



ELSEVIER

Landscape and Urban Planning 58 (2002) 281–295

LANDSCAPE  
AND  
URBAN PLANNING

www.elsevier.com/locate/landurbplan

## Two strategies for conservation planning in human-dominated landscapes

Frank van Langevelde<sup>a,b,\*</sup>, Frits Claassen<sup>c</sup>, Alex Schotman<sup>b</sup>

<sup>a</sup>Department of Environmental Sciences, Land Use Planning Group, Wageningen University, Generaal Foulkesweg 13, 6706 BJ Wageningen, The Netherlands

<sup>b</sup>Department of Landscape Ecology, Alterra Green World Research, P.O. Box 47, 6700 AA Wageningen, The Netherlands

<sup>c</sup>Department of Social Sciences, Operations Research and Logistics Group, Wageningen University, Hollandseweg 1, 6706 KN Wageningen, The Netherlands

### Abstract

This paper discusses the modelling of two strategies for conservation planning in human-dominated landscapes: the enlargement of existing reserve sites and the allocation of stepping stones between these sites. We developed two spatial allocation models that plan new habitat according to these strategies, considering simple ecological rules of thumb to meet the requirements for population sustainability and the suitability of the land for competing land use. The model ENLARGE enlarges the existing sites. The model MENTOR modifies the spatial arrangement of patches by adding new patches that may act as stepping stones between reserve sites. These two models result in different habitat configurations. Both the allocation of stepping stones and the enlargement of existing sites provide a higher percentage of occupied habitat. These models may help to address the question 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. © 2002 Elsevier Science B.V. All rights reserved.

*Keywords:* Allocation model; Spatial optimisation; Habitat fragmentation; Reserve site selection; Metapopulation

### 1. Introduction

Due to the present land use, the habitat of many species is decreased in area and quality and fragmented. When species were not able to adapt to these changes, their numbers declined or they disappeared (Saunders et al., 1991; Andr n, 1994). The decline in biodiversity lead to diverse actions to maintain and improve the remaining nature reserves (Noss et al., 1997). Conservation planning in these human-dominated landscapes

can apply several types of interventions, e.g. to maintain or improve the quality of the reserve sites (the abiotic conditions for plants or the 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. Extensive 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

\* Corresponding author. Tel.: +31-317-477969; fax: +31-317-424988.

E-mail address: f.vanlangevelde@alterra.wag-ur.nl (F. van Langevelde).

discussion: 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)? There are no general guidelines here, but guidelines for a specific case depend on species and landscape characteristics that determine which factors are essential for survival (Frank and Wissel, 1998).

The number and size of the remaining reserves have often become small and they are isolated (Kalkhoven et al., 1995; Hanski et al., 1996). They cannot guarantee persistence of the populations of some species. Local populations of these species are small, exchange of individuals is hampered and local extinction frequently occurs. When there is still a certain exchange of individuals between the remaining sites, local population can survive since they act as part of a metapopulation (Hanski, 1998). Based on these insights, 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). However, it is often not possible to plan large reserves in human-dominated landscapes. The intensity of the use, the availability of the land and the claims of competing land use appear to be limiting factors (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; Csuti et al., 1997). We focus 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 their colonisation probability. For each strategy, we developed a spatial allocation model: ENLARGE for the enlargement strategy and MENTOR for the stepping-stone strategy. In both models, the allocation is based on simple ecological rules of thumb and the suitability of the land for competing land use. In van Langevelde et al. (2000), we briefly discussed the model MENTOR. In this paper, we explain the principles of both models in detail and give some results.

## 2. Modelling competing land uses in conservation planning

### 2.1. Conservation planning in human-dominated landscapes

In human-dominated landscapes, spatial claims of nature conservation and of competing land use, such as agriculture, urbanisation, infrastructure, may conflict. The RSSP should deal with these competing land use (Nevo and Garcia, 1996; Nantel et al., 1998; van Langevelde et al., 2000). In the RSSP, spatial planning can play a role through optimisation of land use allocation. In this context, optimisation of land use allocation aims to enhance the biodiversity through the selection of a reserve network with minimum disadvantages for the competing land uses. 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 woodlots in agricultural landscapes. These 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 these forest fragments are affected by the size of the fragments and the distance to other forest fragments (van Dorp and Opdam, 1987; Enoksson et al., 1995; Bellamy et al., 1998). From the group of birds related to mature deciduous forests, the European nuthatch *Sitta europaea* shows strong effects of area and connectivity on presence (van Dorp and Opdam, 1987; Verboom et al., 1991; Enoksson et al., 1995; Hinsley et al., 1998). If the landscape provides conditions for stable nuthatch populations, we can also expect that most other forest birds are present. We considered the nuthatch as an umbrella species for other forest birds (*sensu* Simberloff, 1998). Therefore, the ecological rules of thumb to allocate habitat using both models were based on the requirements of the nuthatch. In van Langevelde et al. (2000), 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 the distinguished size classes of habitat patches

From (ha)	To (ha)	
	1–3	>3
1–3	1 km	3 km
>3	3 km	3 km

So, our models are 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). 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.

