each gridcell covered by a patch received the number of species that can be expected in the patch.

3 Case study De Leijen

To illustrate the model, we applied it for De Leijen in Noord-Brabant, one of the southern provinces of the Netherlands (figure 2a). The region is 15 x 18 km^2 (27,000 ha). The current landscape is a mosaic of farmland with forests, roads and cities. The dominant land use is agriculture (13,200 ha). Approximately 90% of this farmland is used for dairy farming. Therefore, we considered the suitability of the land for dairy farming. The present land use is intensive (the population density is about 450 persons per km^2) and has caused significant environmental stress (Prov. Noord-Brabant 1992), and as a result the biodiversity has been decreased drastically (Van de Sande 1988, Prov. Noord-Brabant 1992). The actual suitable habitat for the nuthatch covers less than 3% of the total area.

The region and surroundings are expected to be important for the distribution of nuthatch populations in the south of the Netherlands (Post and Ongenae 1990). Based on the habitat map and the distribution of the nuthatch, we could identify 5 areas that are large enough to support a source population for the nuthatch provided that they are part of the network (figure 2c). Two of them are located in the surroundings of De Leijen. Simulations showed that the forest areas in De Leijen are not large enough to provide conditions for source populations without dispersal from the surroundings. Therefore, a habitat network may contribute to regional population survival.

The main objective of conservation planning in De Leijen and surroundings is the preservation of sustainable conditions for biodiversity in a stable and coherent reserve network (Prov. Noord-Brabant 1992). This network contains core nature reserves, nature restoration areas, corridors and multifunctional forests. Since several core nature reserves are located in De Leijen, the study region is an important link in the reserve network of Noord-Brabant (Prov. Noord-Brabant 1992).

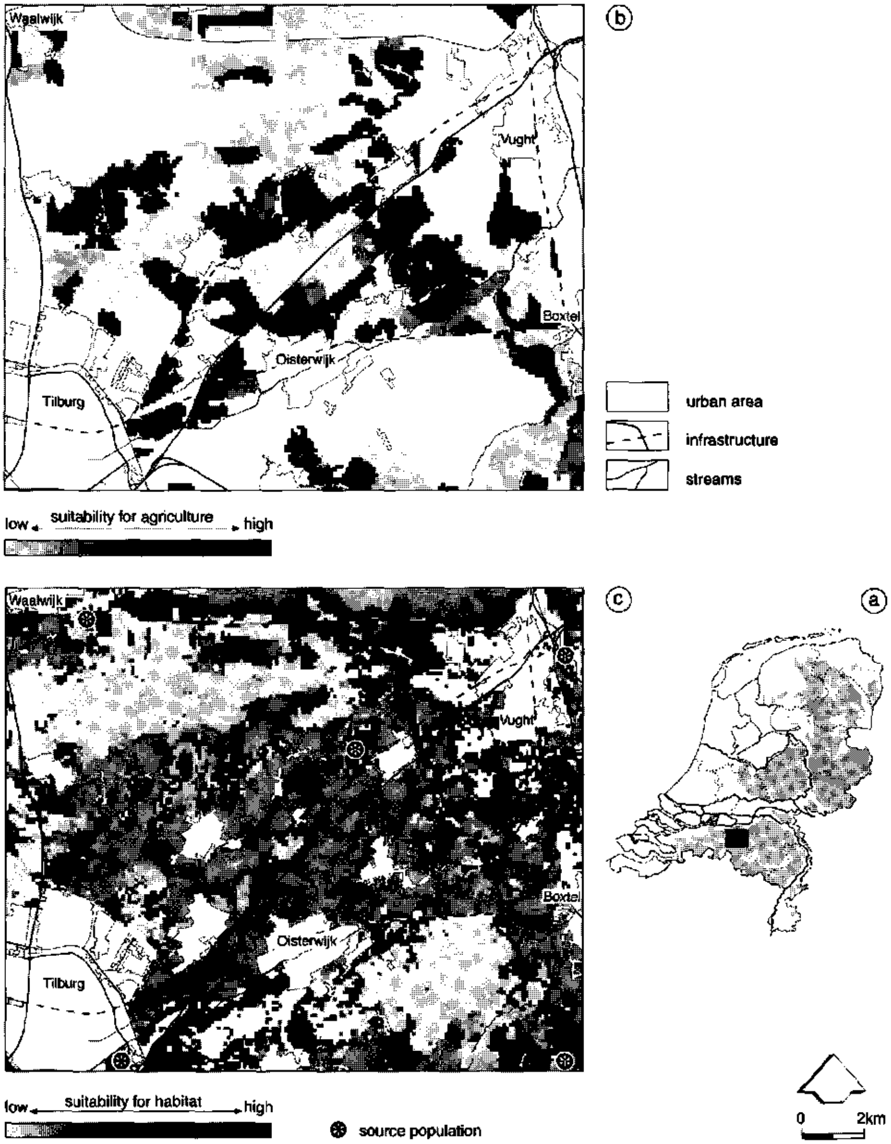

Figure 2 *The location of the study region De Leijen on the Pleistocene sandy soils in the Netherlands (a), the suitability for the highly intensive type of dairy farming in scenario 1 (b) and the suitability for habitat of the nuthatch (deciduous forests) with the distinguished source areas (with source populations) (c). The two markers in the south of the region indicate the locations for connections with source areas in the surroundings of the region.*

A careful reserve site selection in De Leijen may contribute to the realization of this network. Besides the reserve network, the regional policy aims to improve the conditions for agriculture. In this region, spatial planning has to deal with multiple land use with conflicting claims for future development. To illustrate the model MENTOR, we studied the consequences of two existing land use scenarios (CPB 1992, De Groot *et al.* 1994). Can we say something about the opportunities for multiple land use in this region using the spatial optimization model?

The scenarios contain model farm types (the "average farm") which can be expected in the future under the conditions of the scenarios (table 3). Scenario 1 contains a highly productive type of dairy farming, whereas a farmtype with less intensive use is dominant in scenario 2. The two model farm types differ in the size of each farm, the number of dairy cows and their yearly milk production. Based on these characteristics, an index for the intensity of agricultural land use was calculated: [(number of dairy cows x milk production per cow) / farm size]. The intensity of the farm type in scenario 1 was set on 100%. The scenarios varied also in the priority of society given to nature conservation. In scenario 1, a high preference is assigned to agriculture (Wa = 0.9 and Wh = 0.1). In scenario 2, a high preference is given to nature (Wh = 0.9 and Wa = 0.1). The scenarios may differ in the spatial claims for future agricultural land use. For both scenarios, we assumed that the maximum amount of habitat T added to the reserve network is 5% of the area currently used as farmland.

Table 3 *Some characteristics of the two types of dairy farming in scenario 1 and 2 (see text for explanation)*

	Highly intensive farm type	Less intensive farm type
Farm size (ha)	30	60
Number of dairy cows	70	80
Milk production/cow/year (kg)	8500	7500
Index for the intensity of land use (%)	100	50

We mapped the suitability of the land for dairy farming and for deciduous forest based on simple models. These models were based on multi-criteria modelling using map algebra. Several map layers that contained information about characteristics of the land (soil types, groundwater level, vegetation cover, land use, roads, cities) contributed to an overall value per gridcell. We assumed that the suitability within gridcells is uniform. The procedures we used to obtain the suitability maps for nuthatch habitat and dairy farming are enumerated in box 1 and 2.

Box 1 Mapping the suitability of the land for dairy farming

Two criteria were used to map the suitability of the land for the farm types in scenario 1 and 2: the bio-physical and the spatial conditions. These criteria reflect the key processes for optimal production in dairy farming in the Netherlands (Kuijsters and Nieuw-Beerta 1989, Kuijsters and Sparenburg 1990). The bio-physical conditions based on soil type and groundwater level determine the potential yield of the land for grass and maize. Thus, poor bio-physical conditions reduce the potential yield. We used data about the yield reduction for each soil type and groundwater level as found in the Netherlands (Huinink 1993). For both farm types, the potential yield is expressed in economic terms of reduced profits per ha/year (with 0% reduction in potential yield as reference point).

The spatial conditions for dairy farming concerned the percentage of the acreage that each farm can realize adjacent to the farmstead. This percentage is critical for farm management for a reduction of the costs of transportation of milk equipment, manure, fertilizers, etc. To obtain this percentage, the number of farms was determined for both scenarios. The region provides space for 437 farms of type 1 (scenario 1) or 219 farms of type 2 (scenario 2). In our current data, 451 dairy farms were present. Therefore, we removed randomly 14 farms for scenario 1, and 232 farms for scenario 2. The reduction in the number of farms together with the enlargement of the remaining farms is in accordance with the trend of the last decades in farming in the Netherlands. This reduction is expected to be the autonomous development.

In De Leijen, 332 so called farm units were distinguished. Farm units are areas of contiguous farmland that are bounded by 'permanent' landscape elements, such as roads, streams, urban areas, nature reserves. These elements will not be removed in the future. For reasons of concentrated capital investments in and near the farmsteads, we assume that the current location of the farmsteads will not change in the future. So, the size of each unit limits the possibility for individual farms to realize a certain percentage of the farm acreage adjacent to the farmstead. The percentage was calculated as the ratio of the size of the farm unit and the sum of the sizes of the farms within the unit. Dairy farms require a certain percentage of the farm acreage adjacent to the farmsteads, and the remaining acreage preferably close by. Below this percentage, the costs of transportation become very high. For the farm type in scenario 1, the percentage is higher than for the type in scenario 2. When a higher percentage of the farm acreage is near the farmstead, the costs per hectare decrease, and therefore the total added value increases. However, the added value per hectare decreases. Thus, gridcells in a farm unit where the farms can realize a high percentage of the farm acreage near the farmstead have a relatively lower added value. Thus, the suitability of these gridcells for new habitat is higher than the suitability of gridcells in a farm unit where the farms cannot realize this percentage. In other words, it is more difficult for farmers to go from 60% of the farm acreage near the farmstead to 50% than from 90% to 80%.

The suitability Sa_{ij} of gridcell (i,j) for dairy farming was calculated as the sum of the profits due to the bio-physical and the spatial conditions. Figure 2b presents the values of the suitability of the land for the farm type in scenario 1. The highest suitability value (5.0) was assigned to gridcells with both no yield reduction (0%) and a small percentage of the farm acreage adjacent to the farmstead. The lowest value (0.1) was assigned to grids with 30% yield reduction (the highest percentage in the region) and 100% of the farm acreage adjacent to the farmstead. Value 0.0 in the suitability maps for agriculture was assigned to gridcells that contained urban areas, nature reserves, streams and roads. These gridcells cannot be used for agriculture.

4.1 Effects on landscape pattern

As a result of the allocation of the reserve network in De Leijen, the amount of deciduous forest would increase from 741 ha in the present situation to 1029 ha for scenario 1 and 1036 ha for scenario 2 (table 4). In the scenarios, deciduous forests cover about 4% of the total area. The total number of habitat patches increases in both scenarios. Figure 3 shows the number of patches in area classes. Due to the adding of new patches, the number of small patches increases. As a result of the combination or enlargement of existing sites, there is a small increase in larger patches. The changes in amount and configuration of habitat should have consequences for the populations of the nuthatch and species richness in both scenarios.

Box 2 Mapping the suitability of the land for deciduous forests

We used two criteria to determine the land suitability for deciduous forests: the quality of the actual forests as nuthatch habitat and the bio-physical conditions for potential habitat. The quality of the actual forests as habitat could be described by the dominant tree species and its average trunk diameter. Nuthatches prefer mature oaks (*Quercus robur, Q. petraea, Q. rubra*) and beeches (*Fagus sylvatica*) with large trunk diameter (Matthysen 1990, Van Langevelde and Schotman chapter 6). Data on the average trunk diameter were obtained from the Dutch national forest statistics (CBS 1984) and corrected for additional growth of the trees (Van Langevelde and Schotman chapter 6). We applied a regression model that predicts the occupancy probability of nuthatch territories based on these habitat quality variables (Van Langevelde and Schotman chapter 6). We used these predictions for the habitat suitability value of the actual forests F_{ij} of gridcell (i,j).

