Spatial Ecology of the Three-Toed Woodpecker in Managed Forest Landscapes

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The effects of landscape structure and forestry on the abundance and dynamics of boreal forest bird species have been studied widely, but there are relatively few studies in which the spatial structure and quality of the landscape have been related to the spatial ecology of bird species. In this paper, we present methods to measure territory and landscape quality for the three-toed woodpecker *(Picoides tridactylus)* and similar territorial forest bird species based on data from the Finnish multi-source national forest inventory and metapopulation theory. The three-toed woodpecker was studied with territory mapping within an area of 340 square km in southern Finland in 1987–2000. Altogether 195 breeding territory sites were observed. The spatial occurrence of the territories was aggregated, and the highest densities were observed in spruce-dominated old-growth forest areas. Both territory and landscape quality had significant consequences for the occurrence of the three-toed woodpecker. The spatial patterning and permanence of breeding and non-breeding territories were influenced by a combination of spatial dynamics of the species and the quality of the landscape, the latter being much influenced by forestry. The landscape-level spatial occurrence of the three-toed woodpecker in the study area may represent source-sink dynamics. The results of this paper suggest the presence of threshold values at different spatial scales, which may determine the occurrence of the three-toed woodpecker and similar species in managed forest landscapes.

Keywords three-toed woodpecker, territory quality, landscape quality, critical threshold value, metapopulation theory, metapopulation capacity, Finnish National Forest Inventory

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1 Introduction

The habitat preferences and large-scale abundance changes of many boreal forest bird species are relatively well known (v. Haartman et al. 1963–72, Cramp et al. 1977–94, Hagemeier and Blair 1997, Väisänen et al. 1998). The effects of forestry on breeding bird communities have been studied intensively during the past decades (in Finland see e.g. Järvinen et al. 1977, Haila et al. 1980, Helle and Järvinen 1986, Virkkala 1987). There is, however, a relatively small number of studies in which the spatial structure and quality of the landscape have been related to the spatial patterning and dynamics of bird species (Mykrä et al. 2000). In such studies the population ecology and appropriate spatial scales for the species have to be known along with reliable and relevant habitat and landscape data, which makes such studies laborious and difficult to conduct. These studies have, however, proven to be important in increasing our understanding about the population patterns and processes in fragmented landscapes, as demonstrated e.g. by studies on the Spotted Owl *(Strix occidentalis)* in North America (Lande 1988, Thomas 1993), the Capercaillie *(Tetrao urogallus)* in northern Europe (Rolstad and Wegge 1989) and the Nuthatch *(Sitta europea)* in western Europe (Verboom et al. 1991, Van Langevelde 2000).

The three-toed woodpecker *(Picoides tridactylus* (L.)) is a polytypic, widespread woodpecker species that prefers mature, often mixed or conifer-dominated forests with dead or dying trees for feeding and breeding. The species is predominantly a primary hole-nester, relatively resident with some irregular movements usually in autumn and specialised to use bark beetles and other insects found in dead and decaying trees (v. Haartman et al. 1963–72, Dementev and Gladkov 1966, Hogstad 1970, Cramp 1985, Virkkala 1991, Stenberg 1996, Hagemeier and Blair 1997, Fayt 1999). Although the three-toed woodpecker is often considered to be an old-growth forest species, it is probably adapted to natural disturbance dynamics in boreal forests with forest fires and windfalls, which can occasionally produce large amounts of dead wood for its prey insects (Blackford 1955, Yeager 1955, Koplin 1972, Crockett and Hansley 1978, Virkkala et al. 1991, Sorvari 1994, Fayt 1999).

A decreasing trend has been observed in many breeding populations of the nominate subspecies *(P. t. tridactylus)* of northern Europe during the past decades. These population declines, which are probably caused by loss of suitable habitat and the decrease in the quality of the remaining habitat due to forestry practices, indicate problems for the persistence of viable populations in modern managed forest landscape (Dementev and Gladkov 1966, Virkkala et al. 1991, 1994, Nilsson et al. 1992, Stenberg and Hogstad 1992, Angelstam and Mikusiński 1994, Tucker and Heath 1994, Edenius and Elmberg 1996, Väisänen et al. 1998, Svensson et al. 1999).

We present here methods to measure territory and landscape quality for the three-toed woodpecker and other similar species based on data from the Finnish multi-source national forest inventory (NFI) (Tomppo 1991, 1997) and habitat quality measures based on metapopulation theory (Hanski 1999a, Hanski 1999b, Hanski and Ovaskainen 2000). We relate measures of habitat quality to territory type and permanence. Measures of landscape quality in relation to the fraction of suitable habitat occupied allow us to evaluate possible threshold conditions for the persistence of the species in fragmented landscapes.