2.2. Minimising the competition with other land use

It may be obvious that the competition between nature conservation and other land uses will be stronger if 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 optimisation 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. (2000). 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 territory of the species concerned. For each gridcell, we determined the suitability for deciduous forest and dairy farming. The position of each gridcell  $g_{ij}$  is represented by its co-ordinates  $(i, j)$  in which  $i = \{1, \dots, m\}$  and  $j = \{1, \dots, n\}$ . The set of gridcells  $G$  is defined as  $G := \{g_{11}, \dots, g_{mn}\}$ .

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

$$\max \left\{ Z = \sum_{(i,j) \in G_b} [Wh Sh_{ij} x_{ij} + Wa Sa_{ij}(1 - x_{ij})] \right\} \tag{1}$$

subject to:

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

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

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

The integer programming problem formulated in Eqs. (1)–(3) with a single constraint (2) is well known as a so-called knapsack problem (Williams, 1990, 1993; Hillier and Lieberman, 1995). This category of problems can be solved efficiently with dynamic programming (Bellman, 1957). The subset  $G_b$  is different for the allocation of stepping stones and for the enlargement of existing sites. In the next section, 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)

The integer programming problem formulated in Eqs. (1)–(3) extended with constraint (4a) provides a model for the stepping stone strategy, while extended with constraint (4b), it is a model for the enlargement strategy.

Without the constant  $\sum(Wa Sa_{ij})$ , the objective function of Eq. (1) can be rewritten as

$$\max \left\{ Z' = \sum_{(i,j) \in G_b} (Wh Sh_{ij} - Wa Sa_{ij}) x_{ij} \right\} \quad (5)$$

For each gridcell  $g_{ij}$ , the term  $(Wh Sh_{ij} - Wa Sa_{ij})$  in Eq. (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 optimisation criterion for minimising the competition between allocating new habitat and agriculture. van Langevelde et al. (2000) 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., 2000).

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. dairy 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 farm-type 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 existing 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 for conservation planning in human-dominated landscapes

#### 3.1. 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 populations of the species concerned, 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 source 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.

Although the problem in Eq. (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  $10 \times 10$  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.

Let us assume that  $n$  source areas can be distinguished. In the first step, also  $n$  blocks that contain a source area can be distinguished. If two or more source areas are located within one block, the question is if these source areas should be considered separately. The subset  $G_b \subset G$  encloses 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 or 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 follows.

DO FOR all pairs of source areas

- Step 1 Determine the subset  $G_b \subset G$  and  $SV_{\min} = \min_{(i,j)} \{SV | g_{ij} \in G_b\}$
- 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  $G_d := \{g_{ij} \in G_b | SV_{ij} \leq SV_{\min}\}$  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  $g_{ij} = \max_{(i,j)} \{g_{ij} | g_{ij} \in G_d\}$  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  $\Delta SV$  has a crucial impact on the objective value  $Z$  (Eq. (1)) and the computational effort. High values of  $\Delta SV$  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., 2000 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  $\Delta SV$ , the value for  $\Delta SV$  decreased as calculated by  $\Delta SV = (5 - SV_{\min})/5$ . The minimum value for  $\Delta SV$  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.

### 3.2. 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 Eq. (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 maximises overall effectiveness, in our case, the objective value  $Z$  (Eq. (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  $k = 1, \dots, K$  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 Eq. (2)). In advance, which sites will be enlarged with a certain amount of habitat is unknown.

The recursive relationships are defined as

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

$$V_k(t_k) = \begin{cases} \max_{x_k \in G_{T,k}} \{ \mathbf{SV}^T(G_{T,k}) \mathbf{x}_k + V_{k+1}(t_k - \mathbf{x}_k^T \mathbf{l}) \} & \text{for } k = K - 1, K - 2, \dots, 0 \\ 0 & \text{otherwise} \end{cases} \tag{7}$$

in which the term  $V_K(t_K)$  represents the value function of the final stage  $K$ , the transposed vector  $\mathbf{SV}^T(G_{T,k})$  denotes the subtracted values  $\mathbf{SV}_{ij}$  of all gridcells in the subset  $G_{T,k}$ ,  $\mathbf{x}_k \in \mathbb{R}^n$  in stage  $k$  and the transpose  $\mathbf{x}_k^T$  are the decision vectors consisting of the binary decision variables  $x_{ij}$ ,  $\mathbf{l}$  is a vector which elements are all equal to 1, the term  $(t_k - \mathbf{x}_k^T \mathbf{l})$  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  $k = 1, \dots, K - 1$ ). Suppose that the site  $k$  has the size of 1 gridcell with the co-ordinates  $(i, j)$  and one gridcell can be added to this site, than the subset  $G_{1,k}$  for the decision vector  $\mathbf{x}_k^T = (1, 0, \dots, 0)$  is defined as

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

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  $G_{2,k}, \dots, G_{T-1,k}$  for the decision vectors  $\mathbf{x}_k^T = (1, 1, 0, \dots, 0)$  to  $\mathbf{x}_k^T = (1, 1, \dots, 1)$  can be determined in a similar way. The final set  $G_{T,k}$  is defined as  $G_{T,k} = G_{1,k} \cup G_{2,k} \cup \dots \cup G_{T-1,k}$ . 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  $\mathbf{SV}(G_{T,k})$  have to be determined for all stages  $k = 1, \dots, K - 1$ . 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  $\mathbf{SV}_{ij}$ . 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