The bio-physical conditions determine the potentials for habitat. We used data about the potential growth of deciduous tree species for each soil type and groundwater level as found in the Netherlands (Schütz and Van Tol 1990). Based on these data, the classes 'good potential', 'moderate potential' and 'poor potential' could be distinguished for the potential growth of oaks and beeches. These classes provided values for the bio-physical conditions B_{ij} of gridcell (i,j) for the development of habitat. B_{ij} and F_{ij} were scaled between 0 and 5. Since we evaluated scenarios for future developments, the values F_{ij} and B_{ij} were summed as

$$Sh_{ij} = 0.3F_{ij} + 0.7B_{ij}$$

For non-forested areas, $F_{ij} = 0$. The weights 0.3 and 0.7 were chosen following the relative importance in nowadays society regarding the actual and potential suitability. The final suitability map for nuthatch habitat is shown in figure 2c. Gridcells that contained urban areas, streams and roads became value 0. These gridcells were excluded from the RSSP.

4.2 Effects on population survival and species richness

Figure 4 shows the average occupation degree of patches in the present situation and for scenario 1 (with the highly intensive farm type). The average occupation degree per patch is calculated as the ratio between the simulated average number and the maximum number of breeding pairs in each patch. The average proportion of occupied habitat is 23% in the present situation. Due to the planning of new habitat, the average proportion of occupied habitat increases to almost 40% (table 4). As is argued, there is a clear relationship between the average proportion of occupied habitat and the survival of nuthatch populations.

Table 4 *Summary of the results of the allocation of the reserve network in De Leijen based on the two land use scenarios related to the present situation (see text for explanation of these scenarios)*

	Present	Scenario 1	Scenario 2
Effects on landscape pattern			
amount of deciduous forests (ha)	741	1029	1036
number of habitat patches	100	121	121
Effects on nuthatch populations			
proportion of occupied habitat (%)	23	38	38
Effects on dairy farming			
area currently used for dairy farming and assigned as habitat (ha)	0	194	204
estimation of the reduced yields for dairy farming (%, scenario 1 was set on 100%)	0	100	50

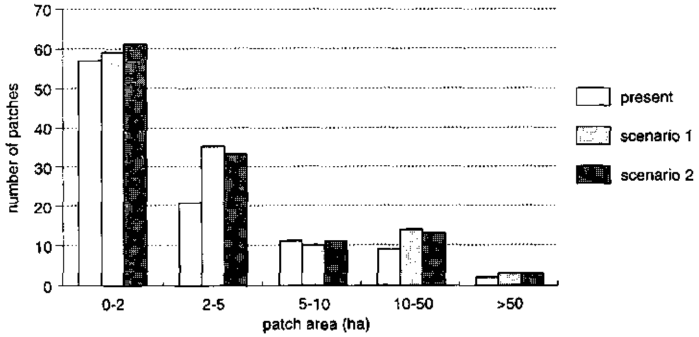

Figure 3 *Number of patches per area class for the present situation and the planned situations under the conditions of the two land use scenarios (see text for explanation of these scenarios)*

Decreased extinction probability (figure 5a) and increased colonization probability (figure 5b) can explain the increase in occupation degree. These figures show the change in number of gridcells with a certain probability value. Especially the colonization probability of the selected set of gridcells changes due to the allocation of the reserve network. The average colonization probability for the set of gridcells increases from 0.23 (s.e. 0.11) in the present situation to 0.64 (s.e. 0.23) in scenario 1 and 0.62 (s.e. 0.24) in scenario 2. We also calculated the expected bird species richness in the patches (figure 6). High numbers of forest birds can be found in more patches due to the addition of new forest.

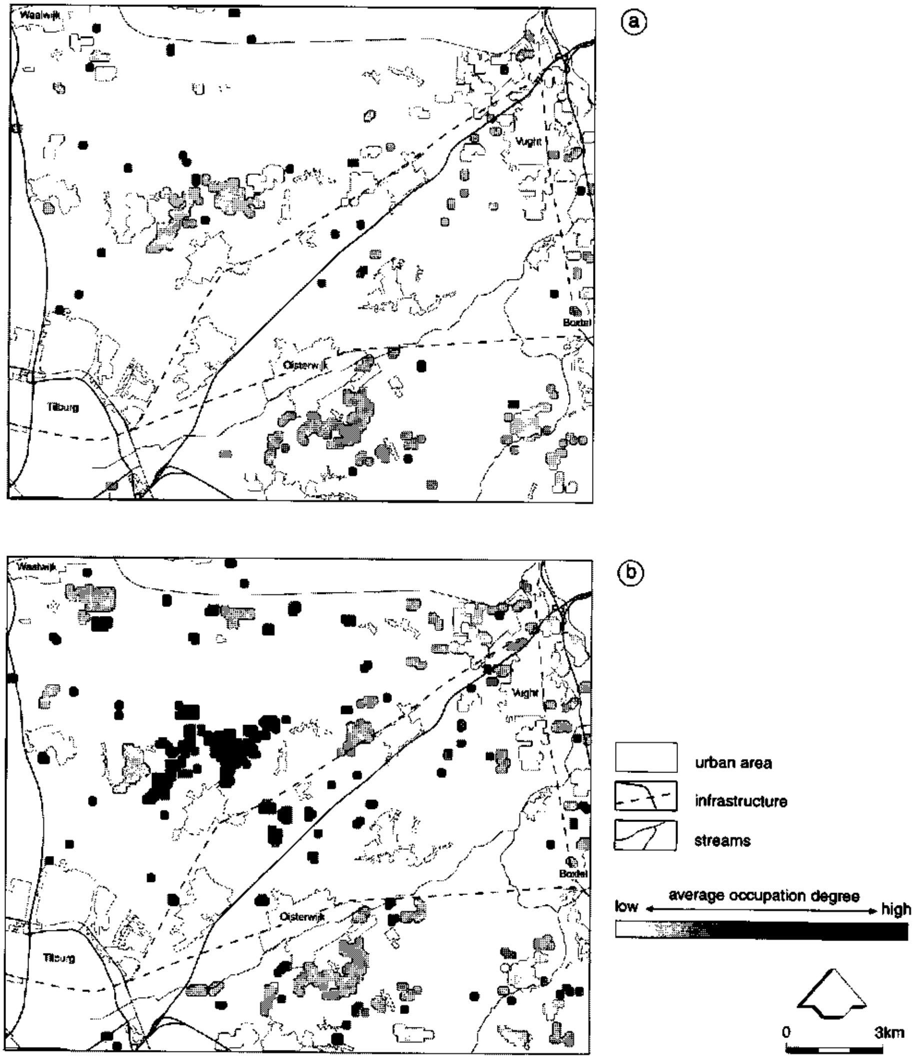

Figure 4 *The average occupation degree of patches for the present situation (a) and the planned situation (b) under the conditions of scenario 1 with the highly intensive type of dairy farming (see text for explanation of this scenario)*

4.3 Effects for agriculture

We assessed the effects for the agricultural use in terms of the number of farms and of the suitability of the land on which new habitat is planned. Based on the area that can be used for agriculture and the average sizes of the farm types (table 3), we calculated the number of farms that can be expected in the future. The planning of new habitat required 194 ha for scenario 1 and 204 ha for scenario 2 (table 4). This is about 1.5% of the total amount of farmland. Despite of constraint (2), it appears that this percentage is enough to connect the selected source areas. Additional new habitat area (94 ha and 91 ha) will be realized in existing reserves, *e.g.*, by enhancing the habitat quality or transformation of the forest vegetation from pine trees to oaks. Thus, the total number of future farms appears to be nearly the same. In scenario 1, a minimum of 6 farms can be expected to disappear (from the total of 437 farms). For scenario 2, the reduction will be 3 farms (from the total of 219 farms).

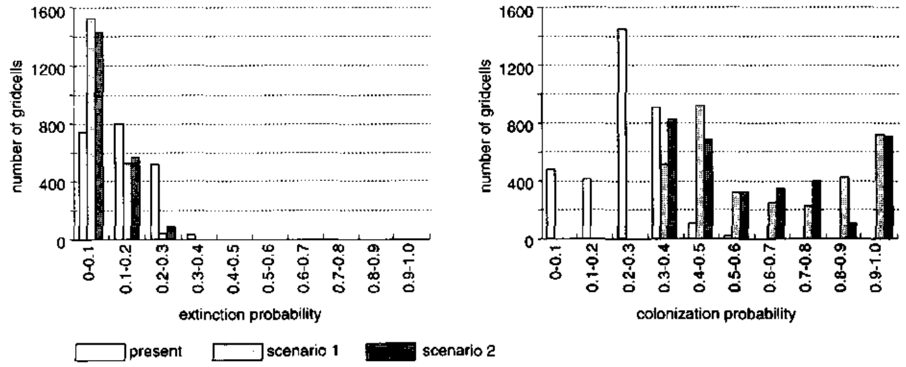

Figure 5 The number of gridcells per class of extinction (a) and colonization (b) probability for the present situation and the planned situations under the conditions of the two land use scenarios (see text for explanation of these scenarios). The size of a gridcell is 1 hectare.

The allocation of future habitat on existing farmland leads to reduced yields. Since the suitability of the land for dairy farming is based on the expected yields for the farmers based on both the biophysical and spatial conditions, we estimated the reduced yields based on the suitability values for agriculture Sa_{ij} of the gridcells that are part of the reserve network. The reduced yield give an indication of the costs for the farmers in scenario 1 related to scenario 2. The area of farmland that is assigned for the reserve network differs slightly between the two scenarios. However, the reduced yields show large differences (table 4). The expected reduction is lower for the farm type in scenario 2. Allocation of new habitat leads to lower costs when the land use in the region is dominated by farm type 2.

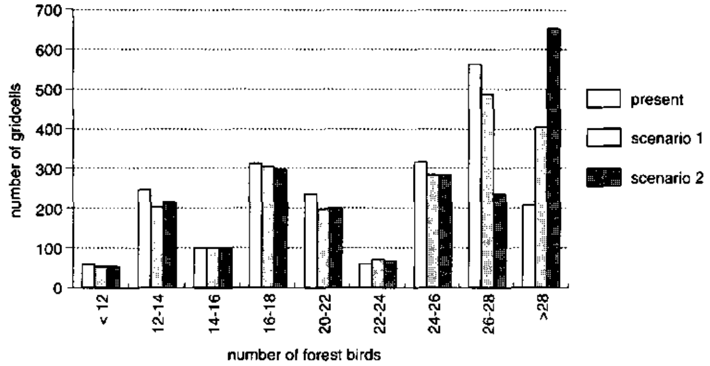

Figure 6 The number of gridcells per class of bird species richness for the present situation and the planned situations under the conditions of the two land use scenarios (see text for explanation of these scenarios). The size of a gridcell is 1 hectare.

5 Discussion

The main objective of many spatial planning efforts in human-dominated landscapes is the allocation of multiple activities in a region. Conservation planning is part of the multiple land use planning. This planning can be approached as an optimization problem, since the suitability of the land and the spatial claims of other land uses should be considered. Optimization models can be used since they are powerful in finding efficient allocations for competing land use (Martínez-Falero *et al.* 1995). In our case, it can offer opportunities to design habitat configurations based on different starting points.

It has been recognized that consideration should be given to population dynamics (Vane-Wright *et al.* 1991, Nicholls and Margules 1993) and competing land use (Bedward *et al.* 1992, Pressey *et al.* 1996, Nantel *et al.* 1998) in the RSSP. Few examples of model approaches known to us consider population dynamics in the selection of a reserve network (Murphy and Noon 1992, Nevo and Garcia 1996, Hof and Flather 1996, Hof and Raphael 1997). They also recognize that connectivity between patches is necessary to maintain viable populations when there are no possibilities to plan large reserves. These models give preference to sites in the proximity of others. However, they cannot be used to allocate stepping stones between habitat patches.

Our objective was to present an approach that deals with ecological guidelines derived from knowledge about population dynamics of a certain species and competing land use in the RSSP. We discussed a model for conservation planning in human-dominated landscapes with minimum consequences for agriculture. To make reserve proposals defensible in light of competing land use, we restricted the maximum amount of farmland to be transformed to wildlife habitat. Population dynamics were introduced by the spatial guidelines for minimum sizes of reserves and threshold distances between reserves. The approach of MENTOR is largely based on the assumption that increasing the degree of connectivity in habitat networks enhances population survival (see also Opdam *et al.* 1993, Hanski *et al.* 1996, Verboom 1996). We acknowledge that our approach is limited to the development of a reserve network that is species-oriented.

