

Scale of habitat connectivity and colonization in fragmented nuthatch populations

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Studies of effects of landscape pattern on population dynamics should consider the spatial scale at which habitat connectivity varies relative to the spatial scale of the species' behavioral response. In this paper, I investigate the relationship between the degree of connectivity of wooded patches measured at different spatial scales and the colonization of these patches by nuthatch *Sitta europaea* populations. I used different threshold distances to calculate the degree of habitat connectivity. A threshold distance is the distance beyond which the probability of successfully bridging the distance by dispersing individuals is assumed to decrease rapidly. The sum of the degree of connectivity over all patches in a region provides a measure for the overall degree of connectivity. Based on this measure, I could first give an indication under what conditions species may experience effects of constrained dispersal in that region. Second, the degree of connectivity of the individual patches was related with the observed colonizations of these patches. The degree of habitat connectivity measured for threshold distances of ca 2.4–3 km best explains the colonization probability of unoccupied patches. These threshold distances give an indication of the distances covered by dispersing nuthatches that led to successful colonizations.

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When the habitat of a species is spatially subdivided, the degree of habitat connectivity is assumed to be an important landscape feature that determines population dynamics (e.g., Fahrig and Merriam 1985, Verboom et al. 1991, Hanski 1994, Schumaker 1996, Gustafson and Gardner 1996, With et al. 1997). In this context, connectivity is the property of habitat patches to maintain exchange of individuals with other habitat patches (Taylor et al. 1993). Due to a low degree of connectivity, dispersal between habitat patches may be constrained. As predicted by metapopulation theory, one of the effects of reduced habitat connectivity is a decrease in the colonization probability of patches (Verboom et al. 1991, Hanski 1994, Hanski and Gilpin 1997). When studying effects of landscape pattern on population responses, however, it is necessary to explic-

itly consider the spatial scale at which habitat connectivity varies relative to the spatial scale of the species' behavioral responses (Fahrig 1992, Doak et al. 1992, Vail 1993, Wiens 1995).

The objective of this paper is to investigate effects of habitat connectivity measured at different spatial scales on population dynamics. Therefore, I used colonization of wooded patches by European nuthatch *Sitta europaea* populations in regions with 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. There is empirical evidence that nuthatch populations are affected by this fragmentation (Van Dorp and Opdam 1987, Verboom et al. 1991, Enoksson et al. 1995, Matthysen and

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Currie 1996, Bellamy et al. 1998). Verboom et al. (1991) already showed that the presence of nuthatch populations in fragmented habitat differed from the predictions based on a 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 of habitat connectivity.

There is often uncertainty about the movement distances of the species concerned in subdivided habitat, e.g., for nuthatches see Matthysen et al. (1995). In this paper, I tested the null hypothesis that the degree of connectivity does not explain colonization of unoccupied habitat patches. For the nuthatches, the degree of connectivity of a patch was measured as a function of the number, size and location of the other patches occupied by nuthatches. First, I used this measure for the degree of connectivity of patches to investigate under what conditions effects of constrained dispersal can be expected in a certain region. Second, the degree of connectivity of patches was related with the observed colonizations of these patches by nuthatches. When an effect of the degree of habitat connectivity on colonization by nuthatches could be demonstrated, I tried to identify the spatial scale at which colonization can be best explained by the degree of connectivity of the patches.

Materials and method

Study regions and time series

The three study regions, Midden Brabant, Zuidwest Drenthe and Noordoost Twente, have wooded patches in a matrix of farmland, predominantly grassland and maize (Fig. 1). In these regions, the area of suitable habitat is < 5% of the total study area. To map the nuthatch habitat in the regions, data of the Dutch national forest statistics were used (Anon. 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 forests is considered as a habitat patch. When the woodlots are < 200 m apart, they were joined to one patch. The size of a patch was defined as the area covered by deciduous forest in the patch. Patches containing < 1 ha habitat were considered too small and excluded from the analysis (cf. Verboom et al. 1991). Figure 2 shows the nearest-neighbor distances and the size of the patches.