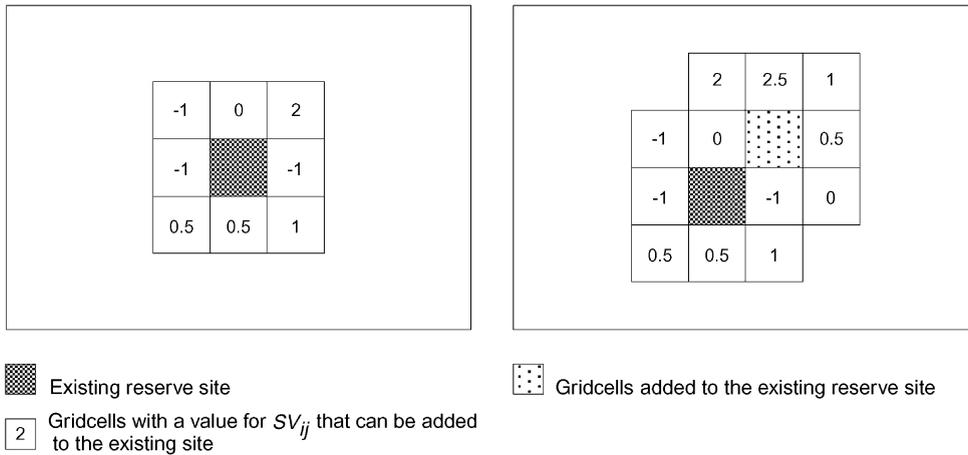


Fig. 1. Selection of the gridcells that can be added to the existing reserve site. The gridcell with the highest value for the subtracted value  $SV_{ij}$  (see text for explanation) is selected to be added to the reserve site. The subset of gridcells increases from which the second gridcell will be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

selected (see Fig. 1). The following algorithm describes the determination of the set  $G_{t,k}$  and the related vector  $\mathbf{SV}(G_{T,k})$ .

Step 1 Set  $G_{0,k} := \{\emptyset\}$  and vector  $\mathbf{SV}^T(G_{T,k}) = (0, \dots, 0)$

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 Eq. (8)

Determine the  $t$ th element  $SV_t(G_{T,k})$  of  $\mathbf{SV}(G_{T,k})$  by

$$SV_t(G_{T,k}) = \max_{(i,j) \in G_{T,k}} \{SV_{ij}\} \tag{9}$$

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

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

END FOR

END FOR

In case two or more adjacent gridcells in the subset  $G_{t,k}$  have the maximum value for  $SV_{ij}$  (Eq. (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  $\mathbf{SV}(G_{T,k})$ .

However, the relationships in (7) do not consider any possible overlap between the stages. As the recursive relationships maximise 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 follows.

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., 2000). Therefore, we used ENLARGE to enlarge the sites in the resulting reserve network.

#### 4. Some 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., 2000). 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).

In Fig. 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 Fig. 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,

Table 2

The number of habitat patches and amount of habitat (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.)<sup>a</sup>

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

<sup>a</sup> 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 ( $W_a = 0.9$ ). Scenario 2 represents a dairy farm-type with less intensive use and a high priority given to nature conservation ( $W_h = 0.9$ ). The number of patches in the present situation is 100 ha and the amount of habitat is 741 ha with 77% optimal habitat.