2 Study Area, Material and Methods

2.1 Study Area

The study area is located in Lammi in southern Finland (61°15´N, 25°00´E; Fig. 1) with a total area of 340 sq km, of which 275 sq km (81%) consists of forest, mostly spruce-dominated coniferous or mixed mature forests. The landscape is a mixture of forests of different ages, agricultural areas, lakes and scattered human settlements with a gradient from a southern agricultural-forest mosaic to northern forest-dominated areas.

2.2 The Three-Toed Woodpecker Data

The three-toed woodpecker has been studied by mapping the numbers and locations of territories

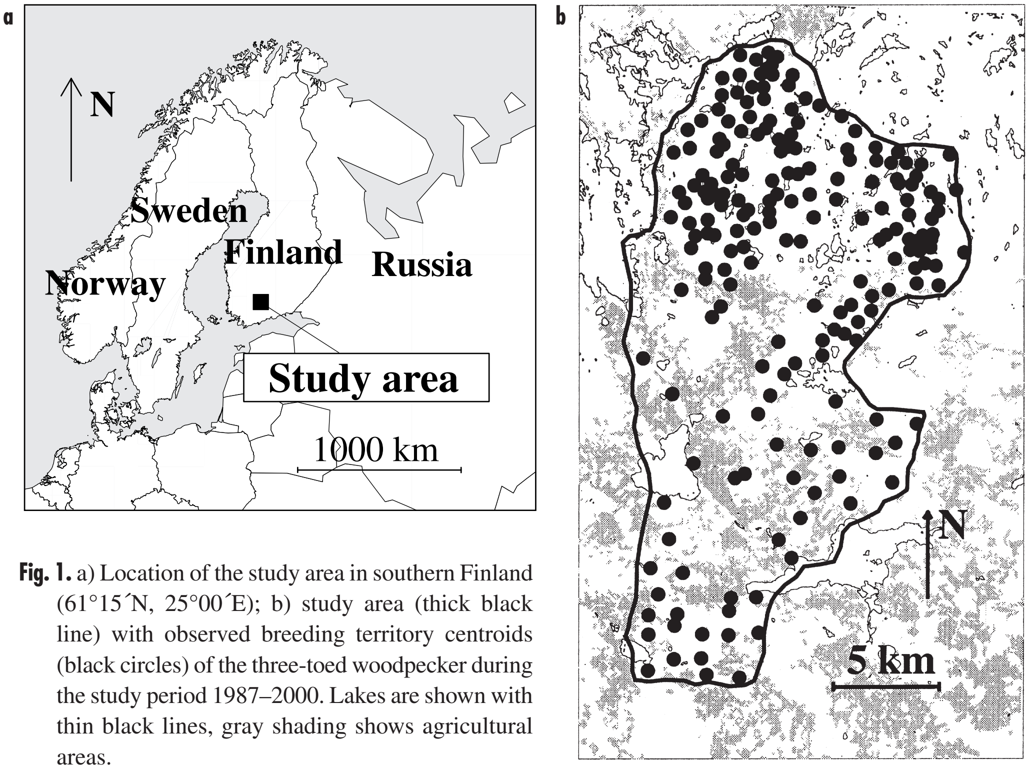

Fig. 1. a) Location of the study area in southern Finland (61°15´N, 25°00´E); b) study area (thick black line) with observed breeding territory centroids (black circles) of the three-toed woodpecker during the study period 1987–2000. Lakes are shown with thin black lines, gray shading shows agricultural areas.

and their type (breeding confirmed, pair detected, only single adult observed) in 1987–2000. The annual censuses were conducted between April 15 and July 15, with a special effort in periods with high detectability of the species: the active drumming period (usually between late April and middle of May) and late nestling period (usually between middle of June and middle of July). Special attention was also paid to fresh feeding signs, which may reveal an occupied territory.

Distinct territories were distinguished from each other by simultaneous observations from neighbouring territories or if simultaneous observations were lacking by distance, which depended on the landscape structure. A minimum distance of 500 m between observations was usually needed to interpret them as different territories if there were no other observations by which territories could be separated. Territory locations were determined by the centroids of field observations. Each territory site studied was mapped 3–5 times during the breeding season and usually several observations of the birds were recorded in a single census. Potential territory sites were mapped usually at least 4–5 times if woodpeckers were not observed to make sure that the site was unoccupied.

