

Research Article

Modelling the effects of dispersal and landscape configuration on population distribution and viability in fragmented habitat

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Abstract

Landscape configuration and dispersal characteristics are major determinants of population distribution and persistence in fragmented habitat. An individual-based spatially explicit population model was developed to investigate these factors using the distribution of nuthatches in an area of eastern England as an example. The effects of immigration and increasing the area of breeding quality habitat were explored. Predictions were compared with observed population sizes in the study area. Our model combined a nuthatch population simulator based on individual behaviour with a grid-based representation of the landscape; nuthatch life cycle and immigration parameters were user selectable. A novel aspect of the model is user-selection of habitat perceptual range. Using a realistic set of parameters, the number of breeding pairs predicted by the model matched observed numbers. According to model simulations, the main cause of nuthatch scarcity in the study area was the inability of patches to support viable populations without immigration from elsewhere. Modelled habitat management, which increased breeding quality habitat in existing woods, lowered the threshold above which the study area population became self-sustaining. The existence of a large core habitat area was critical in producing a self-sustaining population in this landscape, the same area in dispersed small woods failed to sustain populations.

Introduction

In many species, habitat loss and subsequent fragmentation, in association with changing land-use and urbanisation, are major causes of population decline (Saunders et al. 1991; Andr n 1994; Simberloff 1995). Surviving populations may have a scattered distribution, inhabiting discrete habitat patches (With 1997). Extinction in individual patches is a feature of such landscapes and patch

re-colonisation via inter-patch dispersal is essential to maintain the population as a whole (Hanski 1998). In order to reach suitable habitat, individuals are forced to traverse unsuitable and possibly hostile matrix habitat (Zollner and Lima 1999; Ricketts 2001). With dispersal being a key process linking isolated habitat patches (Schippers et al. 1996; Lande et al. 1999), habitat configuration, as well as extent, is important for conservation strategies (Villard et al. 1999; With and King 1999).

Configuration here is defined as ‘the particular spatial arrangement of habitat at a given point in time’ (Villard et al. 1999).

In addition to habitat loss, the process of fragmentation also changes habitat configuration (Wiens 1994), which has been shown to influence the movement patterns of organisms across a range of scales e.g. tenebrionid beetles (*Eleodes obsoleta* Say) (Wiens et al. 1997), ringlet butterflies (*Aphantopus hyperantus* L.) (Sutcliffe and Thomas 1996) and the European badger (*Meles meles* L.) (Schippers et al. 1996). Movement patterns can influence habitat occupancy within patch networks such that the spatial distribution of a population may not be predictable from the distribution of suitable habitat alone (Wiens et al. 1997). Other factors may also result in absence from apparently suitable habitat patches. For example, fragmentation may reduce patch size below a critical persistence threshold e.g. for the hemipteran *Neophilaenus albipennis* (Fabricius) (Biedermann 2004), and/or may cause a loss of connectivity e.g. grey squirrels (*Sciurus carolinensis* Gmelin) (Lurz et al. 2001) and eastern chipmunks (*Tamias striatus* L.) (Henein et al. 1998). Species may be patchily distributed at the edges of their ranges e.g. Alaskan tree species (Lennon et al. 2002) and rare flowering plant species in the Netherlands (Oostermeijer et al. 2002), and as a consequence of recent range changes, e.g. the expansion into the UK of the berberis sawfly (*Arge berberidis* Schrank) (Halstead 2004) and the rhopalid bug (*Brachycarenum tigrinus* Schilling) (Jones 2004). Patch occupancy may also be affected by population size and the availability of colonists (Hinsley et al. 1996).

To aid the prediction of species occupancy and abundance in real landscapes, an individual-based spatially explicit population model (SEPM), named PatchMapper, was developed. A SEPM can be defined as a model that combines a detailed population simulator with an explicit representation of a landscape (Dunning et al. 1995; Ruckelshaus et al. 1996). By simulating the behaviour of individuals in fragmented habitat, individual-based SEPMs have been used to explore the effects of management strategies on population distributions and dispersal (Cain 1985; Liu et al. 1995; Zollner and Lima 1999). The aim of this paper was to use PatchMapper to explore the possible causes of species absence from apparently suitable habitat patches using the nuthatch as an example.