We focused on a single-species approach since the issues of the size, shape, spacing and quality of reserves can only be addressed as a single-species approach with the available knowledge. Generalization of the spatial requirements of an umbrella species into guidelines for reserve design depends on the spatial scale at which interventions are taken and which species group can be considered to be represented by the umbrella species. The strategy as modelled in MENTOR can be used for other species. The first prerequisite is that these species benefit from habitat networks, *i.e.*, the reserve design principles should be valid for the species concerned at the observed spatial scale. The second is that the spatial requirements of these species can be formulated in terms of threshold distances and minimum area (according to table 1).

Moreover, our approach is not limited to agriculture and wildlife habitat. It can be applied in situations where conservation planning deals with competing land use, *e.g.*, between timber harvesting and wildlife habitat (Li *et al.* 1993, Lindenmayer and Possingham 1996). Then, questions appear such as "what part of the wildlife habitat is necessary for population survival?", and "what part can be used for growing timber?". When more species and land use types are involved, the results contribute to solutions for multiple land use. Although the complexity increases, this should be possible since MENTOR is a general model that requires a few input parameters to be specified and a limited amount of data. Moreover, the model can be applied to each scale level depending on the species concerned.

For the case study in De Leijen region, we constructed suitability maps that represent the key processes for both dairy farming in the Netherlands and the population ecology of the nuthatch in fragmented habitat. Relatively simple procedures were applied to map the suitability for agriculture and habitat.

We could describe effects on the landscape pattern, nuthatch populations, bird species richness and dairy farming as a result of the planning of the reserve network. The scenarios computed by MENTOR resulted in an increase in area for the reserve network. The results show a modest change in the number of patches. We were able to assess the results of the allocation model with METAPHOR. We conclude that the application of MENTOR leads to an effective reserve network in the human-dominated landscape of De Leijen concerning the suitability of the land for dairy farming. The results show a doubling of the average proportion of occupied habitat, an increase in colonization probability of patches, a decrease in extinction probability of local populations, and an increase in bird species richness per patch. Whereas, it results in a relatively small amount of land currently used by agriculture: about 1.5% of the total amount of farmland. This percentage appears to be sufficient to connect the source areas, although it does not exceed the constraint of 5% of the area currently used for farming.

The scenarios hardly differ in effects on landscape pattern, on the population characteristics or on bird species richness. Stepping stones had to be allocated to connect pairs of source areas regardless of the intensity of the agricultural land use. Both scenarios provide space for the reserve network with relatively small costs for future dairy farms in terms of amount of land. However, the costs in terms of reduced yields differ largely. The planning of a reserve network in scenario 1 leads to higher costs than in scenario 2. This agrees with assumptions that conservation planning meets less objections when the intensity of the existing land use is low. The effects for agriculture were based on data of model farms. In praxis, individual farms may differ in size or management. This may also lead to differences in costs per farm when plans are realized.

The ability to properly map the suitability of the land has decisive effects on the final results. The suitability maps were solely constructed for the illustration of the model MENTOR. For a refinement of these suitability maps, we can add other factors such as acquisition and management costs and political constraints. We found that our approach is sensitive for maps with many gridcells that have the same suitability value. As is illustrated in table 2, the weighting coefficients *Wa* and *Wh* may have a large impact on the results. However, this is not clearly shown by the land use scenarios, because a relatively small amount of habitat had to be allocated as stepping stones to actual farmland. Regarding their impact on the results, the weighting coefficients can be determined using techniques that are replicable and can differentiate between policy priorities (*e.g.*, Saaty 1980). Spatially explicit assignment of the weighting coefficients is also a further refinement in the application of the model. Priorities for nature conservation may differ between parts of the study region.

We did not account for environmental impacts of land use, *e.g.*, on the habitat quality of the reserve network due to the intensity of land use. An improvement of MENTOR could be to minimize environmental impacts of land uses on the reserve network. This can be modelled, *e.g.*, with the use of weights for incompatibility between land uses (Martínez-Falero *et al.* 1995), or by the selection of locations for the sources of the stress (noise, emission, effects on the groundwater level) at certain distances from the reserve network.

Of course, our approach is not a panacea. Though our approach is, like every model, based on assumptions, it can be used as a baseline against which future developments in land use may be evaluated. Spatial optimization models such as MENTOR can be a supporting tool for formulating alternative land use plans. To assess the effects of the allocation results, evaluation tools are needed. The combination of the allocation model MENTOR and the evaluation model METAPHOR may contribute to prospective solutions for the RSSP and the competing land uses. In general, such combinations provide a useful tool for planners and ecologists to explore the relative merits of alternative land use plans and the dynamics of populations in relation to the amount and spatial configuration. For a study region, this may be of practical significance to explore its opportunities for multiple land use.

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8 TWO STRATEGIES FOR CONSERVATION PLANNING IN HUMAN-DOMINATED LANDSCAPES

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Two strategies for conservation planning in human-dominated landscapes

1 Introduction

Conservation planning in human-dominated landscapes can apply several types of interventions, *e.g.*, to maintain or improve the quality of the reserve sites (abiotic conditions for plants or habitat for animals), to enlarge the area of the sites, to increase the number of the sites, to level barriers between the sites by means of corridors or stepping stones, or to manage buffer zones around the reserves sites. Discussion exists about what interventions are likely to improve the efforts of conservation planning: do changes in the spatial arrangement of habitat influence population persistence, and therefore, biodiversity (Lamberson *et al.* 1994, Lindenmayer and Possingham 1996, Hof and Raphael 1997), are the benefits for species survival higher when few single large reserves exist or several small ones (SLOSS; Diamond 1975, Higgs and Usher 1980, Gilpin and Diamond 1980, Blake and Karr 1984), what are the roles of corridors or stepping stones between reserves (Hobbs 1992, Simberloff *et al.* 1992)?

In human-dominated landscapes, actual reserves can not guarantee population persistence of some species since they are often too small and isolated (Kalkhoven *et al.* 1995, Hanski *et al.* 1996). Then, populations of these species are small, exchange of individuals is hampered and local extinction frequently occurs. Although, there is a general acceptance that actual reserves should be large or at least close together to address effects of environmental stress and habitat fragmentation (Frankel and Soulé 1981, Forman 1995), it is often not possible to plan large reserves in human-dominated landscapes. The intensity of the use, the availability and price of the land appear to be limiting factors.

We focused on two strategies in conservation planning that have a spatial dimension: (1) enlargement of existing reserve sites to decrease the extinction probability of local populations and (2) connecting the existing sites with stepping stones to increase the probability of colonization. For each strategy, we developed a spatial allocation model: ENLARGE for the enlargement strategy and MENTOR for the stepping-stone strategy. The objective of this paper is to present the two models. In these models, we also considered the suitability of the land for competing land uses. The guidelines to plan were based on birds of deciduous forests. We used the requirements of one species, the European nuthatch *Sitta europaea,* that shows strong effects of size and the degree of connectivity of habitat patches (Van Dorp and Opdam 1987, Verboom *et* *al.* 1991, Enoksson *et al.* 1995, Hinsley *et al.* 1998). We considered the nuthatch as an umbrella species for other forest birds (cf. Simberloff 1998).

2 Modelling competing land uses in conservation planning

Conservation planning in human-dominated landscapes

In human-dominated landscapes, spatial claims of nature conservation and of competing land uses, such as agriculture, urbanization, infrastructure, may conflict (Van Buuren and Kerkstra 1993, Cook and Van Lier 1994). The problem what reserve sites should be preserved, the reserve site selection problem (RSSP), should deal with competing land uses (Nevo and Garcia 1996, Nantel *et al.* 1998, Van Langevelde *et al.* chapter 7). In the RSSP, spatial planning can play a role through optimization of land use allocation. In this context, optimization of land use allocation aims to maximize the societal profits of nature conservation through the selection of a reserve network with minimum disadvantages for the other land uses. Among others, the societal profits of nature conservation are to preserve viable populations of some species or a certain degree of biodiversity. The maximum area to be assigned to a reserve network is often restricted, *e.g.*, due to economic, legal or political constraints.

We studied the problem of selecting reserve sites for deciduous forests as patch type to provide long-term conditions for viable populations of the nuthatch, and with agriculture as competing land use. The problem of selecting reserve sites concerning more species or types of land use is principally the same. However, this may require more computational effort.

In Van Langevelde *et al.* (chapter 7), we give an enumeration of the ecological principles that were applied in the spatial allocation models. For forest birds, we distinguish minimum area requirements and maximum threshold distances between pairs of habitat patches (table 1).

Table 1 *Threshold distances for an acceptable probability on successful dispersal of nuthatches between two classes for the size of habitat patches*

	To:	
From:	1-3 ha	> 3 ha
1-3 ha	1 km	3 km
> 3 ha	3 km	3 km

Minimizing the competition with other land use

It may be obvious that the competition between nature conservation and other land uses will be stronger when the suitability of the land for the competing uses is higher. Sites with high suitability for habitat, in our case deciduous forest, should be part of the reserve network. However, they can also have a high suitability for other land use, in our case agriculture. Given that for each site the suitability for habitat of the concerning species and for agriculture can be determined, the two strategies are approached as spatial optimization problems: can the sites with the highest suitability for habitat be added to the existing set of habitat patches so that the patches will be enlarged (strategy 1) or that stepping stones are allocated between the existing habitat patches (strategy 2), and that the suitability of the selected sites for the competing land uses is as low as possible? The final decision about the size and configuration of the reserve network depends on the maximum amount of habitat on farmland that can be added and the ecological guidelines to enlarge existing reserves (strategy 1) and to allocate stepping stones between these reserves (strategy 2).

We constructed suitability maps for deciduous forests as habitat for nuthatches and for agriculture. The suitability maps are the input for both spatial allocation models. The procedure to map these suitabilities is discussed in Van Langevelde *et al.* (chapter 7). In this paper, we do not explain the suitability maps in detail. In fact, any map can be applied in our models that represents the suitability of the land for wildlife habitat and the competing land uses. We divided the landscape into gridcells of 1 ha. The size of the gridcells refers to the minimum area of a nuthatch territory. For each gridcell, we determined the suitability for deciduous forest and dairy farming. The position of each gridcell g_{ij} is represented by its coordinates (i,j) in which $i = \{1, \ldots, m\}$ and $j = \{1, \ldots, n\}$. The set of gridcells G is defined as $G := \{g_{11}, \ldots, g_{mn}\}$.

We defined the following coefficients:

Sh_{ij} ~ the suitability of gridcell g_{ij} for habitat
Sa_{ij} ~ the suitability of gridcell g_{ij} for agriculture

To balance the interest between habitat and agriculture, the suitability of both can be weighted by coefficients. These weights can be interpreted as the priority given by society to agriculture and nature conservation. We used the parameters Wh and Wa as weighting coefficients

Wh ~ the interest of nature conservation
Wa ~ the interest of agriculture

The decision variables are defined as:

x_{ij} ~ a binary variable indicating whether gridcell g_{ij} is assigned as reserve site (x_{ij} = 1) or not ($x_{ij} = 0$)

Now, the allocation problem can be formulated as

$$Max\{Z = \sum_{(i,j)\in G_b} (Wh \cdot Sh_{ij} \cdot x_{ij} + Wa \cdot Sa_{ij} \cdot (1 - x_{ij}))\} \tag{1}$$

subject to

$$\sum_{(i,j)\in G_b} x_{ij} \leq T \tag{2}$$

$$x_{ij} \in \{0,1\} \qquad \forall\, i, j \tag{3}$$

in which T is the available area (*i.e.*, the number of gridcells) of farmland for new habitat

Wh, $Wa > 0$

$Wh + Wa = 1$

the subset $G_b \subset G$ denotes the set of gridcells from which the final configuration of reserve sites will be selected

An integer programming problem like equation (1) to (3) with a single constraint (2) is well known as a knapsack problem (Williams 1990, 1993, Hillier and Liebermann 1995). The subset G_b is different for the allocation of stepping stones and for the enlargement of existing sites. In the section 3, the subset G_b will be explained for both models.