In 50% of the study years, over 70% of the study area was covered with censuses, and all regions of the study area were mapped at least in five years during the study period. The annual territory data were combined to estimate territory centroids and types for the entire study period. The probability of territory occupancy, p_{occ}, was defined for each territory as

$$p_{occ} = \Sigma \text{ years occupied} / \Sigma \text{ years censused} \qquad (1)$$

2.3 Estimation of Forest Parameters with Multi-Source Data

Numerical thematic maps produced by the Finnish multi-source national forest inventory were applied in measuring the territory and landscape quality. The multi-source inventory method utilises satellite images and digital maps in addition to field measurements. Digital maps are used to delineate forestry land from other land use classes. Satellite images, together with field measurements, are used to estimate forestry parameters for the areas of interest. (Forestry land consists of forest land, with mean annual productivity at least 1 m^3/ha, other wooded land, with mean annual productivity at least 0.1 m^3/ha but less than 1 m^3/ha, waste land, mean annual productivity less than 0.1 m^3/ha, and forestry roads and logging yards.) A non-parametric k-nn method has been used in estimation. An essential property of this method is that all inventory variables, typically 100 to 400, can be estimated at the same time for computation units. Another advantage is that area statistics and thematic maps are produced by the same method (Tomppo 1991, 1997).

The multi-source output thematic map data were based on the Finnish NFI field data from the years 1986–88 and its updating from the year 1994. In this updating, 38% of the field plots were re-measured. These re-measured plots were used together with a Landsat TM image (198-17, date July 9, 1994) and with digital map data. The field plot density was one plot per about 700 ha but the multi-source method utilises information outside the test area as well (Tomppo 1991, 1997 and Tomppo et al. 1998; see also the formulas (2) and (3)).

The estimation procedure utilises a distance measure defined in the feature space of the supplementary data (e.g. spectral data space of the image), denoted here by δ, which defines new area weights for each field plot. The weight of field plot i to pixel p is defined as

$$w_{i,p} = \frac{1}{\delta^2_{p_i,p}} \Big/ \sum_{j=1}^{k} \frac{1}{\delta^2_{p_j,p}} \tag{2}$$

if pixel p_i, corresponding plot i, is among the k nearest ones to p, otherwise $w_{i,p}=0$. Here, k is a predefined fixed number.

Within forestry land, the estimate $\hat{m}_p$ of the variable M for the pixel p is defined as

$$\hat{m}_p = \sum_{j=1}^{n} w_{j,p} \cdot m_j \tag{3}$$

where m_j, $j = 1,\ldots,n$, is the value of the variable M in the field plot j corresponding pixel p_j and n the number of the field plots (Tomppo 1991, 1997). Mode value is used instead of mean value for variables of nominal or ordinal scale. The land use classes outside forestry land are transferred directly from digital map file.

2.4 Computation of Landscape Statistics

The themes applied in this study were 1) age of stand (t) (years), 2) volume of pine (*Pinus sylvestris* L.) (v_p) (m^3/ha), 3) volume of spruce (*Picea abies* (L.) Karsten) (v_s), 4) volume of birch (*Betula pendula* Roth and *Betula pubescens* Ehrh.) (v_b), and 5) volume of other broad-leaved trees, mainly aspen (*Populus tremula* L.) and alnus species (*Alnus* spp.) (v_{ob}).

The following functions were applied and computed for each pixel j:

$$w_t = \begin{cases} 0, & \text{if } t < 50 \\ t/100, & \text{if } 50 \le t \le 100 \\ 1, & \text{if } t > 100 \end{cases} \tag{4}$$

where t is the multi-source estimate of the age of the stand in years,

$$w_v = \begin{cases} 0, & \text{if } v < 60 \\ v/200, & \text{if } 60 \le v \le 200 \\ 1, & \text{if } v > 200 \end{cases} \tag{5}$$

where v is the the multi-source estimate of volume of growing stock (tree stem volume),

$$w_s = \begin{cases} 0, & \text{if } w_v = 0 \\ \dfrac{v_s}{200 w_v}, & \text{if } 0 < w_v \text{ and } v_s \le 200 w_v \\ 1, & \text{if } v_s > 200 w_v \end{cases} \tag{6}$$

where v_s is the multi-source estimate of the volume of spruce,

$$w_b = \begin{cases} 0, & \text{if } w_v = 0 \\ \dfrac{v_b + v_{ob}}{100 w_v}, & \text{if } 0 < w_v \text{ and } v_b + v_{ob} \le 100 w_v \\ 1, & \text{if } v_b + v_{ob} > 100 w_v \end{cases} \tag{7}$$

where v_b is the multi-source estimate of the volume of birch and v_{ob} volume of other broad leaved trees.

Let us define

$$a = \begin{cases} w_t \times w_v \times w_s \times w_b \,/\, 16, & \text{if } t \geq 80 \text{ years and } v_s \geq 20 \text{ m}^3 \text{ / ha} \\ 0, & \text{otherwise} \end{cases} \tag{8}$$

(1/16 is the pixel size in hectares), which provides a statistic of territory quality specially designed for the three-toed woodpecker. The functions were defined to appropriately measure features of habitat quality that are considered to be relevant for the three-toed woodpecker (Pakkala et al. 2002).