The nuthatch (*Sitta europaea* L.), a small (c. 22–26 g) cavity-nesting woodland passerine (Nilsson 1976), is thought to be sensitive to fragmentation due to its limited dispersal abilities through unsuitable habitat (Opdam et al. 1985; Enoksson et al. 1995; Matthysen et al. 1995). Here we use it as test species to examine the role of dispersal and habitat configuration in determining habitat occupation. Its scarcity from suitable habitat in an area of eastern England, centred on Monks Wood (52°24' N, 0°14' W) in Cambridgeshire, has been noted in previous studies (e.g. Hinsley et al. 1995; Bellamy et al. 1998). While expanding its range in the UK since the 1970s (Gibbons et al. 1993), and in other parts of Cambridgeshire since the 1980s (Bircham et al. 1994; Clark 1996), the nuthatch is still scarce in the Monks Wood area. The main reason for this absence was thought to be the fragmented nature of suitable habitat and its isolation from other nuthatch populations (Bellamy et al. 1998). This isolation suggested that immigration was a key factor in the maintenance or extinction of the existing nuthatch population within the Monks Woods area (Alderman et al. 2004). Our first objective was to evaluate the importance of immigration in maintaining the existing population and to investigate PatchMapper's ability to predict the abundance of nuthatches in target woods in the study area. The second objective was to determine how much new breeding habitat would be required to decrease a requirement for immigration and create a self-sustaining regional population.

Methods

Study areas

The study area in west Cambridgeshire, in eastern England (Figure 1) was used for nuthatch occupancy and habitat classification surveys by Bellamy et al. (1998). Breeding quality nuthatch habitat, including Monks Wood, was concentrated in the southern half of this study area. To match the model input requirement for ‘square’ landscapes, the test landscape was trimmed to 20 × 20 km (40,000 ha) and adjusted to place Monks Wood at the centre. About 4% (1660 ha) of this landscape was wooded. Within this area, 34 woods were deemed suitable for nuthatch

occupancy (based on the original survey by Bellamy et al. (1998)), containing a total area of approximately 300 ha of breeding quality nuthatch habitat (0.75% of the total landscape area). The definition of breeding quality nuthatch habitat was taken from Bellamy et al. (1998), as mixed deciduous woodland, including oaks, with trees of greater than 30 cm diameter trunks, in which nuthatches have territories of approximately 2 ha. The matrix comprised intensive arable farmland, with large fields bounded by hedgerows (usually well trimmed) and few individual mature trees or rows of trees (Bellamy et al. 1998). The most suitable wooded area within reasonable dispersal distance capable of acting as a source of immigrant nuthatches was thought to be South Rockingham Forest, a large area of mature deciduous forest in Northamptonshire, approximately 12 km to the west of the main study area.

Model description

Coded in Java for portability, PatchMapper is an individual-based SEPM. The landscape can be either dynamic or static, with its structure directly affecting the behaviour of the modelled species. Populations are not directly modelled, but form as a direct consequence of the behaviour of the individuals. Different habitat configurations and

landscape management scenarios can be evaluated with a choice of landscapes, either input from a GIS or user generated. During the run, a real-time (computer) visualisation of the positions of individuals in the landscape is presented to the user. The results of the simulation, in the form of a set of landscape metrics and population demographics, are saved to disk and are also made available for direct display on the screen. The users' selections, entered via a set of interactive screens, control the overall simulation. For this study, PatchMapper combined a nuthatch population simulator with a grid-based representation of the landscape, and is described in more detail below.

Nuthatch simulator

The nuthatch is a resident passerine bird, which lives in pairs throughout the year in mutually exclusive territories (Nilsson 1987; Matthysen 1990; Wesolowski and Stawarczyk 1991; Matthysen and Adriaensen 1998). It is widely distributed throughout Europe and Asia (Pravosudov 1993a; Matthysen 1998). Breeding takes place in spring and the species is usually single brooded (Nilsson 1987; Wesolowski and Stawarczyk 1991). Juvenile nuthatches disperse from the natal site and start territory establishment and pair formation in late summer (Nilsson 1987; Pravosudov 1993b).