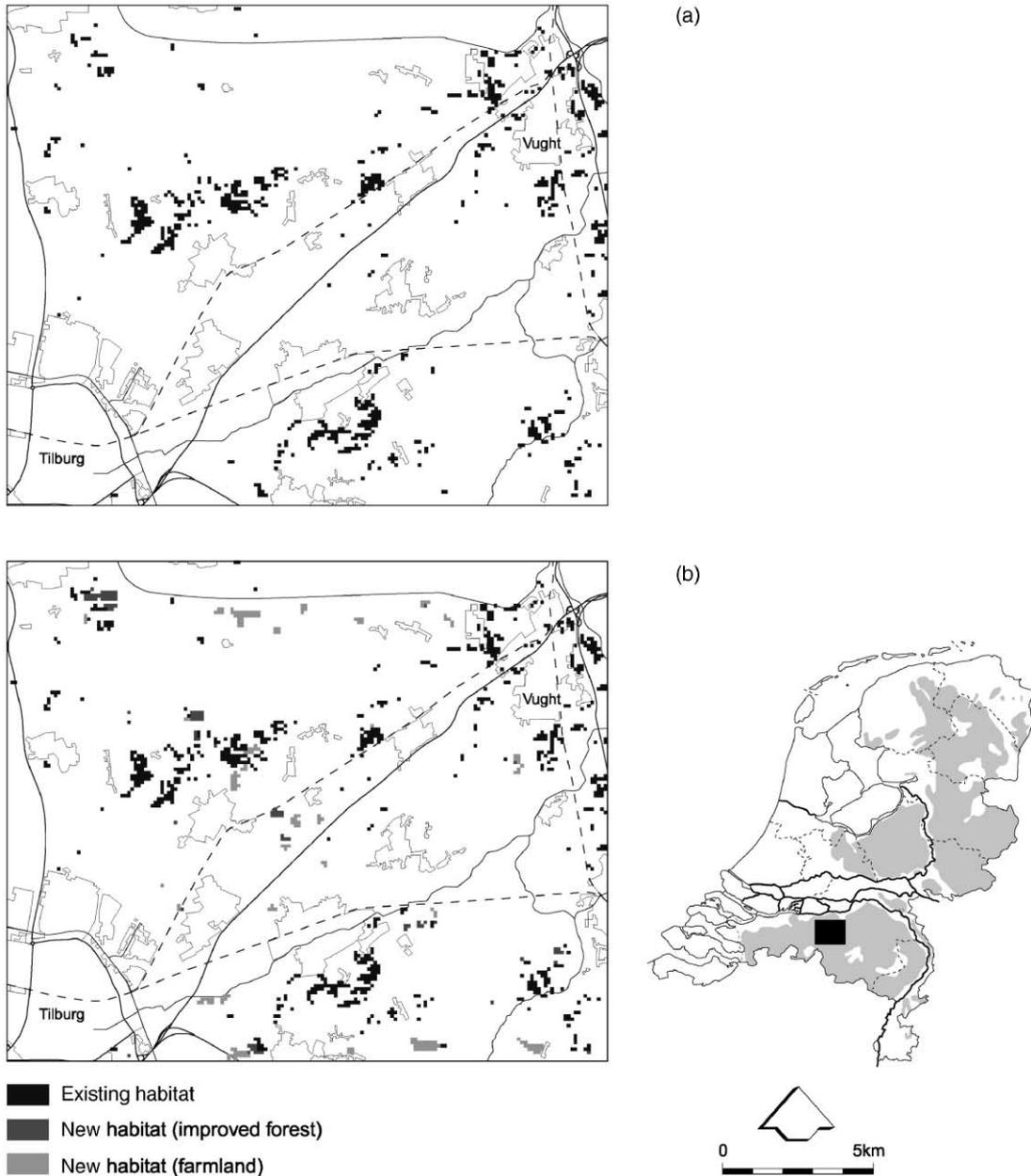
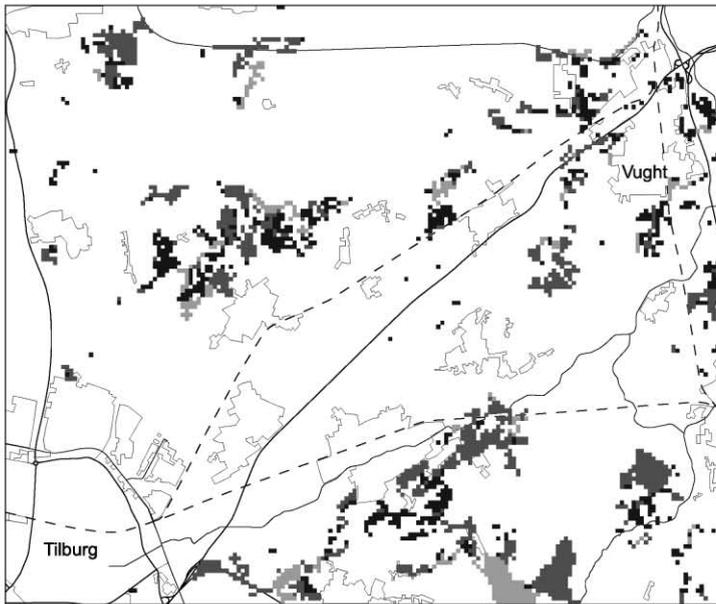
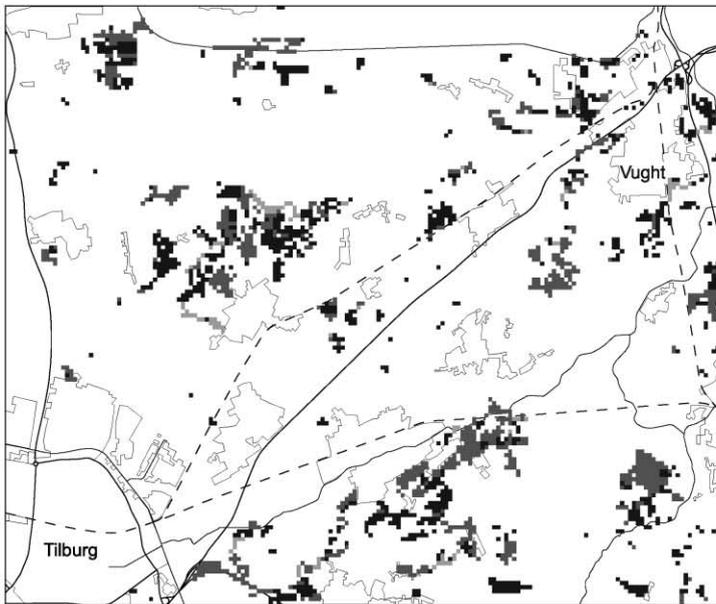


Fig. 2. The present situation (a) and the resulting habitat configurations (b) and (e) from the model MENTOR for the stepping-stone strategy, and (c) and (f) from the model ENLARGE for the enlargement strategy. The habitat configurations (b) and (e) were improved by ENLARGE resulting in (d) and (g). 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, realised 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.