We next define for territory centres i the following measures

$$\text{territory quality } A_i = \sum_{j \in N \cap F} a_j \tag{9}$$

quality of connected habitat

$$\Gamma_i = \sum_{j \in N^c \cap F} a_j \cdot e^{-\alpha d_{ij}} \tag{10}$$

and

$$\text{landscape quality } R_i = A_i \Gamma_i \tag{11}$$

where N is a constant neighbourhood area of the territory i, N^c its complement, F forestry land stratum, d is Euclidean distance in the geographical space (in km) and α a constant. We assume that the contribution of a particular site to the function Γ_i decreases to one half when the distance increases to 1 km, hence we set $\alpha = 0.69$. The sums in the formulas (9) and (10) are computed over the pixels j. The neighbourhood N was restricted to a circle with a radius of 178 m from the observation (i.e. to a size of 10 ha) and N^c to a circle with a radius of 2 km from the observation. The means and variances of the functions A_i, Γ_i and R_i over territory centres i were also computed.

Functions A and Γ describe the quality of the core territory and the quality of the habitat connected to the territory, respectively. The product $R = A\Gamma$ is used in metapopulation theory (Hanski 1999b). In the present context, we use R as a descriptive measure combining the quality of the territory and the connected habitat in a manner that seems biologically justified. The spatial scales were selected to be relevant in relation to the estimated size of typical core areas of breeding territories (radius 178 m gives territory area of 10 ha) and habitat use around territories outside the breeding season in the study area (radius 2 km).

Functions A, Γ and R were computed also for a systematic grid of points 350 m apart from each other and located in forestry land. These results were used to assess whether the functions A, Γ and R computed for the actual territories deviate from the values obtained for systematically sampled points in the study area.

So far we have examined the structure of the landscape at the scale of individual territories. We shall next consider the population scale, which is determined by the range of dispersal of young birds from their natal territory. In this context, we apply the metapopulation theory to the set of potential territory sites in the study landscape. Hanski and Ovaskainen (2000) have introduced the concept of metapopulation capacity, which measures the capacity of a fragmented landscape to support a viable metapopulation. A good approximation of metapopulation capacity λ_M may be calculated as

$$\lambda_M \approx \Sigma R_i^2 / \Sigma R_i \tag{12}$$

that is, the approximation is obtained as a weighted average of the R_i values, the weights being the values themselves (the exact measure λ_M is obtained as the leading eigenvalue of an appropriate matrix; Hanski and Ovaskainen 2000). The metapopulation capacity increases with increasing amount of suitable habitat, but it is also influenced by the spatial configuration of the suitable habitat, e.g. it is generally advantageous for metapopulation persistence if the suitable habitat has an aggregated distribution. We used the metapopulation capacity to describe the quality of forested landscape for the three-toed woodpecker, with the value of α set at 0.3. This value is different from the one used in calculating the quality of the connected habitat in Table 1. In the latter context, we used α to characterize the quality of the immediate surroundings of a particular core territory, which surroundings is used to some extent by the three-toed woodpeckers either during the breeding season or in other times of the year. In the metapopulation context, the value of α is meant to reflect the connectivity of a particular territory to other potential territories, which might send out dispersers to the focal territory should that become empty (Hanski and Ovaskainen 2000). At present, we have little quantitative data on the spatial scales at which the three-toed woodpeckers and their populations operate, but the value of $\alpha = 0.3$ is considered realistic. Note that $\alpha = 0.3$ means that the weight of surrounding areas drops to 5% at a distance of 10 km (see Eq. 10). Fortunately, none of the results reported in this paper is sensitive to the value of α used.

In the analysis of metapopulation size as a function of the metapopulation capacity of the landscape, the former was calculated as a weighted average of the probability of territory occupancy (p_{occ}) values, the weights being elements of the leading eigenvector of the landscape matrix referred to in the above paragraph (see Hanski and Ovaskainen 2000). The metapopulation size thus measured is denoted by p^*_λ.

3 Results

3.1 Territory Numbers, Types and Densities

A total of 195 different territory sites used by the three-toed woodpecker were observed during the study period in 1987–2000 (Fig. 1). Breeding was confirmed at least once at 85 (43%) sites, 13 (7%) sites were territories with a pair observed but no breeding confirmed, and in the remaining 97 (50%) sites only a single, probably unpaired woodpecker was observed during the study period. Territories were predominantly situated in mature spruce-dominated forests, often connected to spruce bogs. The spatial occurrence of the territories was aggregated, and about 80% of the breeding pairs were observed in small groups concentrated in old-growth forest areas.