However, our description of the problem needs some additional constraints. For the stepping-stone strategy, the additional constraint is formulated as:

Distances between the stepping stones connecting existing reserve sites may not exceed the threshold distances (see table 1) (4a)

The additional constraint for the enlargement strategy is:

New habitat should be allocated adjacent to the existing sites (4b)

Without the constant $\Sigma\ (Wa \bullet Sa_{ij})$, the objective function of equation (1) can be rewritten as

$$Max\{Z' = \sum_{(i,j)\in G_h} (Wh \cdot Sh_{ij} - Wa \cdot Sa_{ij}) \cdot x_{ij}\} \qquad (5)$$

For each gridcell g_{ij}, the term $(Wh \bullet Sh_{ij} - Wa \bullet Sa_{ij})$ in equation (5) can be calculated in advance and is called the subtracted value SV_{ij}. In both MENTOR and ENLARGE, the subtracted value SV_{ij} is used as an optimization criterion for minimizing the competition between allocating new habitat and agriculture. Van Langevelde et al. (chapter 7) illustrate the effects of the weighting coefficients Wh and Wa on SV_{ij}. Regarding the principle of calculating the difference between the suitability values, the suitability values should be at one scale in order to make them comparable (see Van Langevelde *et al.* chapter 7).

To illustrate the two models, we applied them in the region De Leijen in the south of the Netherlands. Two land use scenarios were considered for this region. The scenarios varied in the societal priority given to nature conservation and in the types of future agriculture, *i.e.*, diary farms with differences in the intensity of the land use determined by the farm size, number of cows and their milk production. Scenario 1 contains a highly productive type of dairy farming. In this scenario, a low priority is given to nature conservation ($Wh = 0.1$ and $Wa = 0.9$). In scenario 2, a dairy farmtype with less intensive use is dominant. A high priority is given to nature conservation ($Wh = 0.9$ and $Wa = 0.1$). These scenarios are based on scenarios developed by the Dutch governmental office for strategic planning (CPB 1992) and elaborated by the Dutch institute for agriculture economics (De Groot *et al.* 1994). They were used to illustrate differences in the results of the allocation models based on different suitability maps and weighting coefficients.

3 Two Models

Stepping-stone strategy (MENTOR)

The objective of MENTOR is to assign locations for stepping stones between existing reserve sites. The allocation of stepping stones is based on the threshold distances and minimum size of the sites (see table 1) and on the suitability of the land for competing land uses. To obtain a reserve network that supports viable nuthatch populations, the model allocates a path between pairs of selected patches. These selected patches are the "pegs" on which the network hangs. We selected patches, called sources areas, that may support source populations and act as a dispersal source for surrounding patches (cf. Kalkhoven *et al.* 1995). When a distance that exceeds the threshold distance separates existing sites with deciduous forest, they will be connected with stepping stones. The stepping stones contain also deciduous forests. Their size is at least the minimum size and they are located within the predefined threshold distances from other sites. The final path between a pair of source areas is defined as the set of habitat patches (including existing sites and stepping stones) which allows individuals of the species to move from one source area to the other.

Though the problem in equation (1) with the constraints (2), (3) and (4a) can be modelled as an integer programming model (Keuren 1995), it turned out to be difficult to solve. In order to reduce the computational complexity of the stated problem of allocating stepping stones, we applied an heuristic algorithm. Therefore, the problem of searching paths between pairs of source areas was decomposed into two steps at different spatial scales. First, blocks of 10 × 10 gridcells were distinguished. For each block b, the subtracted value SV_b has been calculated as the mean of the 50 gridcells in the block with the highest values for SV_{ij}. In the second step, we used the SV_{ij} of the individual gridcells.

The algorithm of the search module in MENTOR is based on an Add & Drop-heuristic (Dannenbring and Starr 1981). This algorithm was used in both steps. Step 1 results in a subset of blocks which was used as the search direction for the path to be searched in step 2.

Given that n source areas can be distinguished in a study region. In the first step, also n blocks that contain a source area can be distinguished. When two or more source areas are located within one block, the question is if these source areas should be considered separately. The subset $G_b \subset G$ enclosed all gridcells that could be used as stepping stone in the paths between each pair of source areas: gridcells with existing habitat and gridcells with potentials for new habitat. The gridcells which are part of the source areas and which are unsuitable, *e.g.*, the gridcells that contain urban areas, infrastructure, etc., were excluded from the subset G_b. The solution subset $G_s \subset G_b \subset G$ encloses all gridcells actually assigned to the final paths between each pair of source areas.

The algorithm can be described as:

DO FOR all pairs of source areas

Step 1 Determine the subset $G_b \subset G$ and $SV_{\min} = \underset{(i,j)}{Min}\{SV_{ij} \big| g_{ij} \in G_b\}$

Step 2 Add all gridcells in the subset G_b to the solution subset G_s

```
Step 3  Determine the subset $G_d \subset G_b$ as $G_d := \{g_{ij} \in G_b \mid SV_{ij} \leq SV_{min}\}$ and eliminate (Drop) the
        subset $G_d$ from $G_s$.
                IF there exists a path in $G_s$ between the source areas THEN
                $SV_{min} = SV_{min} + \Delta SV$
                in which $\Delta SV$ is sufficiently small
                GOTO Step 3
        END IF

Step 4  Locate the gap in the path that exceeds the threshold distance and the set of gridcells
        from $G_d$ around this gap in which additional gridcells are necessary.
        Add the gridcell $g_{ij} = \underset{(i,j)}{Max}\{g_{ij} \mid g_{ij} \in G_d\}$ to the solution subset $G_s$.
        IF there exists a path between the source areas THEN
                STOP
        ELSE
                GOTO Step 4
        END IF

END FOR
```

It may be obvious that the value of the parameter ΔSV has a crucial impact on the objective value Z (equation 1) and the computational effort. High values of ΔSV lead to a large subset G_d in step 3 of the algorithm. Consequently, each pass of step 3 will substantially reduce the subset G_s, *i.e.*, the number of gridcells in which a path is searched. To limit the computational effort, a large reduction of the subset G_s in each pass may be desirable. However, it may have an adverse effect on the objective value Z'. When gridcells with relatively high SV_{ij} are removed it may be difficult in the successive step 4 to find a path between a pair of source areas with high objective value Z'.

In our case study for the region De Leijen, the values for SV_{ij} were between –5 and 5 due to the chosen scale for Sh_{ij} and Sa_{ij} (see Van Langevelde *et al.* chapter 7 for a description of the suitability maps). Since gridcells with a low value for SV_{ij} have high suitability for agriculture and low suitability for habitat, we started with $\Delta SV = 2$. Each time step 3 was passed and the lower bound SV_{min} was raised with ΔSV, the value for ΔSV decreased as calculated by $\Delta SV = (5 - SV_{min}) / 5$. The minimum value for ΔSV was defined as 0.1.

Further reduction of the computational time has been achieved by including the option to reduce the size of the subset G_b. In subset G_b, MENTOR searches a path between a pair of source areas.

Therefore, a line was drawn between the centres of the two source areas. The subset G_b has been defined as the set of gridcells in the buffer of a certain width around this line.

Enlargement strategy (ENLARGE)

The objective of ENLARGE is to assign locations for enlargement of existing reserve sites. The enlargement of existing reserves is the addition of gridcells for new habitat located directly at the boundary of existing reserve sites. It should consider the suitability of these gridcells for competing land uses.

An efficient way of solving the problem stated in equation (1) with the constraints (2), (3) and (4b) is to use (discrete) dynamic programming. For the enlargement strategy, the subset G_b denotes the subset of gridcells g_{ij} at the boundaries of existing reserve sites. Note that the subset G_b is not predefined, but has to be determined for each set of sites and for each maximum amount of habitat T that can be added. The determination of G_b will be discussed after the explanation of the dynamic programming algorithm. Dynamic programming is a useful mathematical technique for making a sequence of interrelated decisions. It provides a systematic procedure for determining the combination of decisions that maximizes overall effectiveness, in our case, the objective value Z (equation 1).

For an introduction to the terminology and structure of dynamic programming problems, we refer to Hillier and Lieberman (1995). We will suffice to give the relevant recursive relationship $V_k(t_k)$ in any stage $k = 1, \ldots, K$ and state t_k. The stages k represent the existing reserve sites. The state variable t_k in stage k is defined as the amount of habitat available for the enlargement of site k ($0 \leq t_k \leq T$, see equation 2). In advance, which sites will be enlarged with a certain amount of habitat is unknown.

The recursive relationships are defined as

$$V_K(t_K) = 0 \tag{6}$$

$$V_k(t_k) = \begin{cases} \underset{x_k \in G_{T,k}}{Max}\{SV^T(G_{T,k}) \cdot x_k + V_{k+1}(t_k - x_k^T \cdot I)\} & \text{for} \quad k = K-1, K-2, \ldots, 0 \\ 0 \qquad\qquad \text{otherwise} & \end{cases} \tag{7}$$

in which the term $V_K(t_K)$ represents the value function of the final stage K

the transposed vector $SV^T(G_{T,k})$ denotes the subtracted values SV_{ij} of all gridcells in the subset $G_{T,k}$

$x_k \in \mathbb{R}^n$ in stage k and the transpose x^T_k are the decision vectors consisting of the binary decision variables x_{ij}

I is a vector which elements are all equal to 1

the term $(t_k - x^T_k \bullet I)$ describes the transformation of the state variables between two successive stages k and $k + 1$; in other words, it represents the amount of habitat t_{k+1} that is available for enlargement of site $k + 1$

The subsets $G_{T,k}$ of gridcells at any state t_k in stage k or, in other words, the available habitat for enlargement of site k, need some explanation. The gridcells with new habitat for enlargement should be added at the boundaries of the existing sites (the stages $k = 1, \ldots, K - 1$). Suppose that the site k has the size of 1 gridcell with the coordinates (i,j) and 1 gridcell can be added to this site, than the subset $G_{1,k}$ for the decision vector $x^T_k = (1, 0, \ldots, 0)$ is defined as

$$G_{1,k} := \{x_{(i-1,j-1)}, x_{(i-1,j)}, x_{(i-1,j+1)}, x_{(i,j+1)}, x_{(i+1,j+1)}, x_{(i+1,j)}, x_{(i+1,j-1)}, x_{(i,j-1)}\} \qquad (8)$$

So , $G_{1,k}$ is the subset of gridcells adjacent to the concerned site from which 1 gridcell has to be selected as new habitat. The subsets $G_{2,k}, \ldots, G_{T-1,k}$ for the decision vectors $x^T_k = (1, 1, 0, \ldots, 0)$ to $x^T_k = (1, 1, \ldots, 1)$ can be determined in a similar way. The final set $G_{T,k}$ is defined as $G_{T,k} = G_{1,k} \cup G_{2,k} \cup \ldots \cup G_{T-1,k}$. The union of the sets $G_{T,k}$ for all stages k provides the subset G_b.

Prior to solving the recursive relationships (6) and (7), the set $G_{T,k}$ and the related vector $SV(G_{T,k})$ have to be determined for all stages $k = 1, \ldots, K - 1$. In other words, the gridcells that can be added to a given site should be listed in such way that the first gridcell in the list is both adjacent to the existing site and has the highest subtracted value SV_{ij}. This gridcell is likely to be the first one to be added as new habitat. The number of gridcells in $G_{T,k}$ cannot exceed the total available amount of habitat T. After the first gridcell is selected, the number of gridcells in the subset increases from which the second gridcell will be selected (see figure 1). The following algorithm describes the determination of the set $G_{T,k}$ and the related vector $SV(G_{T,k})$:

```
Step 1   Set $G_{0,k} := \{\varnothing\}$
         and vector $SV^T(G_{T,k}) = (0, \ldots, 0)$

Step 2   DO FOR all stages $k < K$
                 Determine subset $G_k \subset G$ enclosing all gridcells of site $k$
                 DO FOR $t = 1$ to $T_k$
                         Determine the subset $G_{t,k}$ from $G_k$ analogous to equation (8)
                         Determine the $t$-th element $SV_t(G_{T,k})$ of $SV(G_{T,k})$ by:

                         $SV_t(G_{T,k}) = \underset{(i,j) \in G_{t,k}}{Max} \{SV_{ij}\}$          (9)
```

$$G_{t,k} := G_{t-1,k} \cup \{ g_{ij} \big| SV_{ij} = \underset{(m,n)\in G_{t,k}}{Max} \{SV_{ij}\} \tag{10}$$

$$G_k := G_k \cup G_{t,k} \tag{11}$$

```
        END FOR
    END FOR
```

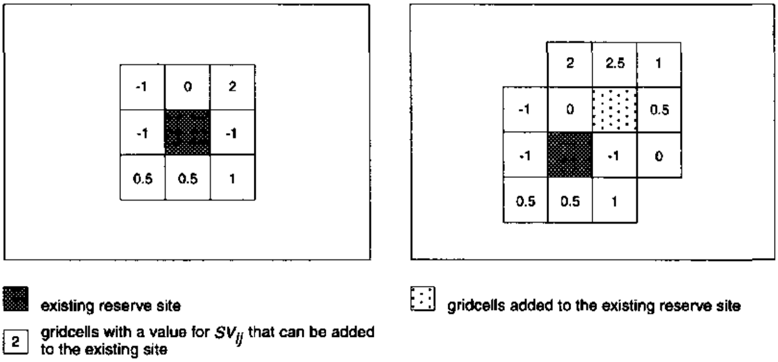

Figure 1 *Selection of the gridcells that can be added to the existing reserve site. The gridcell with the highest value for the subtracted value SV_{ij} (see text for explanation) is selected to be added to the reserve site. The subset of gridcells increases from which the second gridcell will be selected.*

In case two or more adjacent gridcells in the subset $G_{t,k}$ have the maximum value for SV_{ij} (equation 10), the gridcell with the highest value for Sh_{ij} is selected. If this selection contains two or more gridcells, then the gridcell with the lowest value for Sa_{ij} is selected. If still more than one gridcell is selected, the gridcell is selected which is located at the shortest distance to the previous selected gridcell.