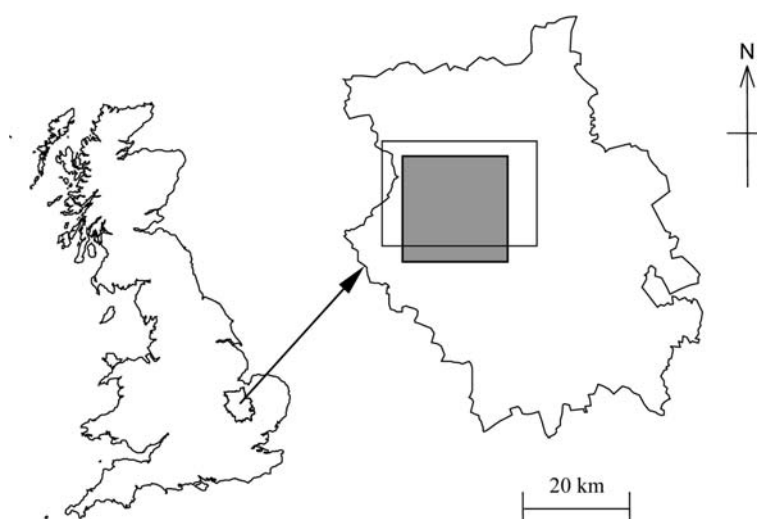


Figure 1. Location of the 20×20 km modelled study area (darker shading) in relation to the 20×25 km study area used by Bellamy et al. (1998), within the county of Cambridgeshire in eastern England, UK (redrawn from Bellamy et al. 1998).

Mortality is highest in the winter (Pravosudov 1993b), leaving territory vacancies. In early spring, pre-breeding dispersal provides a chance for any singleton individuals to form pairs and to occupy existing territories or to form new ones, as appropriate (Matthysen 1989a; Pravosudov 1993a). Territories are usually established before March, when breeding starts (Matthysen 1989b). Once settled, nuthatches are extremely sedentary (Nilsson 1987).

These characteristics, based on parameters taken from the literature (Table 1), were used to model the behaviour of each individual bird, with reference to the quality of the habitat and to landscape structure (see below), an approach in which both landscape structure and species' characteristics govern population sizes and distribution. The overall model flow is given in Figure 2, which also shows the nuthatch parameters used in this study. To model stochastic variation in the demographic and environmental parameters, the summer and winter mortality probabilities, along with the probability of successfully rearing young (breeding success) and the number of successfully fledged young, were sampled from a uniform distribution between the upper and lower limits given in Figure 2. The simulation was based on a yearly cycle, with population size, dispersal mortality, average age and other demographic statistics recorded at the end of each 'year'.

When the simulation is first run, breeding quality habitat cells are grouped into territories.

Such cells are chosen at random, to provide different shaped territories, with the proviso that all cells within the territory group adjoin at least one other cell along a side (rather than a corner). The size of the territory, in number of cells, is user-selectable, with the number of territories per patch limited solely by the amount of breeding quality habitat present in the patch. This means that some cells may remain unallocated, even though of breeding quality. Each group of cells has one 'main' cell. All other cells in the territorial group (called territory cells) record the location of their 'main' cell. Once initialised, territories do not change, reflecting observations that territorial boundaries change little throughout the year (Matthysen 1986; Wesolowski and Stawarczyk 1991; Pravosudov 1993b). The 'main' cell is also used to store occupancy details, such as gender, age of each occupant and whether the territory is occupied by a pair or has a vacancy. During dispersal, a nuthatch locates a habitat cell. Information is gleaned from the territory's 'main' cell, either directly if on the 'main' cell, or indirectly by obtaining its location from a 'territory' cell. If a suitable vacancy exists, then the territory is occupied and marked as such in the 'main' cell. If not, the dispersing nuthatch moves on in search of further suitable habitat. To model territorial establishment during late summer of the same year as fledging (Figure 2), individuals do not disperse a set number of steps, but carry