Annual densities (calculated for 40–50 km^2 areas) varied between 0.45–0.69 pairs/km^2 of woodland in the northern parts and between 0.02–0.14 pairs/km^2 of woodland in the southern parts of the study area. Highest densities, 4–5 pairs/km^2, were observed in natural old-growth forests of the Evo area, i.e. in the northern parts of the study area.

3.2 Is There a Connection Between Territory Quality and the Probability of Territory Occupancy?

There is a highly significant ($p < 0.001$; $n = 195$) positive correlation between territory occupancy p_{occ} and territory quality A_i ($r_s = 0.30$), p_{occ} and quality of connected habitat Γ_i ($r_s = 0.22$) and p_{occ} and landscape quality R_i ($r_s = 0.31$; Fig. 2). There are significant differences in mean territory quality ($\overline{A}$) between the territory types (Table 1; one-way AOV, $F_{3,\,2349} = 128.7$, $p < 0.001$). The quality of the breeding territories was higher and that of the landscape without territories lower than in the other groups (Tukey test, $p < 0.05$). Also the mean quality of the connected habitat ($\overline{\Gamma}$) differed between territory types (Table 1; one-way AOV, $F_{3,\,2349} = 53.7$, $p < 0.001$); the quality of breeding territories was significantly higher than that of the other types of territories (Tukey

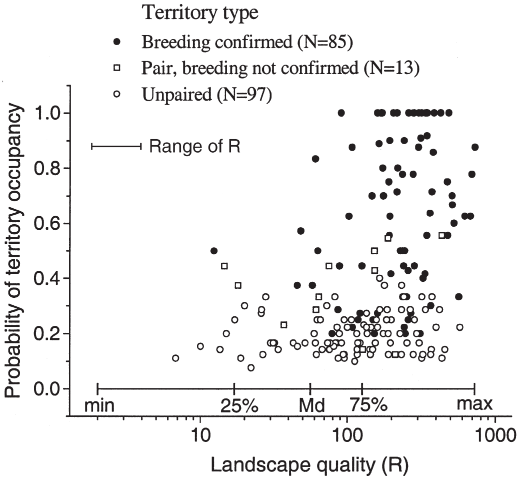

Fig. 2. The landscape quality R and the probability of territory occupancy p_{occ} of the three-toed woodpecker during the study period 1987–2000. Solid line indicates the range of R, its quartiles and median computed from a grid of points located in forestry land 350 m apart from each other.

Table 1. Quality measures and probabilities of territory occupancy of different types of territories of the three-toed woodpecker and the corresponding values of the landscape without territories (mean ± SD). P-values refer to tests of mean quality (one-way AOV) and occupancy measures (Kruskal-Wallis one-way AOV), respectively. Values of 'no territory' were assessed using a systematic grid of points located in forestry land 350 m apart from each other and with a distance > 300 m from woodpecker territory centres.

Territory type (N)	Territory quality A	Quality of connected habitat Γ	Landscape quality R	Probability of territory occupancy p_{occ}
Breeding confirmed (85)	3.07 ± 1.37	88.9 ± 23.5	285.3 ± 167.7	0.63 ± 0.28
Pair observed (13)	1.92 ± 1.30	66.0 ± 20.8	140.1 ± 121.1	0.35 ± 0.15
Unpaired (97)	2.11 ± 1.21	71.8 ± 26.3	164.2 ± 129.8	0.20 ± 0.07
No territory (2158)	1.05 ± 1.03	56.7 ± 25.4	71.2 ± 90.9	0
Difference between means, P-value	< 0.001	< 0.001	< 0.001	< 0.001

test, $p < 0.05$), but no other single group differed significantly from the others (Tukey test, $p > 0.1$). The landscape quality R showed a similar pattern with the other quality measures: a significant difference in mean landscape quality ($\overline{R}$) between habitat types (Table 1; one-way AOV, $F_{3, 2349} = 158.8$, $p < 0.001$); and the quality of breeding territories was higher and that of landscape without territories lower than in the other groups (Tukey test, $p < 0.05$). The probability of territory occupancy differed significantly between territory types (Table 1; Kruskal-Wallis one-way AOV, $H_2 = 109.9$, $p < 0.001$), and all pairwise probabilities of territory occupancy differed significantly from each other (Dunn's non-parametric a posteriori test with unequal sample sizes; breeding vs. pair: $p < 0.05$; breeding vs. unpaired: $p < 0.001$; pair vs. unpaired: $p < 0.05$).

The general pattern observed indicates a threshold value of landscape quality for territory occupancy (Fig. 2.). There is also a qualitative change in territory type as the landscape quality increases: most breeding territories are located in high-quality landscapes.