From a computational point of view, the recursive relationships (6) and (7) are rather easy to solve. In fact, it turns out that the computational complexity is substantially less than the determination of the set $G_{T,k}$ and the related vector $SV(G_{T,k})$.

However, the relationships in (7) do not consider any possible overlap between the stages. As the recursive relationships maximize the cumulative subtracted values SV_{ij}, it is likely that gridcells with high values for SV_{ij} are reached from more than one reserve site, especially when these sites are located near to each other. When the purpose of the model ENLARGE is to add T ha of new habitat to the existing sites, then this possible overlap has to be removed.

Adjusting the recursive relationships (7) in order to cope with this possible overlap requires a multi-dimensional state-space which in turn has a dramatic influence on the computational complexity of the problem. For this reason, we developed an iterative procedure to exclude any possible overlap. This procedure is implemented as

```
Step 1   $k = 1$
         and $n = 0$

Step 2   DO WHILE $t_k > 0$
                 Solve (6) and (7)
                 Count the number $n$ of uniquely allocated gridcells
                 $t_k = t_k - n$
         END WHILE
```

The model ENLARGE has been applied for two purposes. The first was to enlarge the existing reserve sites. The second can be regarded as an improvement step of the stepping-stone strategy. As result of the model MENTOR not all available amount of habitat T has to be assigned as stepping stones to the reserve network (Van Langevelde *et al.* chapter 7). Therefore, we used ENLARGE to enlarge the sites in the resulting reserve network.

4 Results

The two models were applied for two land use scenarios in the study regions De Leijen. For both scenarios, the maximum amount of habitat on farmland T added to the reserve network was set on 1.5% of the area currently used as farmland (198 gridcells), 2.5% (330 gridcells) and 5% (660 gridcells). Table 2 presents the number of the patches, the amount of habitat and the percentage high quality habitat per configuration. As can be observed, the number and size of the patches differ between the stepping-stone strategy and the enlargement strategy.

In the suitability mapping, we differentiated between a good, moderate and poor potential of the bio-physical conditions of soil and ground water level for the growth of oaks *Quercus robur*, *Q. petraea* and *Q. rubra* and beech *Fagus sylvatica* (Van Langevelde *et al.* chapter 7). Based on this distinction, we assumed that gridcells with good and modest potentials can support high quality habitat and gridcells with poor potentials provide low quality habitat (table 2).

Table 2 *The number of habitat patches and amount of habitat (in ha) and the percentage of optimal habitat in the two scenarios as result of MENTOR for the stepping-stone strategy, and of ENLARGE for the enlargement strategy, and of a combination of both (Comb.). The amount of available habitat on farmland T was set on 198, 330 and 660 gridcells. Scenario 1 contains a highly productive type of dairy farming and a high priority given to agriculture (Wa = 0.9). Scenario 2 represents a dairy farmtype with less intensive use and a high priority given to nature conservation (Wh = 0.9). The number of patches in the present situation is 100 and the amount of habitat is 741 ha with 77% optimal habitat.*

Scenario	Model	$T = 198$			$T = 330$			$T = 660$		
		Number	Amount	%	Number	Amount	%	Number	Amount	%
1	MENTOR	121	1029	71	-	-	-	-	-	-
	ENLARGE	60	1905	64	53	2163	41	46	2597	36
	Comb.	-	-	-	81	2035	36	66	2511	30
2	MENTOR	121	1036	73	-	-	-	-	-	-
	ENLARGE	64	1482	68	57	1639	51	54	2024	46
	Comb.	-	-	-	89	1613	47	78	1979	38

In figure 2, the present situation (a) and several resulting configurations of habitat are presented for T = 330 gridcells. The results of MENTOR are the configurations (b) and (e) for the two scenarios. The amount of new habitat on farmland does not exceed 1.5% of the total amount of farmland (table 2). The model ENLARGE resulted in the configurations (c) and (f). The configurations (d) and (g) are the result of the combined application of MENTOR and ENLARGE. We allowed that existing reserve sites could be transformed to deciduous forests. In the region De Leijen, there is a policy to transform planted pine forests, dominated by Scots pine *Pinus sylvestris*, to deciduous forests. In figure 2, a distinction is made between new habitat in existing reserve sites as result of these transformations and new habitat on farmland.

The resulting habitat configurations were evaluated with the spatially explicit population model METAPHOR (Verboom 1996). With this model, the percentage of the amount of habitat that will be occupied by nuthatches could be estimated. The percentage of occupied habitat is assumed to be a measure for population sustainability. For the evaluation, we assumed that nuthatches need twice the amount of habitat to establish a territory in low quality habitat than in high quality habitat.

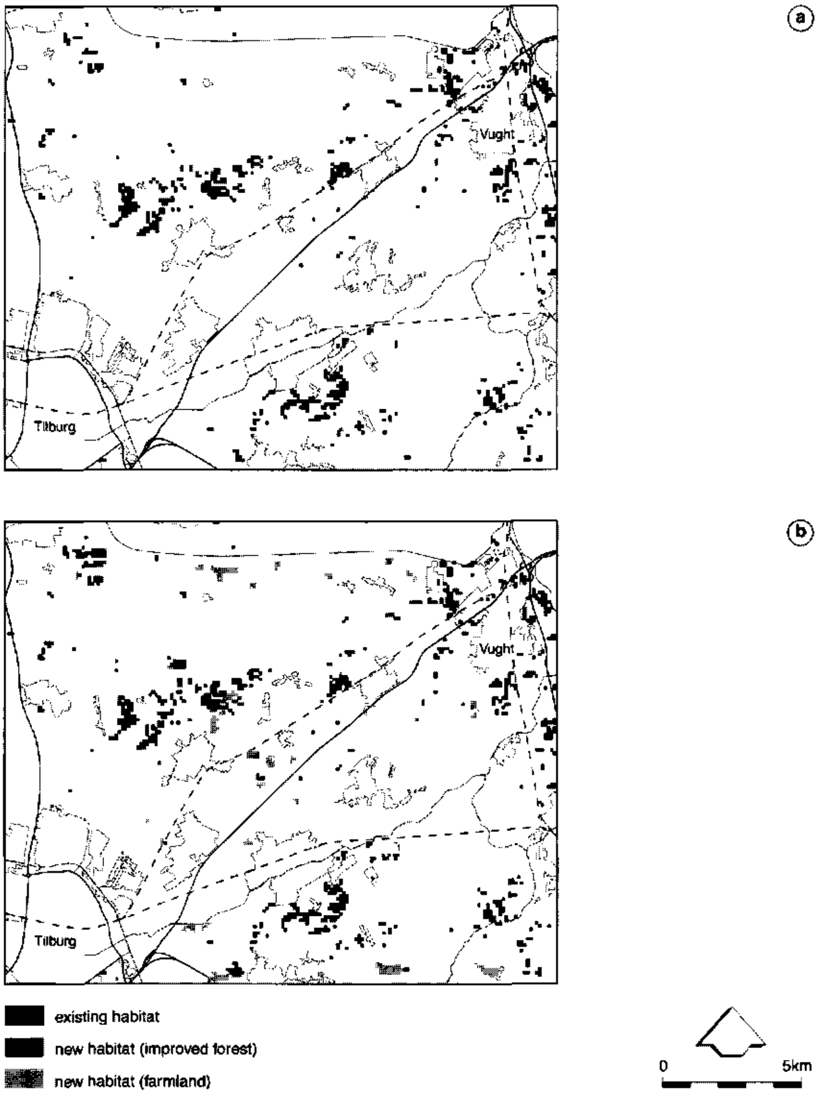

Figure 2 *The present situation (a) and the resulting habitat configurations (b) and (e) from the model MENTOR for the stepping-stone strategy, and (c) and (f) from the model ENLARGE for the enlargement strategy. The habitat configurations (b) and (e) were improved by ENLARGE resulting in (d) and (g). The configurations (b), (c) and (d) are based on scenario 1 with a highly productive type of dairy farming and configurations (e), (f) and (g) based on scenario 2 with less intensive dairy farming. New habitat is planned in existing reserve sites, realized by transformation of the cover types to deciduous forests, and on farmland. The maximum amount of habitat on farmland T was set on 330 gridcells.*