(c)



(d)

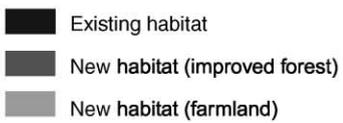
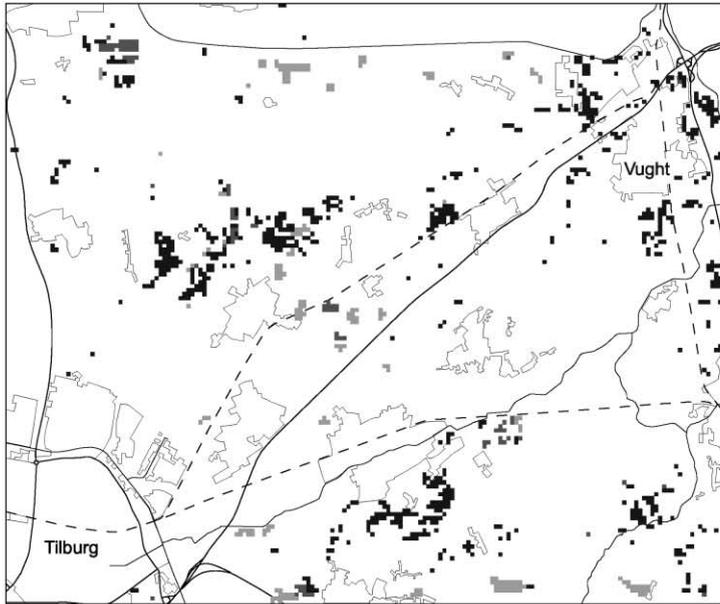
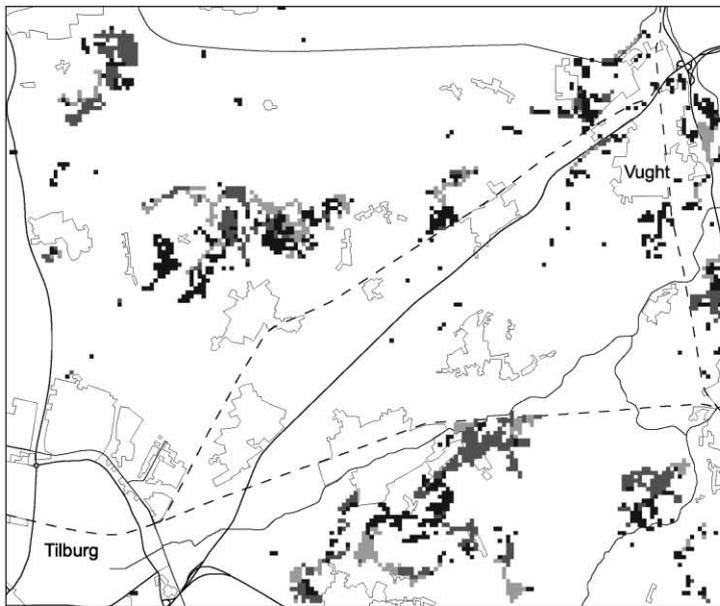


Fig. 2. (Continued).



(e)



(f)

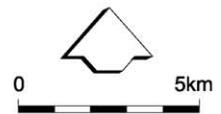
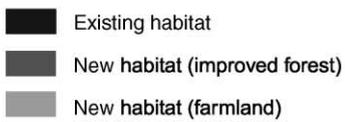


Fig. 2. (Continued).