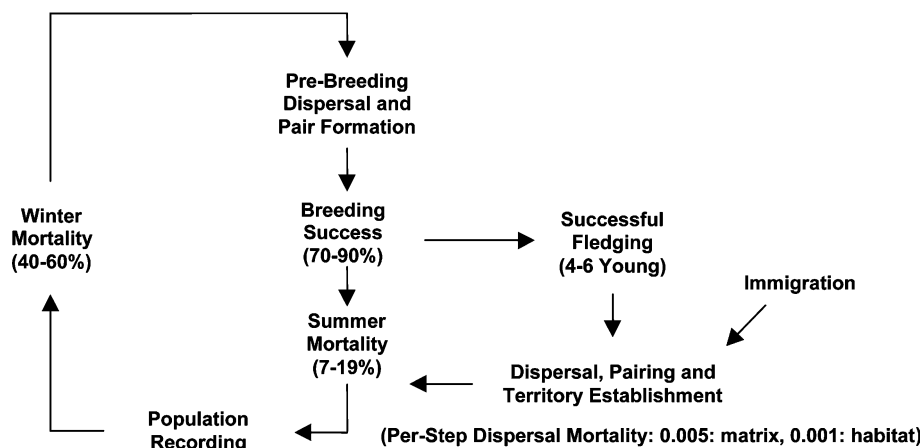


Figure 2. The nuthatch lifecycle as modelled by PatchMapper. The immigration input allows individuals to disperse from distant sources into the study area. The parameters are taken from the literature (see text and Table 1) and vary stochastically over their ranges during the simulation, as described in the text.

Table 1. Published sources of demographic and territorial characteristics of the nuthatch (*Sitta europaea*) used to parametrise PatchMapper's nuthatch simulator.

Territory size (ha)	Winter mortality (%)	Summer mortality (%)	Annual mortality (%)	Breeding success (%)	Mean brood size/female	Mean fledged young/female	General study area	Reference
	46	15	50			3.72 (SD = 1.5)	Belgium	Matthysen (1986)
		9–17	54	72% (SD = 16.5)			Sweden	Nilsson (1987)
	30–60		58–64				Belgium	Matthysen (1989b)
2.08 (Breeding Habitat)			50	58–89	6.2		Belgium	Matthysen (1990)
			40–50	72 (Sweden)			Poland	Wesolowski and Stawarczyk (1991)
				83 (SW Germany)				
30 (21–41)			32.8 (mean)	57.5 (41.9–78.2)	5.97 (4.83–7.4)	5.11 (3.6–6.33)	Siberia	Pravosudov (1993a)
			43	91 (UK)			Siberia	Pravosudov (1993b)
1–2 (Breeding Habitat)						4.26	Belgium	Matthysen et al. (1995)
							UK	Bellamy et al. (1998)
1.58–1.85					6–8		Belgium	Currie and Matthysen (1998)
				75	6.5	5	Belgium	Matthysen and Adriaensen (1998)

The parameters used for the simulations in this study are given in Figure 2.

on moving until either a suitable territorial vacancy is found, or mortality occurs.

Dispersal in PatchMapper is governed by a set of inter and intra-patch dispersal rules. Dispersing nuthatches search for habitat, traversing the matrix with a correlated random walk in which small turns are made at intervals. On leaving the natal site, individuals are each assigned a dispersal direction, chosen at random from the set of cardinal and quadrantal directions. The disperser moves one cell in the dispersal direction and then one cell in an orthogonal direction, determined at random from a uniform distribution. On leaving the patch, dispersers 'look' for habitat within an arc of 180°, and up to a distance determined by a user-selectable perceptual range (see below). If a habitat patch is detected, the disperser moves directly to that patch, if not, it resumes the search, dispersing in a random direction. During a simulation, individuals may disperse from natal patches or immigrate into the study area from the landscape boundary. In both scenarios, dispersers are searching for suitable vacant territory and therefore use the same inter-patch movement rules. When a habitat patch is encountered, it is searched for breeding quality habitat. If none is found, the search is resumed for a new patch. If breeding habitat is found, then depending on its occupancy status, a new territory is established, a pair formed or, if no suitable vacancy exists, the disperser is forced to search for further suitable habitat within the wood, or to search the matrix for another wood. The resultant inter-patch dispersal paths were nearly straight 'zig-zags' across the landscape. The scale chosen for modelling the landscape (1 cell = 1 ha, see the population viability tests section below) meant that features smaller than 1 ha could not be modelled. During dispersal across the matrix, it is likely that a nuthatch would take shelter in single trees or small woods and the actual dispersal path would therefore most likely be more 'zig-zag' than straight. Such dispersal paths are more realistic than straight ones (Samways 1989) and increase the chance of habitat detection (Forman 1995; Zollner and Lima 1999).