In a logistic regression model of breeding (breeding confirmed; $n = 85$) versus non-breeding territories (unpaired or pair observed but no breeding confirmed; $n = 110$), the regressions with A, Γ or R as independent variables were all positive and highly significant ($p < 0.001$). R was the best explanatory variable in the model; A and Γ were highly correlated ($r = 0.49$, $p < 0.001$), and adding Γ to a model with A did not make the model essentially better.

3.3 The Landscape Level: Metapopulation Capacity and the Fraction of Landscape Occupied

The study area was divided into eight subareas (Fig. 3a). The division was mainly based on natural borders (lakes, built areas, agricultural and other open land areas). There was a significant positive correlation between the metapopulation capacity of the landscape and the fraction of landscape occupied ($r_s = 0.98$, $n = 8$, $p < 0.01$; Fig. 3b). This empirical result suggests that there is critical quality threshold for the occurrence of the three-toed woodpecker at the landscape level.

4 Discussion

Our results demonstrate that landscape structure at different spatial scales is important for the capacity of managed forests to retain the three-toed woodpecker. The observed patterns also suggest that threshold values exist both in terms of the quality of the core territory as well as the larger landscape for the occurrence of the woodpecker. Because the distribution of territories is aggregated and the majority of permanent breeding territories are located in old-growth forest areas, high-quality forest areas are important for the regional woodpecker population. The relatively stable aggregated distribution of territories reflects the situation of the three-toed woodpecker in managed forest landscapes: the species

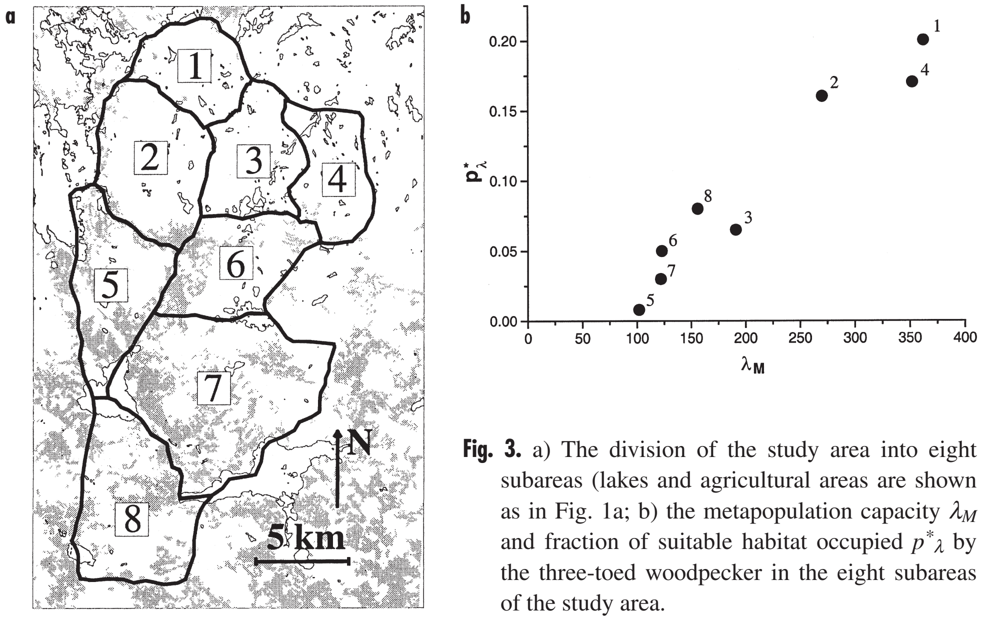

Fig. 3. a) The division of the study area into eight subareas (lakes and agricultural areas are shown as in Fig. 1a; b) the metapopulation capacity λ_M and fraction of suitable habitat occupied $p^*\lambda$ by the three-toed woodpecker in the eight subareas of the study area.

is largely restricted to the most favourable habitat fragments that are still left, but because of lack of natural disturbance dynamics new suitable habitats created by forest fires or windfalls are rare. In low-quality landscapes the territories are often short-lived and are usually hold by unpaired birds.