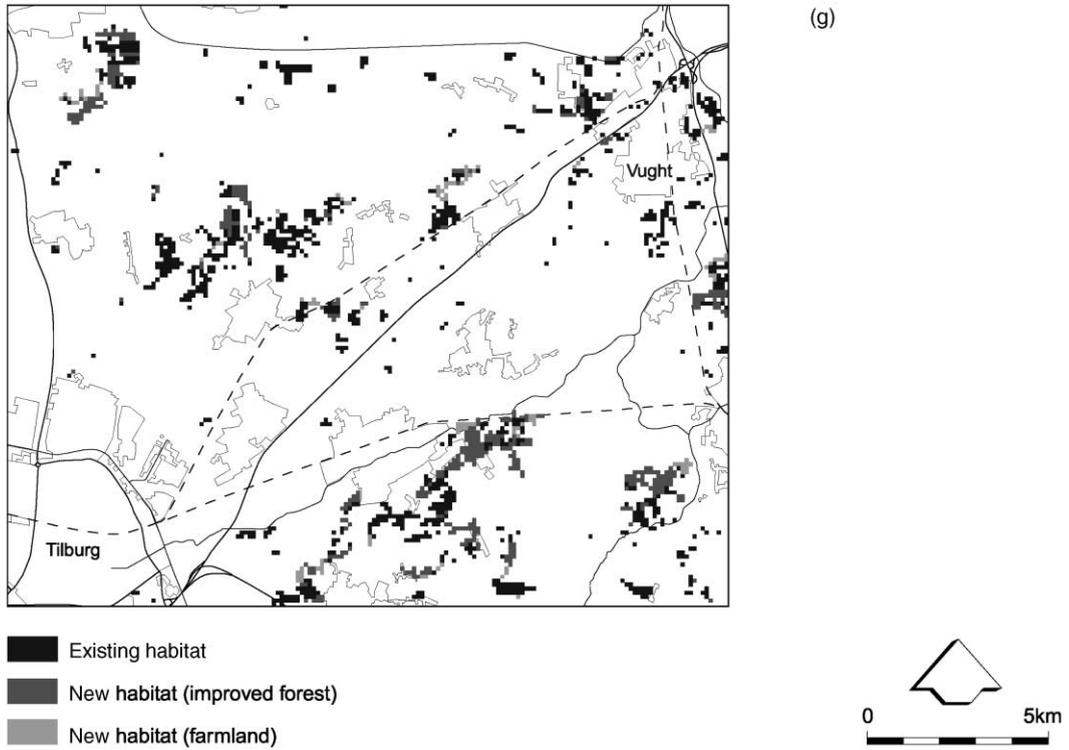


Fig. 2. (Continued).

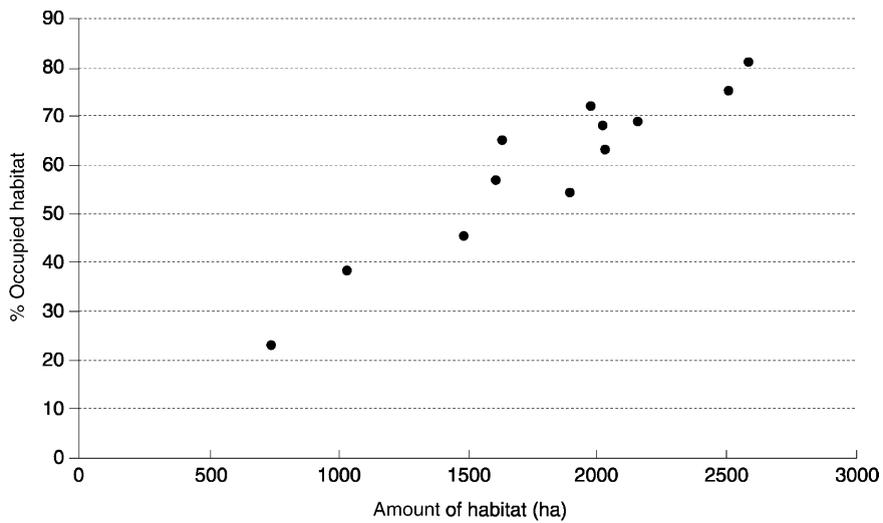


Fig. 3. Relationship between the amount of habitat in the configurations corrected for differences in habitat quality (Table 2) and the percentage of occupied habitat (Table 3).

Table 3

The percentage of occupied habitat resulting from METAPHOR in the present situation (23) and the two scenarios as result of MENTOR for the stepping-stone strategy, ENLARGE for the enlargement strategy, and a combination of both (Comb.)<sup>a</sup>

Scenario		T		
		198	330	660
1	MENTOR	38	–	–
	ENLARGE	54	69	81
	Comb.	–	63	75
2	MENTOR	38	–	–
	ENLARGE	45	65	68
	Comb.	–	57	72

<sup>a</sup> See Table 1 for further explanation.

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.

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 Fig. 3.

## 5. Discussion

In this paper, we present two spatial optimisation models for conservation planning in human-dominated landscapes. These models were developed for two different strategies in conservation planning: one strategy focuses on the enlargement of existing reserve sites and the other strategy on the allocation of stepping stones between these sites. The model ENLARGE enlarges the existing sites. The model MENTOR modifies the spatial arrangement of patches by adding new patches that may act as stepping stones between reserve sites. These models may help to address the relevant question 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.

Spatial optimisation 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. If the RSSP 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) can be applied (see Csuti et al., 1997 for a review of these selection algorithms). In contrast to other reserve selection approaches, our models minimise the competition between interventions to add new habitat and competing land uses.

The model MENTOR was developed with the ecological rules of thumb derived from the population dynamics of the nuthatch (van Langevelde et al., 2000). Here, the allocation of stepping stones depend on the threshold distances between pairs of habitat patches and the minimum size of the sites. The model ENLARGE is not directly linked to the guidelines for one species. Species specific requirements in ENLARGE are represented by the distance from the boundary of existing reserve sites and the gridcells with new habitat. In our application, the gridcells with new habitat should be allocated at the boundary of the existing sites (see Fig. 1). Both models can be applied for other patch types and for other species.

To illustrate the two models, we applied them in the study area 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 number 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 differs between the scenarios (Fig. 2). For a proper comparison of the effects of both strategies on population performance, two issues should be reconsidered related to our present analysis. First, we allowed new habitat to be realised 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 realised 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 issue 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 result 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, 1999), 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 (Fig. 3). When the amount of habitat is relatively low, stepping stones are recognised to play a role in increasing connectivity of empty patches and reducing extinction of local populations (Fahrig and Merriam, 1985; Lefkovich 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; Venier and Fahrig, 1996; Fahrig, 1998; van Langevelde, 1999). Then, the necessity of stepping stones to facilitate the exchange of individuals between the existing patches decreases.