The distance over which a particular species is able to distinguish between different landscape elements has been variously defined as its 'radius of detection' or 'reactive distance' (Cain 1985; Adler and Nuernberger 1994), 'detection distance'

(Fahrig 1988) or, more recently, its ‘perceptual range’ (Zollner and Lima 1997; Zollner 2000).

For a dispersing individual, the shorter its perceptual range, the longer the time it spends in the matrix before locating a habitat patch. This increases the chance of dispersal mortality through factors such as resource depletion and increased risk of predation (Lima and Zollner 1996; Schooley and Wiens 2003). Perceptual range interacts with physical connectedness to determine the effective connectivity of the landscape and thus may play a key role in species’ responses to habitat fragmentation.

To incorporate effects of landscape structure on dispersal patterns (Travis and French 2000), a habitat perceptual range mechanism was included in the basic dispersal rules, allowing the disperser to move directly to the nearest wood, if within the specified range. The perceptual range algorithm searched all cells within the user-selected perceptual range, fanning out progressively from the origin. Implicit in the concept of habitat perceptual range is the species’ field of view. Other modelling studies discussing perceptual range looked directly ahead (Zollner and Lima 1999) or used a 360° field of view (Cain 1985; Fahrig 1988), but published coverage of this subject is sparse. For the tests in this study, a 90° field of view was employed, as a compromise between computational efficiency and ensuring that cell coverage was a factor in the resultant model behaviour (Figure 3). The bird moved to the habitat cell nearest the origin. If more than one cell was found at the same distance, a random choice was made to avoid any directional biasing. The distance at which a disperser perceives a wood should represent the actual habitat perceptual range, but this is not known for the nuthatch (or for many other species) and such data are difficult to estimate (Wennergren et al. 1995). A distance of 2 km was assumed as a suitable perceptual range for a nuthatch. This distance corresponds to the maximum distance over which a human observer at ground level in a similar landscape was able to clearly identify woods (Alderman pers. obs.). To simulate nuthatches flying at canopy height, the observations were taken from hilltops.

In reality, dispersing individuals are not constrained by arbitrary study area dimensions, they can both leave and enter the study area. PatchMapper models emigration by ‘losing’ an individual once it

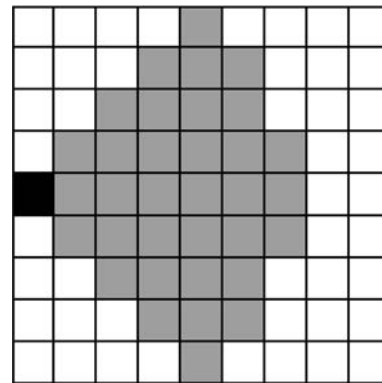


Figure 3. Example search coverage for a disperser with a six-cell perceptual range using a 90° field of view, including corrections for cell diagonal and side dimensions. The black cell is the search origin.

crosses the landscape edge (an absorbing boundary). To model immigration into the landscape, from a nearby external source for example, both the direction of immigration and its rate were made user-selectable. Immigration takes place in the ‘summer’, with an individual nuthatch entering the landscape from a position chosen at random along a landscape edge. The position was sampled from a uniform distribution, with gender alternating for each immigrant. Immigration rate is modelled as a yearly number of immigrants and is user-selectable, as is immigration direction, which can be from one of the cardinal or quadrantal compass points or from all points.