Time series of territory occupancy by nuthatches in the breeding season were available for the three re-

gions: from 1990 to 1992 for Midden Brabant by Post et al. (unpubl.), from 1982 to 1995 for Zuidwest Drenthe by Van Dijk (unpubl.), and from 1988 to 1994 for Noordoost Twente by 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. Colonization was recorded when a patch was unoccupied in the breeding season of a certain year and occupied in the breeding season of the next year. 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). In this context, a graph is a geometrical figure consisting of points (vertices) and lines (edges) that connect some of these points. The habitat patches in the regions were considered as vertices in such a network and the relationships between the patches 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, more than one distance should be investigated. I analyzed a range of distances to determine what distance best explains the observed patterns.

Varying the threshold distances when constructing the graphs results in different scales of fragmentation (Fig. 3). With low threshold distance, disjointed subsets of habitat patches can then be distinguished. When subsets are disjointed, the assumption is that a patch in one subset has no functional relationship with a patch in another subset. The size of the subsets is the number of vertices in it (Van Langevelde et al. 1998).

Measuring the degree of habitat connectivity

In this paper, I consider graphs with n vertices and m edges. The length of the edges w_{ij} between two vertices i and j is measured in kilometers. 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. (1998) derived matrix-based parameters for the degree of connectivity of the individual patches. These parameters deal with the distance to

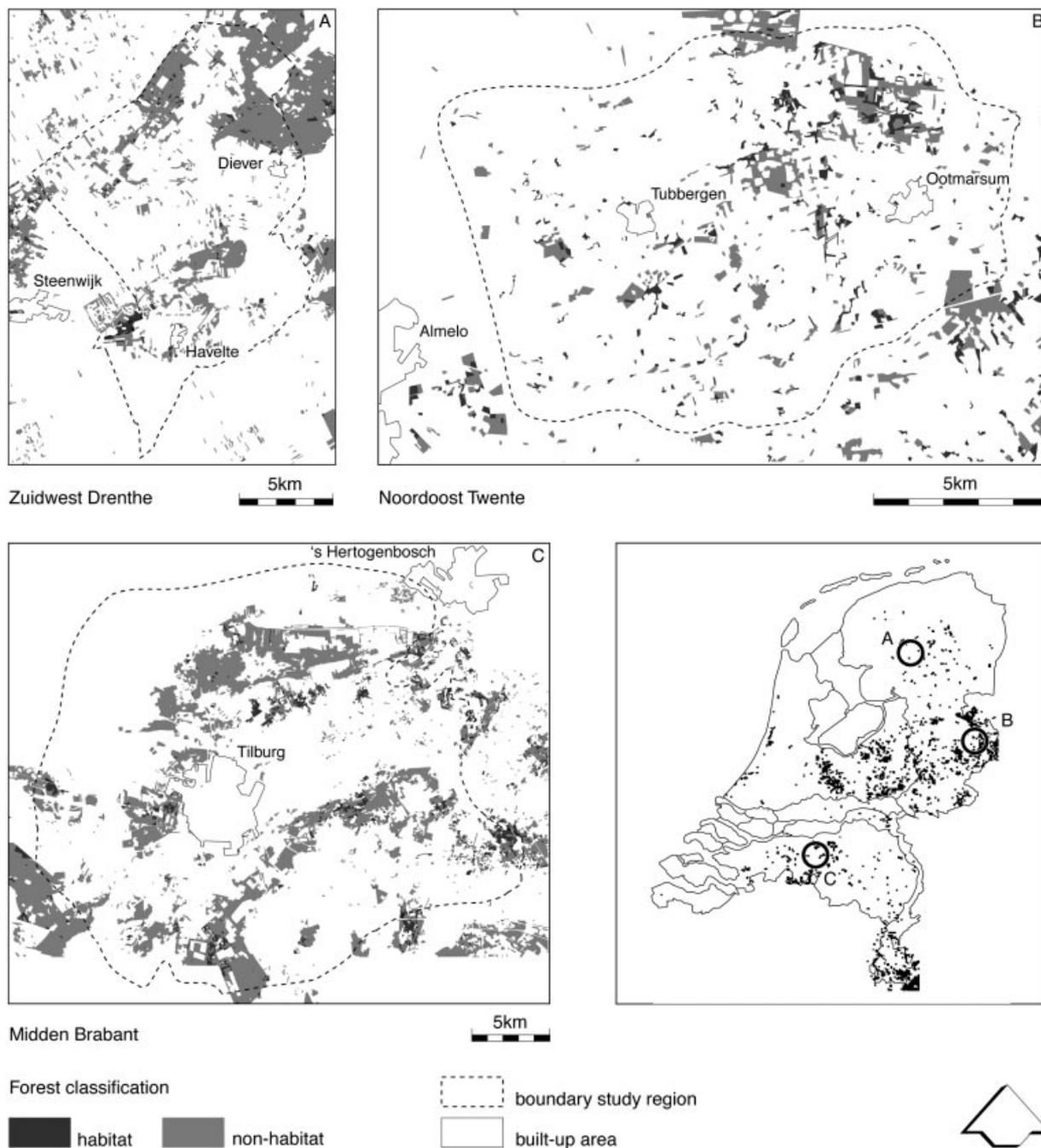
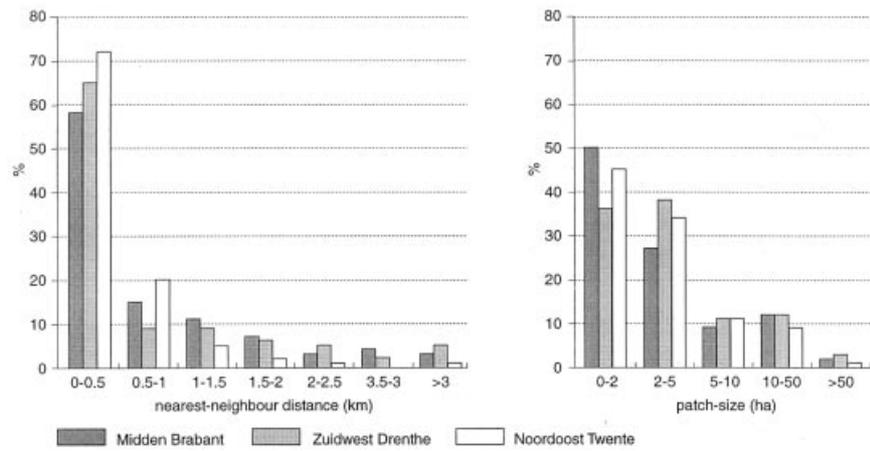