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. 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. The output of the models can be used as a baseline against which future developments in land use may be evaluated. They may provide a useful tool for landscape planners and ecologists to explore the relative merits of alternative land use plans.

## Acknowledgements

We like to thank Leo Aarnink, Paul van Beek, Teun Jansen, Rob Jongman, Anke Keuren, Joke van Lemmen-Gerdessen, Hubert van Lier, Jan Smits and Gerard Sparenburg for their contributions.

## References

- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportion of suitable habitat: a review. *Oikos* 71, 355–366.
- Bedward, M., Pressey, R.L., Keith, D.A., 1992. A new approach for selecting fully representative reserve networks: addressing efficiency, reserve design and land suitability with an iterative analysis. *Biol. Conserv.* 62, 115–125.
- Bellamy, P.E., Brown, N.J., Enoksson, B., Firbank, L.G., Fuller, R.J., Hinsley, S.A., Schotman, A.G.M., 1998. landscape structure and climate on local distribution patterns of the nuthatch (*Sitta europaea* L.). *Oecologia* 115, 127–136.
- Bellman, R.E., 1957. *Dynamic Programming*. Princeton University Press, New York.
- Blake, J.G., Karr, J.R., 1984. Species composition of bird communities and the conservation benefit of large versus small forests. *Biol. Conserv.* 30, 173–187.
- Cook, E.A., van Lier, H.N. (Eds.), 1994. *Landscape Planning and Ecological Networks*. ISOMUL 6F, Elsevier, Amsterdam.
- CPB, 1992. *Scanning the Future: A Long-Term Scenario Study of the World Economy*. SDU, The Hague.
- Csuti, B., Polasky, S., Williams, P.H., Pressey, R.P., Camm, J.D., Kershaw, M., Kiester, A.R., Downs, B., Hamilton, R., Huso, M., Sahr, K., 1997. A comparison of reserve selection algorithms using data on terrestrial vertebrates in Oregon. *Biol. Conserv.* 80, 83–97.
- Dannenbring, D.G., Starr, M.K., 1981. *Management Science: An Introduction*. McGraw-Hill, New York.
- De Groot, N.S.P., van Hamsvoort, C.P.M.C., Rutten, H. (Eds.), 1994. *Voorbij het Verleden. Drie Toekomstbeelden voor de Nederlandse Agribusiness, 1990–2015*. LEI-DLO, The Hague.
- Diamond, J.M., 1975. The island dilemma: lessons of modern biogeographic studies for the design of nature reserves. *Biol. Conserv.* 7, 129–146.
- Enoksson, B., Angelstam, P., Larsson, K., 1995. Deciduous forest and resident birds: the problem of fragmentation within a coniferous forest landscape. *Landscape Ecol.* 10 (5), 267–275.
- Fahrig, L., 1998. When does fragmentation of breeding habitat affect population survival? *Ecol. Model.* 105, 273–292.
- Fahrig, L., Merriam, G., 1985. Habitat patch connectivity and population survival. *Ecology* 66, 1762–1768.
- Forman, R.T.T., 1995. *Land Mosaics: The Ecology of Landscapes and Regions*. Cambridge University Press, Cambridge.
- Frank, K., Wissel, C., 1998. Spatial aspects of metapopulation survival—from model results to rules of thumb for landscape management. *Landscape Ecol.* 13, 363–379.
- Frankel, O.H., Soulé, M.E., 1981. *Conservation and Evolution*. Cambridge University Press, Cambridge.