We used landscape information sampled in the middle part of the study period, which leads to some inaccuracy in the results, as there have been substantial changes in the landscape during the 14-year study period. A decreasing trend is evident in the total population size of the three-toed woodpecker during the study period, and about 50% of the decrease can be attributed directly to habitat and landscape changes, mostly caused by forestry practices (Pakkala et al. 2002). The habitat and landscape measures that were used here do not directly reflect the density of small-scale habitat elements, e.g. the amount of suitable dead or dying wood for feeding and breeding, which may be important for territory permanence (Hogstad 1970, Amcoff and Eriksson 1996, Fayt 1999). Although landscape dynamics and small-scale quality attributes of territories may have a relatively small effect on the general pattern of our results, a more detailed analysis is needed to study the spatial dynamics of territory occupancy in dynamic landscapes (T. Pakkala et al., in prep.). Relatively low age thresholds have been applied in the formulas (3) and (7) due to a tendency towards mean of the multi-source estimates (Tomppo et al. 1998). A method has been currently derived to reduce this effect (Halme and Tomppo 2001). This new method with multi-temporal estimates will be applied in the forthcoming studies. Pixel-level root mean square errors of the k-nn estimates are often high due to several error sources. The error decreases rapidly when the area in question increases (Tomppo 1997, Tomppo et al. 1998). The effect of the estimation error on the derived estimates of landscape statistics may be lower than the errors of the forest resource estimates themselves due to the fact that only few estimate classes have been utilised.

Our results indicate that the persistence of the three-toed woodpecker in larger regions requires that the quality of the forested landscape exceeds a threshold value (Fig. 3). In other words, the species is likely to be completely missing from a region where high-quality sites occur so sparsely that the landscape-level condition is not met. Within our study area, the southern part appears to be close to the threshold value. The three-toed woodpecker has bred in the southern part during the study period, but the numbers have continuously declined, most likely due to the fact that the quality of the forest landscape has also declined. In fact, recalling that the occurrence of the species is expected to track environmental changes with a shorter or longer time delay (Hanski 2001), the current situation in the southern part may already be below the threshold value. It is also possible that the presence of the three-toed woodpecker in the southern part of the study area is due to migration from the northern part, thus representing source-sink dynamics (Pulliam and Danielsson 1991).

References

Amcoff, M. & Eriksson, P. 1996. Förekomst av tretåig hackspett Picoides tridactylus på bestånds- och landskapsnivå. Summary: Occurrence of Three-toed Woodpecker Picoides tridactylus at the scales of forest stand and landscape. Ornis Svecica 6: 107–119.

Angelstam, P. & Mikusiński, G. 1994. Woodpecker assemblages in natural and managed boreal and hemiboreal forest – a review. Annales Zoologici Fennici 31: 157–172.

Blackford, J.L. 1955. Woodpecker concentration in burned forest. Condor 57: 28–30.

Cramp, S. 1985. The birds of the Western Palearctic, vol. 4. Oxford University Press, New York.

— , Perrins, C.M. & Simmons, K.E.L. (eds.). 1977–94. The birds of the Western Palearctic, vols. 1–9. Oxford University Press, New York.

Crockett, A.B. & Hansley, P.L. 1978. Apparent response of Picoides woodpeckers to outbreaks of the pine bark beetle. Western Birds 9: 67–70.

Dementev, G.P. & Gladkov, N.A. (eds.). 1966. Birds of the Soviet Union. Israel Progr. for Scientific Translations, Jerusalem.

Edenius, L. & Elmberg, J. 1996. Landscape level effects of modern forestry on bird communities in North Swedish boreal forests. Landscape Ecology 11: 325–338.

Fayt, P. 1999. Available insect prey in bark patches selected by the Three-toed Woodpecker Picoides tridactylus prior to reproduction. Ornis Fennica 76: 135–140.

von Haartman, L., Hildén, O., Linkola, P., Suomalainen, P. & Tenovuo, R. 1963–72. Pohjolan linnut värikuvin. Otava, Helsinki.

Hagemeier, W.J.M. & Blair, M.J. (eds.). 1997. The EBCC atlas of European breeding birds. Their distribution and abundance. T & AD Poyser, London.

Haila,Y., Järvinen, O. & Väisänen, R.A. 1980. Effects of changing forest structure on long-term trends in bird populations in SW Finland. Ornis Scandinavica 11: 12–22.

Halme, M. & Tomppo, E. 2001. Improving the accuracy of multi-source forest inventory estimates to reducing plot location error – a multi-criteria approach. Remote Sensing of Environment 78: 321–327.

Hanski, I. 1999a. Habitat connectivity, habitat continuity, and metapopulations in dynamic landscapes. Oikos 87: 209–219.

— 1999b. Metapopulation ecology. Oxford University Press, Oxford.

— 2001. Extinction debt and species credit in boreal forests: modelling the consequences of different approaches to biodiversity conservation. Annales Zoologici Fennici 37: 271–280.

— & Ovaskainen, O. 2000. The metapopulation capacity of a fragmented landscape. Nature 404: 755–758.

Helle, P. & Järvinen, O. 1986. Population trends of North Finnish landbirds in relation to their habitat selection and changes in forest structure. Oikos 46: 107–115.