Fig. 1. The three study regions Zuidwest Drenthe (A), Noordoost Twente (B) and Midden Brabant (C) with fragmented habitat for the nuthatch *Sitta europaea*. The location of the regions is indicated on the map with deciduous forests in The Netherlands. In Zuidwest Drenthe 66 habitat patches were distinguished,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

Fig. 2. Percentage of patches per class of nearest-neighbor distances and of patch sizes in the three study regions.



other patches and the size and spatial configuration of the subset to which the habitat patches are connected. To measure the degree of habitat connectivity, the matrix S' is defined, $S' = (s'_{ij})$. This matrix provides the shortest-weighted paths between pairs of vertices: where s'_{ij} is the reciprocal of the cumulative edge length of the shortest path between two vertices i and j , $s'_{ij} = 1/\Sigma w_{ij}$. To measure the degree of connectivity of the vertices, the vector s' can be obtained by multiplying matrix S'

with the vector 1

$$s' = S'1 \quad (1)$$

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

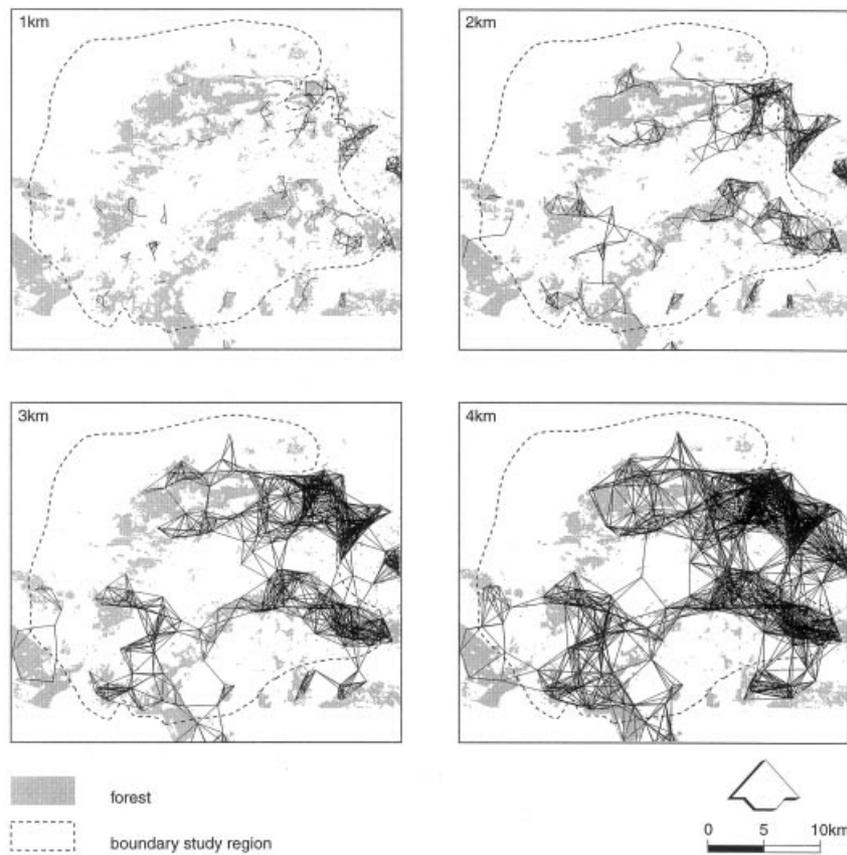


Fig. 3. Some graphs of the nuthatch habitat network in Midden Brabant for the threshold distances 1, 2, 3 and 4 km. The vertices in the graphs represent the centers of the habitat patches. An edge between two vertices indicates that the distance between the vertices is less than or equal to the specified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

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 patch 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 b can be calculated in the same way as shown in eq. (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 s' with 1 (Van Langevelde et al. 1998)

$$\hat{s}' = s'^T \mathbf{1} \quad (2)$$

The dispersion \hat{s}' is a property of the distribution of inter-patch or inter-network distances in a certain region.

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 center 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 analysis

With logistic regression, the presence or absence of a colonization of a patch 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. Since differences between the regions exist in population level and size of the region (which affect the connectivity parameter s'_{ij}), the regions were added as binary factors in the regression analyses. The size of the patches, A_i , 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. 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 individuals which led to successful colonizations.

Results

For each threshold distance, the dispersion \hat{s}' was calculated based on the degrees of connectivity s'_i of the