- Gilpin, M.E., Diamond, J.M., 1980. Subdivision of nature reserves and the maintenance of species diversity. *Nature* 285, 567–568.
- Hanski, I., 1998. Metapopulation dynamics. *Nature* 396, 41–49.
- Hanski, I., Thomas, C.D., 1994. Metapopulation dynamics and conservation: a spatially explicit model applied to butterflies. *Biol. Conserv.* 68, 167–180.
- Hanski, I., Moilanen, A., Gyllenberg, M., 1996. Minimum viable metapopulation size. *Am. Nat.* 147, 527–541.
- Harrison, S., Fahrig, L., 1995. Landscape pattern and population conservation. In: Hansson, L., Fahrig, L., Merriam, G. (Eds.), *Mosaic Landscapes and Ecological Processes*. IALE-Studies in Landscape Ecology, Vol. 2. Chapman & Hall, London, pp. 293–308.
- Higgs, A.J., Usher, M.B., 1980. Should nature reserves be large or small? *Nature* 285, 568.
- Hillier, F., Lieberman, G.J., 1995. *Introduction to Operations Research*, 6th Edition. McGraw-Hill, New York.
- Hinsley, S.A., Bellamy, P.E., Fry, G., Gabrielsen, L., McCollin, D., Schotman, A., 1998. Geographical and land-use influences on bird species richness in small woods in agricultural landscapes. *Global Ecol. Biodivers. Lett.* 7, 125–135.
- Hobbs, R.J., 1992. The role of corridors in conservation: solution or bandwagon? *Trends Ecol. Evol.* 7, 389–392.
- Hof, J., Flather, C.H., 1996. Accounting for connectivity and spatial correlation in the optimal placement of wildlife habitat. *Ecol. Model.* 88, 143–155.
- Hof, J., Raphael, M.G., 1997. Optimisation of habitat placement: a case study of the Northern Spotted Owl in the Olympic Peninsula. *Ecol. Appl.* 7 (4), 1160–1169.
- Kalkhoven, J.T.R., van Apeldoorn, R.C., Foppen, R.P.B., 1995. Fauna en natuurdoeltypen minimumoppervlakte voor kernpopulaties van doelsoorten zoogdieren en vogels. IBN-report 193, Wageningen.
- Keuren, A., 1995. Ontwikkeling van model voor toewijzing van gronden aan landbouw en natuur. Department of Mathematics, Agricultural University, Wageningen.
- Lamberson, R.H., Noon, B.R., Voss, C., McKelvey, K.S., 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the Northern Spotted Owl. *Conserv. Biol.* 8, 185–195.
- Lefkovich, L.P., Fahrig, L., 1985. Spatial characteristics of habitat patches and population survival. *Ecol. Model.* 30, 297–308.
- Lindenmayer, D.B., Possingham, H.P., 1996. Modelling the interrelationships between habitat patchiness, dispersal capability and metapopulation persistence of the endangered species, Leadbeater's possum, in south-eastern Australia. *Landscape Ecol.* 11, 79–105.
- Margules, C.R., Nicholls, A.O., Pressey, R.L., 1988. Selecting networks of reserves to maximise biological diversity. *Biol. Conserv.* 43, 63–76.
- Murphy, D.D., Noon, B.R., 1992. Integrating scientific methods with habitat conservation planning: reserve design for Northern Spotted Owls. *Ecol. Appl.* 2 (1), 3–17.
- Nantel, P., Bouchard, A., Brouillet, L., Hay, S., 1998. Selection of areas for protecting rare plants with integration of land use conflicts: a case study for the west coast of Newfoundland, Canada. *Biol. Conserv.* 84, 223–234.
- Nevo, A., Garcia, L., 1996. Spatial optimisation of wildlife habitat. *Ecol. Model.* 91, 271–281.
- Noss, R.F., O'Connell, M.A., Murphy, D.D., 1997. *The Science of conservation planning. Habitat conservation under the Endangered Species Act*. Island Press, Washington, DC.
- Opdam, P., van Apeldoorn, R., Schotman, A., Kalkhoven, J., 1993. Population responses to landscape fragmentation. In: Vos, C.C., Opdam, P. (Eds.), *Landscape Ecology of a Stressed Environment*. IALE-Studies in Landscape Ecology, Vol. 1. Chapman & Hall, London, pp. 145–171.
- Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. *Biol. Conserv.* 1, 18–30.
- Simberloff, D., 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? *Biol. Conserv.* 83, 245–257.
- Simberloff, D., Farr, J.A., Cox, J., Mehlman, D.W., 1992. Movement corridors: conservation bargains or poor investments? *Conserv. Biol.* 4, 493–504.
- van Dorp, D., Opdam, P.F.M., 1987. Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecol.* 1, 59–73.
- van Langevelde, F., 1999. Habitat connectivity and fragmented nuthatch populations in agricultural landscapes. Ph.D. Thesis, Agricultural University, Wageningen.
- van Langevelde, F., Schotman, A., Claassen, F., Sparenburg, G., 2000. Competing land use in the reserve site selection problem. *Landscape Ecol.* 15, 243–256.
- Venier, L.A., Fahrig, L., 1996. Habitat availability causes the species abundance–distribution relationship. *Oikos* 76, 564–570.
- Verboom, J., 1996. *Modelling Fragmented Populations: Between Theory and Application in Landscape Planning*. IBN Scientific Contributions 3, Wageningen.
- Verboom, J., Schotman, A., Opdam, P., Metz, J.A.J., 1991. European nuthatch metapopulations in a fragmented agricultural landscape. *Oikos* 61, 149–156.
- Williams, H.P., 1990. *Model Building in Mathematical Programming*. Wiley, New York.
- Williams, H.P., 1993. *Model Solving in Mathematical Programming*. Wiley, New York.

**Frank van Langevelde** is currently working as Postdoc at the Department of Landscape Ecology, Alterra Green World Research. He is interested in spatial aspects of population and community ecology. This paper is part of his PhD thesis “Habitat connectivity and fragmented nuthatch populations in agricultural landscapes” defended in 1999 at Wageningen University.

**Frits Claassen** teaches Operations Research (OR) and Logistics at Wageningen University. His main interests include the application of quantitative methods and decision support systems to real-life problems.

**Alex Schotman** is Landscape Ecologist at the Department of Landscape Ecology, Alterra Green World Research. His specialisation is in the field of population responses to landscape fragmentation, in particular, in birds. He studied the effects of habitat fragmentation on the European Nuthatch (*Sitta europaea*).