The predator most likely to be encountered by dispersing nuthatches is the sparrowhawk (*Accipiter nisus*) (Newton 1986), although other avian predators such as kestrel (*Falco tinnunculus*) and hobby (*F. subbuteo*) may also be a threat. Vulnerability, once pursued, would be greater in the open than in woodland. Taking this into consideration, in conjunction with published dispersal mortality estimates (Pulliam et al. 1992; Liu et al. 1995), arbitrary per-step dispersal mortality probabilities equivalent to 0.05 km^{-1} were chosen for dispersal within the matrix and 0.01 km^{-1} for within-habitat dispersal. (Per-step mortality is the chance that mortality occurs during dispersal, applied at each movement step.) Dispersal in PatchMapper is modelled as movement from one cell to another. The step size for the tests used in this study was 100 m (1 cell = 1 ha, see the population viability tests section below), which meant

that mortality probabilities of 0.005 and 0.001 were applied at each step in the matrix and habitat respectively.

Landscape modelling

PatchMapper models landscapes in a square celled lattice of 100×100 , 200×200 , 300×300 or 600×600 cells. The landscapes used for the tests in this study were 200×200 cells and were imported from a GIS.

Habitat quality may differ within patches, resulting in variations in population density within a patch. Therefore, in addition to shape and location, patch quality should also be modelled. To meet these requirements, PatchMapper uses two landscapes for each simulation, one for habitat structure and the other for habitat quality. The structural landscape is a binary representation of habitat and matrix, in the form of a cartographic view of the landscape representing all woods in the study area. The quality landscape is the same resolution as the structural landscape, with four possible states, allowing up to four levels of habitat quality to be modelled. The two lattices are coupled. During dispersal, reference is made to the structural lattice and if the individual is on a habitat cell, reference is made to the corresponding cell in the quality lattice to determine whether or not to settle.

For this study, the landscape was modelled with three elements: target habitat, non-target habitat and matrix. Target habitat represents breeding quality woodland habitat. Non-target habitat represents woodland that is unsuitable for breeding, but the difference between breeding quality and non-target woodland cannot be determined from a distance. The matrix represents non-wooded areas, unsuitable for occupancy by nuthatches. The breeding quality habitat areas could support 2 ha territories. Note that individual woods can contain both target and non-target habitat.

Tests

First, the importance of immigration into the study area was examined, followed by a comparison of the predictions of PatchMapper to observed

numbers of nuthatches in target woods (*model comparison tests*). Secondly, the effects of increasing the area of breeding quality habitat on nuthatch population persistence were examined (*population viability tests*). These tests were intended to demonstrate the effects of feasible habitat management plans, rather than to provide a long-term prediction of actual nuthatch population sizes. The tests are described in detail as follows.

Model comparison

To investigate the role of immigration in population persistence in the study area, the model was run with no immigration (from outside the study area). Emigration still applied, meaning that birds were lost as they crossed the study area boundary. The scenario consisted of 100 runs of 100 yearly cycles per run and the results were used to calculate the mean time to extinction for the study area population.

The most likely direction of immigration into the study area was westerly (from South Rockingham Forest), but the immigration rate itself was unknown. The comparison tests therefore took the form of a sensitivity analysis, measuring the mean population sizes in Monks, Holland, Wennington and Rolts Woods for immigration rates from 0 to 60 birds per annum. The upper range limit of 60 birds was thought to be well above the most likely actual rate, with the test therefore spanning the actual rate. Tests were run over 10,000 cycles for each tested value, using the presumed nuthatch perceptual range of 2 km. The mean population size in each wood was recorded for each test.

Population viability

To determine the effects of increasing the amount of breeding quality habitat in the study area on the long-term viability of the nuthatch population, three sets of tests were carried out. In the first set, the amount of breeding quality habitat in the six largest woods in the test landscape which already contained breeding habitat (Figure 4b) was increased (Figure 4a). In these tests, any non-breeding habitat was changed to breeding habitat in existing woods, but without any increase in the

total area of woodland, making the whole area of each wood suitable for breeding (Table 2). In the second test (the 'All Small' option), all the woods in the study area with the exception of the three largest woodland patches (Monks Wood, Holme Fen and Woodwalton Fen, the latter two woods marked Fens in Figure 4a), were upgraded to breeding quality habitat in the same manner. This option provided a total of 1099 ha breeding habitat spread over 232 smaller woods, removing the influence of the large habitat patches. (In this instance, Monks Wood retained its existing breeding quality habitat area of 40 ha.)