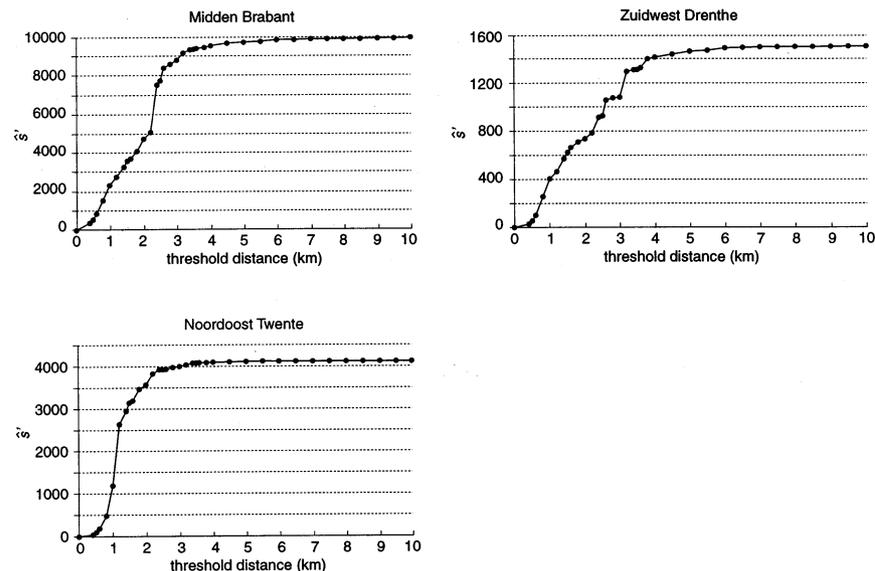


Fig. 4. The dispersion \hat{s}' or overall degree of connectivity of habitat patches for the European nuthatch in the three study regions calculated for different threshold distances.

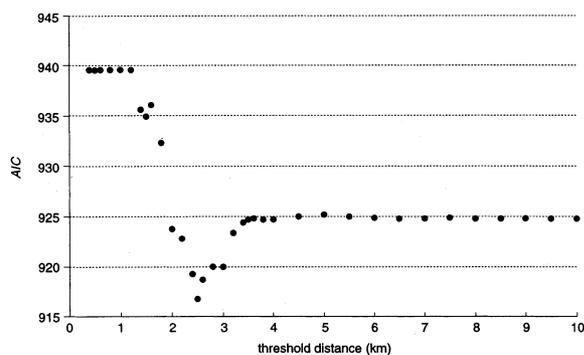


Fig. 5. The values for the Akaike's Information Criterion (AIC) of the regression models for colonization where the degrees of connectivity b_i calculated for the different threshold distances were added one by one. The minimum model to which b_i was added contained the size of the patches, the region 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) based on the threshold distance of 2.5 km. 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; $R_{adj}^2 = 21\%$).

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
$A_i \times NT$	0.582 (0.139)	***

individual habitat patches for these distances. In Fig. 4, the dispersion \hat{s}' for the set of patches with deciduous forest is presented per study region. In the study regions, the amount and spatial configuration of this habitat type is assumed to be constant, whereas the threshold distance to construct the graphs is varied. The absolute value of \hat{s}' depends upon the number of patches and the distances between them (Van Langevelde et al. 1998). The change in the value of \hat{s}' with the threshold distances provides an indication of the change in overall degree of habitat connectivity in a region. I assumed that the mean dispersal distances of species correspond with certain threshold distances. Then, one can derive the range of dispersal distances for which the habitat type in a certain region can be considered as fragmented. Thus, where effects of constrained dispersal can be expected.

For the studied habitat type in the three regions, the dispersion \hat{s}' is relatively constant for the threshold distances larger than ca 3.5 km (Fig. 4). This means that if the mean dispersal distance of forest species is more

than this distance, the habitat can be considered as not fragmented. The resulting distance may be partly explained by the lack of data about habitat and the occupation of nuthatches > 3 km outside the study regions. The main reason is that 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. 1998).

When a species found in deciduous forests has a dispersal distance above this threshold of 3.5 km, the forests in Midden Brabant can be considered as 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 ca 4 km and in Noordoost Twente ca 2.5 km. The latter region is less fragmented from the point of view of habitat connectivity. (This region has on average the smallest nearest-neighbor distances, see Fig. 2).

To investigate the effects of constrained dispersal on colonization of patches by nuthatches in those regions, Fig. 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 threshold distances between 0.4 and 10 km is: not significant for b_i calculated for threshold distances < 1.4 km; $p < 0.05$ for b_i calculated for threshold distances between 1.4 and 1.6 km; $p < 0.01$ for b_i calculated for the threshold distance of 1.8 km; $p < 0.001$ for b_i calculated for the threshold distances > 1.8 km (two sided t-test).

The models with the degrees of connectivity b_i calculated for the threshold distances 2.4–3 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, this 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. The degree of connectivity b_i calculated for threshold distances > 3 km still significantly explains colonization. With higher threshold distances, also the potential influx of individuals from remote patches determines the degree of connectivity of a certain patch. As argued above, the potential influx of individuals from nearby patches remains high relative to the one from remote patches.