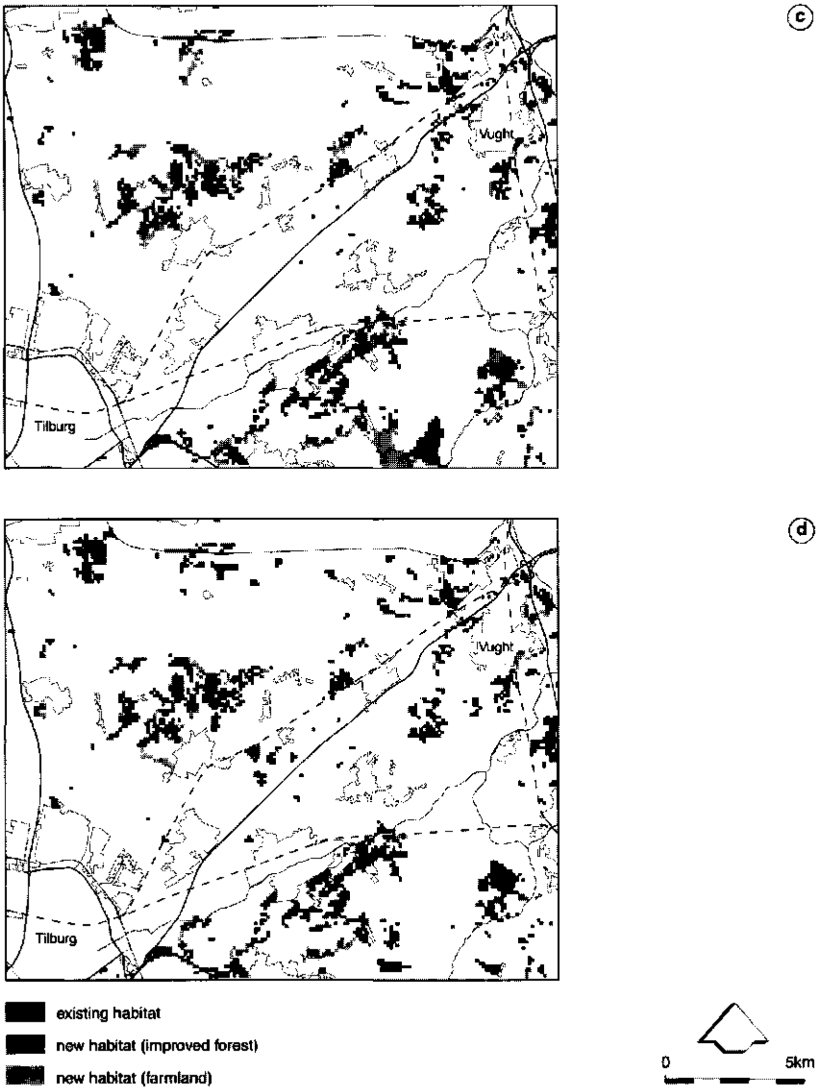

Figure 2 *continued*

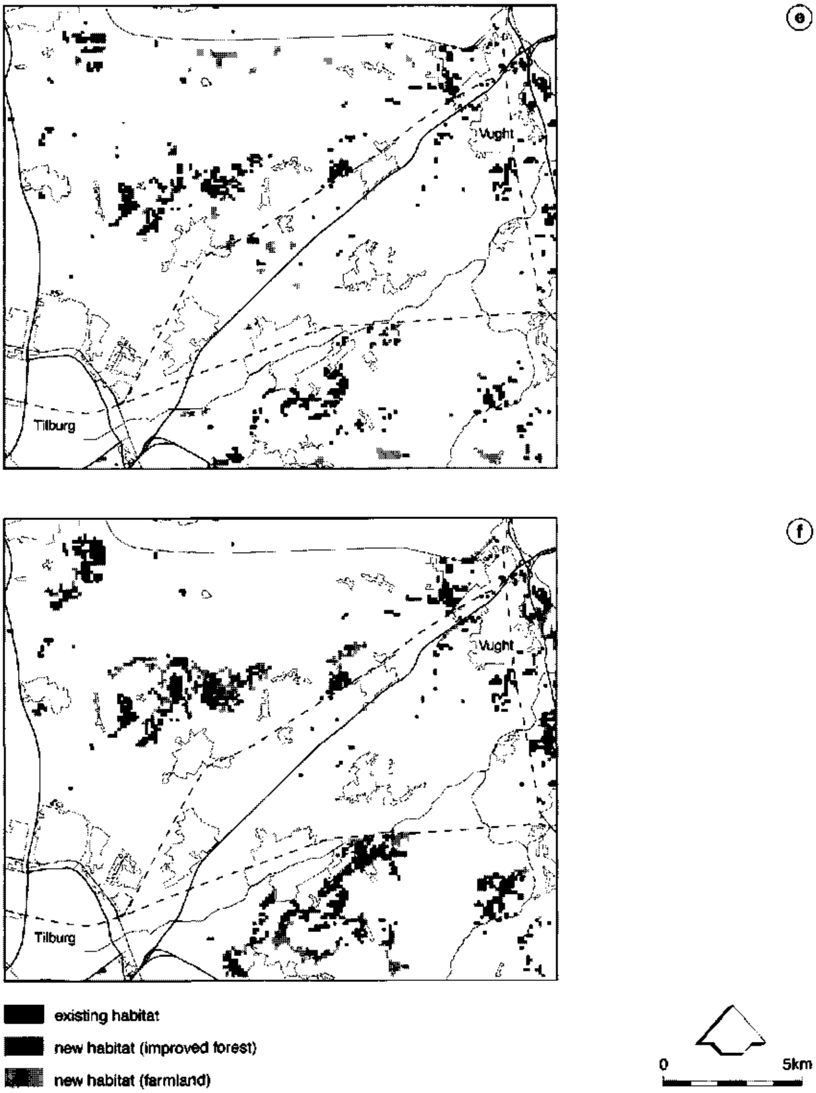

Figure 2 *continued*

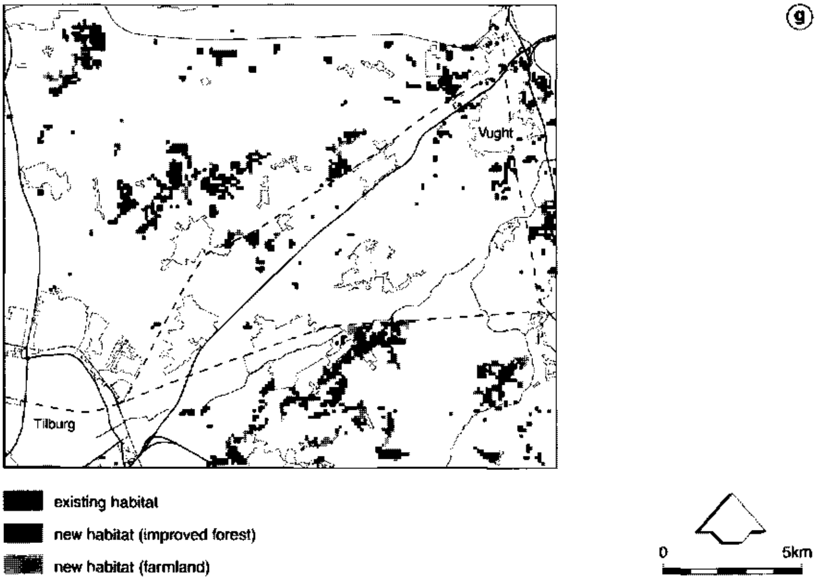

Figure 2 *continued*

In table 3, the percentage of occupied habitat is given for each habitat configuration. These values cannot be compared due to differences in amount and quality of habitat. Therefore, the amount of habitat corrected for differences in quality, and the resulting percentage of occupied habitat are drawn in figure 3.

Table 3 *The percentage of occupied habitat resulting from METAPHOR in the present situation and the two scenarios as result of MENTOR for the stepping-stone strategy, and of ENLARGE for the enlargement strategy, and of a combination of both (Comb.). See table 1 for further explanation.*

			$T = 198$	$T = 330$	$T = 660$
Present		23			
Scenario 1	MENTOR		38	-	-
	ENLARGE		54	69	81
	Comb.		-	63	75
Scenario 2	MENTOR		38	-	-
	ENLARGE		45	65	68
	Comb.		-	57	72

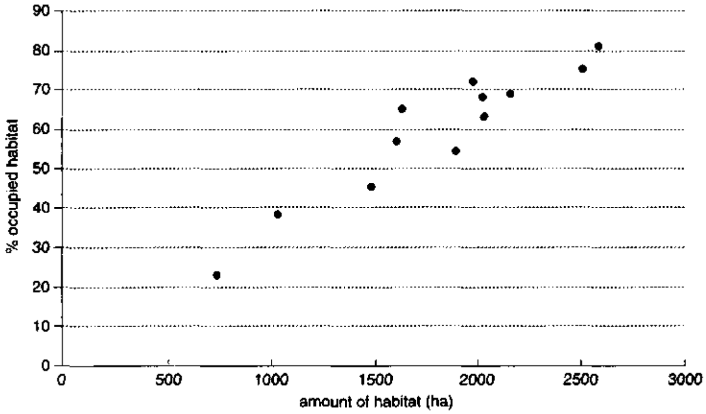

Figure 3 Relationship between the amount of habitat in the configurations corrected for differences in habitat quality (table 2) and the percentage of occupied habitat (table 3)

5 Discussion

In this paper, we presented two spatial optimization models for conservation planning in human-dominated landscapes. These models were developed for two different strategies in conservation planning: strategy 1 focuses on the enlargement of existing reserve sites and strategy 2 on the allocation of stepping stones between these sites.

Spatial optimization can be used if the configuration of habitat is not specified (Hof and Flather 1996, Hof and Raphael 1997) or new habitat can be added. It can offer opportunities to design habitat configurations based on different starting points, *e.g.*, as formulated in scenarios. When the reserve site selection problem is reduced to select those patches that have to be protected against further development of other land uses, algorithms as advocated by Margules *et al.* (1988) or Scott *et al.* (1993) can be applied. See Csuti *et al.* (1997) for a review of these selection algorithms. In our models, we minimize the competition between interventions to add new habitat and competing land uses.

The model MENTOR was developed with the ecological guidelines derived from the population dynamics of the nuthatch (Van Langevelde *et al.* chapter 7). The model ENLARGE is not directly linked to the guidelines for one species. The only variation that is implemented in ENLARGE is the distance from the boundary of existing reserve sites and the gridcells with new habitat. In our model, the gridcells with new habitat should be allocated at the boundary of the existing sites (see figure 1). Thus, both models can be applied for other patch types and for other species.

To illustrate the two models, we applied them in a case in the region De Leijen in the south of the Netherlands. This resulted in several different habitat configurations. The effects on landscape structure and on population performance were described. The numbers of patches in the results of MENTOR and of ENLARGE for the two scenarios are almost equal (table 2). However, the location of the patches differ between the scenarios (figure 2).

For a proper comparison of the effects on population performance, there are two confusing factors. First, we allowed new habitat to be realized in existing reserve sites by transformation of the actual cover types to deciduous forest. The model MENTOR for the stepping-stone strategy could assign existing reserve sites as stepping stones assuming that the vegetation cover of these sites will be transformed to deciduous forest. When this happens, connection between the selected source areas may be realized without claiming farmland. The model ENLARGE could also add gridcells that should be transformed when these were located at the boundary of existing sites with deciduous forest. The second confusing factor is that we differentiated in high and low quality habitat in the total amount of habitat. Although both factors are realistic options for conservation planning, it may confuse the comparison of the resulting habitat configurations. It seems that the percentage of occupied habitat by nuthatches is higher when the habitat patches are enlarged. However, the total amount of habitat and the amount of high quality habitat is higher for these configurations compared to the ones that results from the model MENTOR. Moreover, the enlargement of the patches will also lead to a decrease in the inter-patch distances (Harrison and Fahrig 1995, Van Langevelde chapter 5), especially when several small patches are joined into one large patch.

As result of both models, the amount of habitat and the percentage of occupied habitat increases (figure 3). When the amount of habitat is relatively low, stepping stones are recognized to play a role in increasing connectivity of empty patches and reducing extinction of local populations (Fahrig and Merriam 1985, Lefkovitch and Fahrig 1985, Opdam *et al.* 1993, Hanski and Thomas 1994). As can be expected, the spatial configuration of habitat becomes less important when the amount of new habitat increases (Andrén 1994, 1996, Venier and Fahrig 1996, Fahrig 1998, Van Langevelde chapter 5). Then, the necessity of stepping stones to facilitate the exchange of individuals between the existing patches decreases.

In this paper, we presented two models for conservation planning in human-dominated landscapes. These models result in different habitat configurations. Depending on the characteristics of the species, the landscape in which interventions are planned, and economic, legal or political constraints, one can apply a model to enlarge existing sites or to connect these sites with stepping stones.

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9 DISCUSSION

Discussion

1 Introduction

In this thesis, I report on a study of effects of habitat fragmentation at population and individual level and opportunities to address these effects by planning ecological networks. The objective of the research is to contribute to an improved knowledge about the effects of fragmentation and defragmentation of habitat on populations, in particular effects of differences in the degree of habitat connectivity on colonization and habitat selection. The main question of the research was: do networks of patches contribute to population sustainability of species in fragmented habitat? The hypothesis was that the degree of habitat connectivity is a crucial feature to constitute an ecological network since it determines processes at population and individual level in fragmented populations. The main research question was split up into three questions:

1) What variables can measure the degree of connectivity of the habitat patches? When insufficient connectivity constrains dispersal in fragmented habitat, it will be reflected by the colonization patterns of the species. Are differences in the degree of connectivity related to the probability that patches are colonized?
2) When insufficient connectivity constrains dispersal in fragmented habitat, habitat selection will deviate from optimal selection. Is habitat selection limited in landscapes with fragmented habitat?
3) When networks of patches can mitigate effects of habitat fragmentation by enhancement of the degree of connectivity, how can they be optimally allocated in agricultural landscapes that meets both the requirements for population sustainability and takes into consideration the suitability of the land for competing land uses?

This thesis provides scientific knowledge as foundation for the application of the spatial concept of ecological networks. The first and second research questions contribute to the problem detection of fragmentation effects: is dispersal a problem in fragmented habitat? For the species for which this is true, an understanding of metapopulation dynamics is crucial for effective conservation. The third research question contributes to solutions for species which populations are affected by habitat fragmentation.

The research was restricted to deciduous forest fragments in Dutch agricultural landscapes. For this patch type, I focused on fragmentation and defragmentation effects in populations of the European nuthatch *Sitta europaea*. The majority of this thesis deals with the nuthatch as subject of study. In chapter 4, effects of differences in the degree of connectivity on colonization of empty patches by nuthatch populations are studied. In chapter 6, hypotheses about limited habitat selection in nuthatch populations in fragmented habitat were tested with empirical data. In chapter 7 and 8, the requirements of the nuthatch were used as guidelines for conservation planning based on two spatial allocation models. Although the nuthatch is not a red list species or its habitat is seriously threatened, it is a useful model species for my research. The nuthatch is a habitat specialist and sensitive for fragmentation of its habitat. I could illustrate the effects of habitat connectivity on colonization of empty patches and habitat selection and of defragmentation on population sustainability. Other species, birds, mammals, insects, may show similar effects of fragmentation and defragmentation of their habitat.