Hogstad, O. 1970. On the ecology of the Three-toed Woodpecker Picoides tridactylus (L.) outside the breeding season. Nytt Magasin for Zoologi 18: 221–227.

Järvinen, O., Kuusela, K. & Väisänen, R.A. 1977. Effects of modern forestry on the number of breeding birds in Finland 1945–1975. Silva Fennica 11: 284–294. (In Finnish with English summary).

Koplin, J.R. 1972. Measuring predator impact of woodpeckers on spruce beetles. Journal of Wildlife Management 36: 308–320.

Lande, R. 1988. Demographic models of the Northern Spotted Owl (Strix occidentalis caurina). Oecologia 75: 601–607.

Mykrä, S., Kurki, S. & Nikula, A. 2000. The spacing of mature forest habitat in relation to species-specific scales in managed boreal forests in NE Finland.

Annales Zoologici Fennici 37: 79–91.

Nilsson, S.G., Olsson, O., Svensson, S. & Wiktander, U. 1992. Population trends and fluctuations in Swedish woodpeckers. Ornis Svecica 2: 13–21.

Pakkala, T., Tomppo, E. & Hanski, I. 2002. Territory characteristics of the three-toed woodpecker in forest landscapes in southern Finland. (Unpublished manuscript).

Pulliam, R.H. & Danielson, B.J. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. American Naturalist 137: 50–66.

Rolstad, J. & Wegge, P. 1989. Capercaillie (Tetrao urogallus L.) populations and modern forestry – a case for landscape ecological studies. Finnish Game Research 46: 43–52.

Sorvari, V.-M. 1994. Kitsin paloalue – pohjantikkojen paratiisi. Summary: Kitsi forest area – a paradise for Three-toed Woodpeckers. Linnut 4: 28–32.

Stenberg, I. 1996. Nest site selection of six woodpecker species. Fauna Norvegica, Ser. C. Cinclus 19: 21–38.

— & Hogstad, O. 1992. Habitat use and density of breeding woodpeckers in the 1990's in More og Romsland county, western Norway. Fauna Norvegica, Ser. C. Cinclus 15: 49–61.

Svensson, S., Svensson, M. & Tjernberg, M. 1999. Svensk fågelatlas. Vår Fågelvärld, supplement 31. Stockholm.

Thomas, J.W. 1993. Viability assesments and managements considerations for species associated with late-successional and old-growth forest of the Pacific Northwest. The Report of the Scientific Analysis Tea. USDA Forest Service, Portland, OR.

Tomppo, E. 1991. Satellite image-based national forest inventory of Finland. International Archives of Photogrammetry and Remote Sensing 28: 419–424.

— 1997. Application of remote sensing in Finnish National Forest Inventory. In: Kennedy, P. J. (ed.). Application of remote sensing in European forest monitoring. International Workshop, Vienna, Austria, 14th–16th October 1996. Proceedings. European Commission. p. 375–388.

— , Katila, M., Moilanen, J., Mäkelä, H. & Peräsaari, J. 1998. Kunnittaiset metsävaratiedot 1990–94. Metsätieteen aikakauskirja – Folia Forestalia 4B/1998: 619–839. (In Finnish).

Tucker, G.M. & Heath, M.F. 1994. Birds in Europe. Their conservation status. BirdLife Conservation Series 3. BirdLife International, Cambridge.

Väisänen, R.A., Lammi, E. & Koskimies, P. 1998. Muuttuva pesimälinnusto. Summary: Distribution, numbers and population changes of Finnish breeding birds. Otava, Keuruu.

Van Langevelde, F. 2000. Scale of habitat connectivity and colonization in fragmented nuthatch populations. Ecography 23: 614–622.

Verboom, J., Schotman, A., Opdam, P. & Metz, J.A.J. 1991. European nuthatch metapopulations in a fragmented agricultural landscape. Oikos 61: 149–156.

Virkkala, R. 1987. Effects of forest management on birds breeding in northern Finland. Annales Zoologici Fennici 24: 281–294.

— 1991. Population trends of forest birds in Finnish Lapland in a landscape of large habitat blocks: consequences of stochastic environmental variation or regional habitat alteration? Biological Conservation 56: 223–240.

— , Heinonen, M. & Routasuo, P.1991. The response of northern taiga birds to storm disturbance in the Koilliskaira National Park, Finnish Lapland. Ornis Fennica 68: 123–126.

— , Rajasärkkä, A., Väisänen, R.A., Vikholm, M. & Virolainen, E. 1994. Conservation value of nature reserves: do hole-nesting birds prefer protected forests in southern Finland? Annales Zoologici Fennici 31: 173–186.

Yeager, L.E. 1955. Two woodpecker populations in relation to environmental change. Condor 57: 148–153.

Total of 44 references