The results also show that the colonization probability of large patches in Noordoost Twente is higher than of smaller ones. 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 or less competition for holes and predation. In Noordoost Twente, Schotman (unpubl.) 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 may be due to the relatively low degree of connectivity of the patches in these regions (Figs 2 and 4): nuthatches are not able to locate and select territories in large patches better than in small patches (Van Langevelde 1999).

Discussion

Conditions where dispersal is constrained

The results give an indication under what conditions species may experience effects of constrained dispersal in the studied regions. As is shown in Fig. 4, relatively small changes in the threshold distances may lead to large changes in the overall degree of connectivity. When the mean dispersal distance of a species is less than the threshold distances in this range, reduced colonization probability of unoccupied patches due to constrained dispersal can be expected. Several studies show that there are thresholds in the landscape for population persistence (e.g., Andr en 1994, 1996, With and Crist 1995, Gustafson and Gardner 1996, Metzger and D ecamps 1997, Keitt et al. 1997, With et al. 1997). Mostly by theoretical studies, it is shown that there are critical thresholds in the degree of habitat connectivity beyond which movement through the landscape suddenly becomes unlikely. When the degree of connectivity of the patches is calculated at different spatial scales as in this paper, it can be expected that such critical thresholds will be revealed as a property of the studied habitat distribution in the region. One can then assess for which species this habitat may be fragmented since one species may perceive a given habitat distribution as highly fragmented (dispersal distances are less than the critical threshold in \hat{s}) while the distribution appears relatively connected to others that interact with the landscape at another spatial scale. Such analysis may address questions like "what species groups can be expected when the observed habitat type is spatially subdivided at certain spatial scale?"

Effects of the degree of habitat connectivity on colonization

The results of the regression analyses for the nuthatch data 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 ca 1.4 km or more (Fig. 5). Regarding the values for AIC, the degrees of connectivity calculated for threshold distances between 2.4 and 3 km best explain the colonization patterns. I rejected the null hypothesis because the degree of connectivity explains the colonization of unoccupied habitat patches by nuthatches.

The results agree with the study of Verboom et al. (1991). They found that the colonization probability of unoccupied patches depends upon 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 Meeuwssen 1994, Enoksson et al. 1995). They also use the amount of habitat in a radius of several kilometers around the patch of observation.

The reason for the analyses of the nuthatch data in this paper is that uncertainty exists about the dispersal behavior 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 kilometers: 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 nestlings disperse at least 3 km from the natal territory. Matthysen et al. (1995) could not estimate an actual distance distribution due to the small sample size, but conclude that the median dispersal distance of must be several km at least in highly fragmented habitat. 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 1999) 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 the dispersal behavior is to assume that an indication of the covered distances can be derived from colonization patterns obtained with long-term observations.

Measuring the degree of connectivity

For such studies, information should be available about dispersal rate and distances, and about the behavior of dispersing individuals in relation to landscape pattern. 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, Schumaker 1996, Schippers et al. 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 then often related to 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: 1) the number or size of sources, or the area of habitat within a certain distance (Verboom et al. 1991, Vos and Stumpel 1995); 2) the distance to the nearest occupied patch and its size or local population size (Gustafson and Gardner 1996); 3) the distances to all occupied patches and their sizes or local populations (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. This parameter can then be used to explicitly incorporate the spatial scale in measuring the degree of habitat connectivity, when the size of the subsets of connected patches varies due to different threshold distances.

In general, the approach is suitable for matching a certain population characteristic that reflects the dispersal process with the degree of connectivity of patches. Depending on the dispersal characteristics of the species concerned, also other patch-specific parameters can be considered, such as size, shape, quality, permeability of patch boundaries. I considered solely the size of the patch. Besides a judgement on whether a certain wooded patch is suitable or not, the quality of a patch is often difficult to determine. In literature, there is no evidence that parameters such as patch shape and permeability can be considered as relevant for nuthatches. 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. This may provide a refined measure of the degree of connectivity of individual patches.

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