2 Connectivity and colonization in fragmented habitat

Effects of the degree of habitat connectivity on populations are the central theme in this thesis. Extensive empirical and theoretical research shows that the degree of habitat connectivity is an important feature for population dynamics in landscapes with fragmented habitat. Fragmented populations often show large fluctuations in density and can only survive if dispersal is sufficient to colonize empty patches (*e.g.*, Gilpin and Hanski 1991, Hansson 1991, Opdam 1991, Opdam *et al.* 1993, Taylor *et al.* 1993, Adler and Neurnberger 1994, Andrén 1994, 1996, Fahrig and Merriam 1994, With and Crist 1995, Hanski and Gilpin 1997). Then, local populations are connected as a metapopulation. The degree of connectivity is crucial in the metapopulation theory (Levins 1970, Opdam 1990, Hanski and Gilpin 1997).

The first research question contains actually two questions that are strongly connected. To investigate the effects of connectivity on colonization of empty patches, one should first determine what parameters for measuring the degree of connectivity should be used. As is enumerated in chapter 4, several parameters for the degree of connectivity exist. To assess the effects of fragmentation, the phenomena that will be explained, in my case colonization patterns, should be studied at the proper spatial scale. As in a sensitivity analysis, I varied the spatial scale of movement by nuthatches. Therefore, varying threshold distances were used beyond which it is assumed that the probability of successful dispersal rapidly decreases. As a result of varying the threshold distances, disjoint subsets of patches can be distinguished that differ in size (number of patches).

In spatial analysis, parameters that have their origin in the mathematical graph theory are often applied to measure the degree of connectivity of locations (or accessibility in geographical studies). In chapter 3, I derived parameters for the degree of connectivity of patches that can deal with the size and spatial configuration of the subset to which the patch is connected to. The degree of connectivity of the patches as measured by these parameters can be related to data of patch occupancy, colonization, pair success, etc. Moreover, the sum of the degree of connectivity of all patches in the landscape provides a measure for the overall degree of connectivity. Varying the threshold distance for which this overall degree of connectivity is calculated can give an indication of the critical threshold of the habitat configuration in the observed landscape. Species with dispersal behaviour that cannot bridge this threshold distance may deal with effects of constrained dispersal.

The parameters were used to study the relationships between colonization of empty patches by nuthatches and their degree of connectivity measured at different spatial scales. Further research may show if the graph-theoretical parameters are also useful in other spatially explicit studies on population responses.

A reduced tendency to dispersal or a limited dispersal capacity has not been demonstrated in nuthatches (Matthysen *et al.* 1995). However, several studies provide indirect evidence that dispersal success is not optimal in fragmented habitat (Van Dorp and Opdam 1987, Verboom *et al.* 1991, Enoksson *et al.* 1995, Matthysen and Currie 1996, Bellamy *et al.* 1997, 1998). In this thesis, I also showed indirectly that dispersal is constrained in fragmented habitat since colonization of empty patches depends on the degree of connectivity. Colonization probability is lower in patches with low degree of connectivity. The effects of connectivity on colonization underpin the metapopulation theory for nuthatch populations in fragmented habitat. This was also shown by Verboom *et al.* (1991), although they do not include difference in the spatial scale. It appeared that the degree of connectivity measured with the threshold distance of 2.4 to 3 km best explained the colonization patterns. These distances can be seen as an indication of the dispersal distances of nuthatches.

Knowledge about effects of the degree of habitat connectivity on colonization can be used in conservation planning. It implies that enhancing the degree of habitat connectivity in networks of patches, *i.e.*, by allocating stepping stones between the patches, may increase the colonization probability of these patches. This may support the relevance of networks of patches that enhance the population sustainability. When guidelines for conservation planning are needed to decide how much dispersal is enough, also other spatial determinants of population dynamics should be included, such as the size of the patches. The enlargement of the existing patches may result in a decrease of the extinction risk decreases and of the need for immigrants.

3 Limited habitat selection in fragmented habitat

Habitat selection in fragmented habitat was the second process studied in this thesis, which may be affected by the degree of connectivity. Understanding the factors affecting habitat selection has direct implications for the conservation of species living in fragmented habitat. When apparently suitable habitat in the fragments is unoccupied, one can question if the habitat quality is sufficient for breeding or individuals cannot find this habitat?

Differences in habitat quality and the effects on population level are often studied in the context of source-sink dynamics (Pulliam 1988, Pulliam and Danielson 1991, Pulliam 1996). However, variation in habitat quality and its influence on selection is rarely considered at landscape level (Lima and Zollner 1996). In metapopulations, patches are often assumed to have equal quality (but see Gyllenberg and Hanski 1997). In chapter 5, a theoretical study to habitat selection in patchy landscapes is presented. In this study, the responses of two species that differ in dispersal capacity are compared. I showed that patch selection depends on the degree of connectivity of the patches when the dispersal distance is small related to the distances between the patches. The selection of habitat by the model species with small dispersal distances is not optimal compared to what can be expected as optimal selection. This theoretical study generated the hypothesis that habitat selection is limited in fragmented habitat. I could test this hypothesis with empirical data of nuthatches in regions with fragmented habitat and with contiguous habitat.

For nuthatches, several studies demonstrate that the quality of fragments is sufficient for breeding (Matthysen and Currie 1996, Matthysen and Adriaensen 1998, Schotman in prep.). In chapter 6, we concluded that habitat selection is limited in nuthatch populations in fragmented habitat compared to populations in contiguous habitat. When the degree of habitat connectivity is low, the quality of the occupied territories related to the quality of the available territories is lower than in territories with high degree of connectivity, especially when the population level is low. We showed that on average a lower breeding success can be found in territories with low degree of connectivity. Among other factors such as increased demographic and environmental stochasticity, limited habitat selection in fragmented habitat may result in a lower growth rate and population density than in contiguous habitat.

Besides a lower colonization probability, limited habitat selection is the second indirect evidence in this thesis for constrained dispersal of nuthatches in fragmented habitat. Enhancing the degree of connectivity in networks of patches may increase the selection of habitat and the population density. This may positively affect population sustainability.

4 Allocating ecological networks in agricultural landscapes

In many planning efforts, it is assumed that ecological networks enhance the population sustainability. Therefore, one often refers to the metapopulation theory. Metapopulation theory provides answers to questions about the effects of spatial determinants on population dynamics that are relevant for conservation planning (chapter 2 and 7). For this thesis, I also took the metapopulation theory as starting point. Based on the results in this thesis and other research, it can be concluded that when it is shown that the degree of connectivity affects population dynamics, networks of patches contribute to the population sustainability of these species in fragmented habitat, especially when the habitat patches are small.

The third research question about how networks of patches can be allocated in agricultural landscapes is addressed in chapter 7 and 8. Therefore, we developed two spatial allocation models that plan new habitat considering ecological guidelines and the suitability of the land for competing land uses. The model MENTOR can modify the spatial arrangement of patches by adding new patches that may act as stepping stones. Chapter 7 showed that the allocation of stepping stones provide a higher percentage of occupied habitat. The model ENLARGE enlarges the existing sites. In chapter 8, the two models are presented. We were not able to compare the results of the two models. An interesting question for further research is under which conditions the allocation of stepping stones has a higher contribution to population sustainability than the enlargement of the existing sites.

Both the models MENTOR and ENLARGE can also be applied for other species with different spatial requirements at different spatial scales, *e.g.*, to assign the locations where hedgerows or herbaceous vegetation are needed for the population persistence of birds, mammals, insects, or the locations of new ponds for amphibians regarding the location of their winter habitat.

For sustainable multiple land use, knowledge about ecological effects of the land use is needed, including the future spatial claims of the land uses (Jongman 1996). Besides the ongoing environmental stress, important constraints for realizing Dutch nature policy are the availability and the price of the land as result of the claims of agriculture, urbanization and transportation (RIVM *et al.* 1997). Optimization of land use allocation is one of the possible solutions for conservation planning. This solution agrees with the trend of nature conservation by land owners and users. They are more and more involved in the management of nature reserves. For both nature conservation and agriculture, the objective is sustainable use of the land so that the benefits are considerable for nature conservation and the costs as low as possible for agriculture.

Spatial optimization models as presented in this thesis can be used if the configuration of habitat is not specified or new habitat can be added. Spatial optimization can provide alternative spatial layouts for ecological networks that meet the requirements of the species concerned. The alternatives can then be compared based on simulation by spatially explicit population models (Schippers *et al.* 1996, Verboom 1996, Hanski and Simberloff 1997). The combination of spatial allocation models and spatially explicit population models undoubtedly provide knowledge for the long-term conservation of populations. Note that the spatial allocation models should be used as a starting point for spatial planning not as a result of it.

5 Concluding remarks

The results of this study provide evidence that the degree of habitat connectivity is a crucial feature to constitute an ecological network. When networks of patches enhance the degree of habitat connectivity, positive effects on population sustainability can be expected. I could also give an indication at what spatial scale the degree of habitat connectivity affects the processes at population and individual level as observed for nuthatches.

In this thesis, I contributed to an improved problem detection of effects of habitat fragmentation and explore opportunities for defragmentation of habitat trough optimization of land use allocation in human-dominated landscapes. Several topics deserve more attention in future research to spatially explicit populations:

- Analysis of the effects of limited habitat selection in fragmented populations on population development.
- Development of metapopulation models that includes differences in habitat quality.
- Analysis of the conditions in terms of the amount or spatial configuration of habitat where either the allocation of stepping stones or the enlargement of existing sites is preferred as strategy for conservation planning in human-dominated landscapes.
- Extension of the reserve site selection problem for groups of species in human-dominated landscapes.

For a proper application of the knowledge about effects of fragmentation and defragmentation of habitat, it should be considered that the general characteristics of scientific knowledge are reduction and abstraction. Via analysis, the studied reality is reduced to one or a few aspects. In this research, these aspects are formulated in the three research questions. Abstraction is the simplifying of the complex reality to achieve understanding by observation, where variation in conditions of the studied phenomena is kept as constant as possible. These phenomena can occur everywhere when the conditions agree with the ones as selected in the research.

However, understanding and prediction do not necessarily guarantee control, since we can only stimulate the occurrence of phenomena as far as we are able to satisfy the necessary conditions. Other limitations of applying scientific knowledge can appear when empirical results are extrapolated beyond the observed range of variation in the variables. For example, extrapolation can be problematic to other geographical regions that differ in history of land development or in traits of species.

One way to bring scientific knowledge with all its uncertainties into planning is the use of guidelines and spatial concepts. These can serve as a bridge to translate knowledge into action. I provided knowledge that contributes to the spatial concept of ecological networks. The application of such scientific knowledge is surrounded by the uncertainty under what conditions guidelines and spatial concepts can be used. However, this deficient knowledge can still contribute to planning since uncertainty is a crucial aspect with which planners should deal with. They ask questions like 'what will be dominant developments in the future, what do we know about the processes that should be intervened?'. The opportunities to know and direct future developments are limited. Modelling alternative land use plans as advocated in this thesis can be used to explore these opportunities. With the knowledge about the effects of fragmentation and defragmentation, this study may be a step forward to enhance and preserve biodiversity.

SUMMARY

Summary

In agricultural landscapes, the habitat of many species is subject to fragmentation. When the habitat of a species is fragmented and the distances between patches of habitat are large relative to the movement distances of the species, it can be expected that the degree of habitat connectivity affects processes at population and individual level. In this thesis, I report on a study of effects of habitat fragmentation and opportunities to mitigate these effects by planning ecological networks. The objective of the study is to contribute to an improved knowledge about the effects of fragmentation and defragmentation of habitat on populations, in particular effects of differences in the degree of habitat connectivity on colonization and habitat selection. The main question of the research was: do networks of patches contribute to population sustainability of species in fragmented habitat?

The development of planning for nature in the Netherlands is sketched in the second chapter. It is illustrated with the spatial concepts for the rural areas that landscape planning became landscape ecological based. After this chapter, I addressed three questions that were derived from the main question.

The first question was: what variables can measure the degree of connectivity of habitat patches and are the differences in the degree of connectivity related to the colonization probability of patches? Therefore, habitat patches and the distances between these patches were modelled as networks. In landscapes with fragmented habitat for a certain species, these networks appear as so-called nonconnected networks consisting of disjointed subsets of patches. Between these subsets, exchange of individuals happens seldom of never. We derived parameters that measure the degree of connectivity of the patches in those networks. The parameters can deal with the size (the number of elements) and the spatial configuration of these subsets. One of the parameters was used to investigate the relationship between the degree of connectivity measured at different spatial scales and colonization of unoccupied patches by the nuthatch *Sitta europaea* in three regions in the Netherlands. To vary the spatial scale, I used threshold distances as maximum dispersal distances for which the degree of habitat connectivity was calculated. Habitat patches are assumed to be connected when the distances between the patches are less than this threshold distance. The degree of habitat connectivity measured for threshold distances of approximately 2.4 to 3 km best explains the differences in the colonization probability of unoccupied patches. These threshold distances give an indication of the distances covered by dispersing nuthatches that led to successful colonizations. Moreover, I could give an indication of the range of threshold distances where effects of constrained dispersal can be expected in the three regions.

The second question was: is habitat selection limited in landscapes with fragmented habitat? Therefore, effects of the degree of habitat connectivity on the selection of territories were investigated. Based on a spatially explicit individual-based model, it could be hypothesized that habitat selection is limited when the degree of connectivity is low. This hypothesis was tested with empirical data of nuthatches in four regions in the Netherlands. One of the regions can be considered as the reference region with contiguous habitat where dispersal is not constrained. The habitat quality for nuthatches could be measured by the mean trunk diameter of oaks and beeches. We concluded that selection of territories is limited in fragmented habitat compared to selection in contiguous habitat. The quality of the occupied territories in fragmented habitat is lower than in contiguous habitat. This is especially the case when the population level is low. We showed that a lower average breeding success can be found in territories with low degree of connectivity. The results indicate the absence of a negative feedback between population level and the average breeding success in fragmented habitat, which contributes to the increased extinction probability of populations. Among other factors, limited habitat selection in fragmented habitat may thus result in a lower population density than in contiguous habitat.

The degree of habitat connectivity can increase due to the allocation of new habitat. This may mitigate the effects of fragmentation. The third question was: how can networks of patches be optimally allocated in agricultural landscapes that both meets the requirements for population sustainability and takes into consideration the suitability of the land for competing land uses? We developed two spatial allocation models that plan new habitat considering ecological guidelines of minimum patch sizes and maximum threshold distances and the suitability of the land for competing land uses. The model MENTOR adds new patches that may act as "stepping stones" between reserve sites. The model ENLARGE enlarges existing sites. We showed that both the allocation of stepping stones and the enlargement of existing sites provide a higher percentage of occupied habitat. An interesting question for further research is under which conditions either the allocation of stepping stones or the enlargement of existing sites is preferred as strategy for conservation planning in human-dominated landscapes.

The results of the research provide evidence that the degree of habitat connectivity determines both the colonization probability of unoccupied patches and the selection of habitat. They also give an indication at what spatial scale the degree of habitat connectivity affects these processes as observed for nuthatches. When through networks of patches the degree of habitat connectivity can be enhanced, positive effects on population sustainability can be expected. This thesis contributes to an improved problem detection of effects of habitat fragmentation and explores opportunities for defragmentation of habitat and optimization of land use allocation in human-dominated landscapes. With the knowledge about the effects of fragmentation and defragmentation, this study may be a step forward to enhance and preserve biodiversity.

SAMENVATTING

Samenvatting

Als gevolg van ontwikkelingen in het landgebruik kan het leefgebied (of het habitat) van een planten- of diersoort worden versnipperd. Versnippering betekent voor deze soort dat het habitat te vinden is in kleine plekken die vaak ver van elkaar liggen. Bovendien is het gebied tussen de habitatplekken vaak ongeschikt voor het doortrekken, rusten of foerageren. Naast te kleine leefgebieden, kan versnippering problematisch zijn als de afstanden tussen de habitatplekken relatief groot zijn vergeleken met de afstanden die individuen kunnen afleggen. In dergelijke situaties mag worden verwacht dat de mate van verbinding van habitatplekken van invloed is op processen zoals kolonisatie van onbezette plekken en de selectie van habitat. De mate van verbinding (of de "connectivity") van de habitatplekken houdt in dat uitwisseling van individuen tussen deze plekken mogelijk is.

In dit proefschrift wordt verslag gedaan van een onderzoek naar effecten van habitatversnippering en mogelijkheden om deze effecten tegen te gaan door de planning van ecologische netwerken. Een ecologisch netwerk is een verzameling van plekken met habitat voor een bepaalde soort die in zekere mate met elkaar verbonden zijn doordat individuen van deze soort zich van de ene plek naar de andere kunnen verplaatsen.

Het doel van dit onderzoek is het vermeerderen van kennis over effecten van versnippering van habitat en het tegengaan van deze effecten, met name over de effecten van variatie in de mate van verbinding van de habitatplekken op kolonisatie en habitatselectie. De centrale vraag van het onderzoek was: dragen netwerken van habitatplekken bij aan de duurzaamheid van populaties van soorten in versnipperd habitat?

In hoofdstuk 2 is de ontwikkeling van planning voor natuur in Nederland geschetst. De ontwikkeling dat de ruimtelijke planvorming meer en meer werd onderbouwd door de landschapsecologie is geïllustreerd aan de hand van de ruimtelijke planconcepten voor de landelijke gebieden. (Een planconcept is een idee hoe de ruimte zou kunnen worden ingericht.)

In de volgende hoofdstukken worden drie vragen behandeld die zijn afgeleid van de centrale vraag.

De eerste vraag was: welke variabelen kunnen worden gebruikt om de mate van verbinding van habitatplekken te meten en zijn verschillen in de mate van verbinding gerelateerd aan de kans dat deze plekken worden gekoloniseerd? Om deze vraag te beantwoorden werden de habitatplekken en de afstanden tussen deze plekken gemodelleerd als netwerken. In landschappen met versnipperd habitat bestaan deze netwerken uit deelverzamelingen van habitatplekken waartussen niet of zelden uitwisseling van individuen plaats vindt. We leidden variabelen af die de mate van verbinding van habitatplekken in dergelijke netwerken kunnen meten. Deze variabelen baseren de mate van verbinding op de omvang (het aantal elementen) en de ruimtelijke configuratie van de deelverzamelingen van habitatplekken. Eén van de variabelen is gebruikt om de relatie te onderzoeken tussen de mate van verbinding van de habitatplekken gemeten op verschillende ruimtelijke schaalniveau's en de kolonisatie van de plekken door de boomklever *Sitta europaea* in drie regio's in Nederland. De boomklever is een zangvogel van oude loofbossen. Het habitat van boomklevers in een cultuurlandschap is vaak versnipperd. Voor het variëren van de ruimtelijke schaal heb ik gebruik gemaakt van grenswaarden voor de afstand tussen plekken waarover dispersie (eenmalige verplaatsingen naar een voortplantingsgebied) nog kan plaats vinden. Verondersteld werd dat tussen habitatplekken een verbinding mogelijk is als de afstand tussen deze plekken kleiner is dan de grenswaarde voor de dispersie-afstand. De mate van verbinding van habitatplekken gemeten met grenswaarden voor de dispersie-afstand tussen 2,4 en 3 km verklaart het best de verschillen in kolonisatiekans van onbezette habitatplekken. Deze grenswaarden geven een indicatie van de afstanden afgelegd door boomklevers die hebben geleid tot succesvolle kolonisaties. Bovendien kon ik voor de drie regio's een indicatie geven van de dispersie-afstanden waarbij effecten van versnippering te verwachten zijn.

De tweede vraag was: is habitatselectie beperkt in landschappen met versnipperd habitat? Om deze vraag te beantwoorden zijn de effecten van de mate van verbinding van het habitat op de selectie van territoria onderzocht. Met behulp van een ruimtelijk expliciet model dat het gedrag van individuen simuleert, kon de hypothese worden afgeleid dat habitatselectie beperkt is wanneer de mate van verbinding laag is. Deze hypothese is getest met empirische gegevens over boomklevers in vier regio's in Nederland. Eén van deze regio's kan worden beschouwd als de referentieregio met aaneengesloten habitat waar dispersie niet beperkt is. De kwaliteit van het habitat van boomklevers kon worden beschreven met behulp van de stamdikte van eiken en beuken. We concluderen dat selectie van territoria door boomklevers in versnipperd habitat beperkt is vergeleken met de selectie in aaneengesloten habitat. De gemiddelde kwaliteit van de bezette territoria in versnipperd habitat is lager dan van de bezette territoria in aaneengesloten habitat. Dit is met name het geval als het populatieniveau laag is. We lieten zien dat in territoria met een lage mate van verbinding gemiddeld een lager broedsucces wordt gevonden. Deze resultaten geven een indicatie dat een negatieve feedback tussen het populatieniveau en het gemiddeld broedsucces afwezig is in versnipperd habitat, hetgeen bijdraagt aan de toegenomen kans op extinctie van een populatie. Naast andere factoren kan deze beperkte habitatselectie in versnipperd habitat leiden tot een lager populatieniveau dan in aaneengesloten habitat.

De mate van verbinding van het habitat kan toenemen door het plaatsen van additionele habitatplekken. Hierdoor kunnen effecten van habitatversnippering worden tegengegaan. De derde vraag was: hoe kunnen netwerken van habitatplekken optimaal worden geplaatst in cultuurlandschappen zodat ze voldoen aan zowel de eisen voor een duurzame populatie als rekening houden met de ruimtelijke claims van andere landgebruiksvormen? We ontwikkelden hiervoor twee ruimtelijke allocatiemodellen die nieuw habitat kunnen plannen, waarbij rekening wordt gehouden met ecologische richtlijnen voor minimale omvang van plekken en maximale afstanden ertussen en met de geschiktheid van het gebied voor concurrerende landgebruiksvormen. Het model MENTOR voegt nieuwe habitatplekken toe die als "stepping stones" tussen natuurgebieden kunnen worden gebruikt. Deze stepping stones zijn kleine habitatplekken tussen bestaande gebieden die kunnen worden gebruikt voor verplaatsingen tussen deze gebieden. Het model ENLARGE vergroot bestaande natuurgebieden. We lieten zien dat zowel het plaatsen van stepping stones als het vergroten van bestaande gebieden resulteren in een hoger percentage van bezet habitat. Een interessante vraag voor vervolgonderzoek is onder welke condities ofwel de plaatsing van stepping stones ofwel het vergroten van bestaande natuurgebieden de beste strategie is voor het natuurbeleid in cultuurlandschappen.

De resultaten van het onderzoek bieden het bewijs dat de mate van verbinding van het habitat zowel de kolonisatiekans van onbezette plekken als de selectie van habitat bepalen. Ze geven ook een indicatie op welk ruimtelijk schaalniveau de mate van verbinding invloed heeft op deze processen zoals is bestudeerd voor de boomklever. Zodra door netwerken van habitatplekken de mate van verbinding van de plekken kan worden verhoogd, kunnen positieve effecten op de duurzaamheid van populaties worden verwacht. Dit proefschrift draagt bij aan de kennis voor het vaststellen van effecten van habitatversnippering en verkent mogelijkheden voor het tegengaan van deze effecten en het optimaliseren van het landgebruik in cultuurlandschappen. Met de kennis over de effecten van habitatversnippering en het tegengaan van deze effecten is dit onderzoek een stap voorwaarts in het streven om de biodiversiteit te verhogen en te bewaren.

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Curriculum vitae

François van Langevelde was born on 30 August 1968 in Oosterhout (Noord-Brabant, the Netherlands). In 1987, he graduated from the secondary school Nassau Scholengemeenschap in Breda (the Netherlands). The same year, he started his study Land and Water Use (Cultuurtechniek) at the Wageningen Agricultural University (the Netherlands). During his graduate studies, he did research projects at the (former) departments Agricultural Economics, Physical Planning and Rural Development, Nature Conservation, and Vegetation Science, Plant Ecology & Weed Science of this university. He obtained his Ir-degree, equivalent to MSc, *cum laude* in 1993.

After graduation, he directly started as a researcher in training (Aio) his doctoral research that resulted in this thesis. For this research, he spent three months in 1993 at the department of Environmental Planning of the Arizona State University in the United States. During the period as Aio, he supervised graduate students and contributed to several courses. From 1997 to 1998, he worked as a landscape ecologist at the Laboratory for Soil and Groundwater Research of the National Institute of Public Health and the Environment (RIVM). He is currently appointed as a postdoc applied mathematics in the FLARE-project (Fundamentals of African Rangeland Economies in Kenya and Burkina Faso) at the Tropical Nature Conservation and Vertebrate Ecology Group of the Wageningen Agricultural University.