The third test was devised to explore whether the nuthatch population could be made self-sustaining by increasing the area of breeding quality habitat in a single wood. Monks Wood (number 6 in Figure 4b) was chosen for these tests because it contains the largest area of existing breeding quality habitat in the study area. Starting with the existing 40 ha of breeding habitat, this area was increased in increments of 10 ha (equating to five nuthatch territories) up to the maximum existing wood area of 157 ha. For each increase, the landscape was seeded with the maximum possible number of nuthatches and the simulation run with no immigration, for a total of 100 runs of 100 yearly cycles. The mean fraction of remaining population was calculated for each increase in area of breeding habitat at

25, 50, 75 and 100 years after the start of the simulation.

Results

Model comparison

The first model comparison test revealed that without immigration, the study area population became extinct after a mean of $8 \text{ years} \pm 0.5 \text{ years}$ (95% CI over 100 runs). Therefore, immigration into the study area was a vital factor in maintaining the existing nuthatch population and needed to be included in the model.

As expected, the predicted population sizes in Monks, Holland, Wennington and Rolts Woods increased with increasing immigration rate (immigration from the west, perceptual range of 2 km). The results showed a lower threshold at approximately 10 individuals per annum, below which the numbers of immigrants reaching the woods were too low to support a population (Figure 5). The results also showed an upper threshold at approximately 30–40 individuals per annum, when the number of immigrants 'saturated' the woods (Figure 5). The maximum observed numbers were 2 pairs in Monks Wood, 1 pair in Wennington Wood and 0.5 pairs in Holland and Rolts Woods.

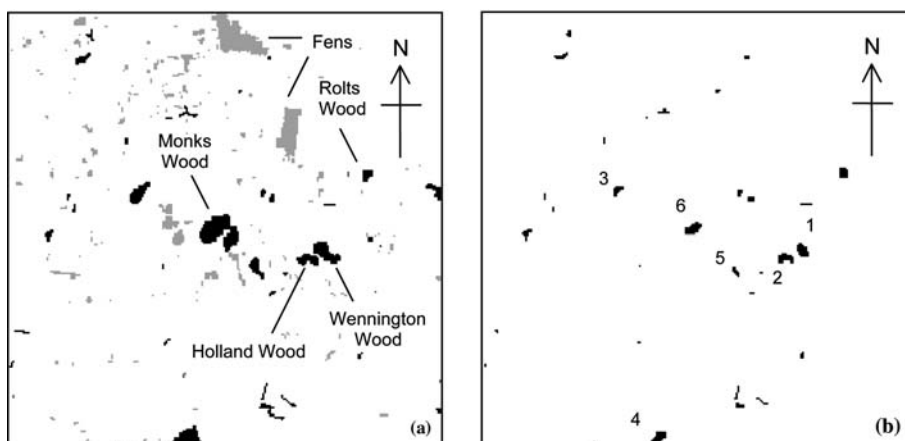


Figure 4. The structural and quality landscapes used with PatchMapper for the model tests. The landscapes are modelled using a 200×200 cell grid, with Monks Wood positioned at the centre, representing a 20×20 km landscape (1 cell = 1 ha). The structural landscape (a) is a binary representation of the landscape, comprising woods (potential habitat) and matrix. For illustration, woods containing suitable habitat are shown in black, with all other woods shaded light grey. Woods of particular relevance to the study are individually labelled. The quality landscape (b) represents the areas of habitat of sufficient quality to support nuthatch territories. Data extracted from survey results by Bellamy et al. (1998).

Population viability

The results of increasing the area of breeding habitat in selected woods are given in Figure 6. For clarity, not all results are shown. With the current amount of breeding quality habitat, the population lasted approximately 10 years. This increased to approximately 20 years when breeding habitat in woods 1–5 (Figure 4b) was increased to occupy the whole of each wood. However, the population only became self-sustaining over the long-term, when the amount of breeding habitat in Monks Wood (wood number 6) was also increased to occupy the whole wood.

The ‘All Small’ option provided the largest increase in breeding quality habitat of the three tests

(1099 ha compared with 573 ha for the ‘wood 6 option’ (Table 2)). Of the 232 woods altered by this option, 117 were below 2 ha and hence too small to support a breeding pair, 90 woods were from 2 to 10 ha, leaving 25 woods above 10 ha. Young produced in the smaller woods have little option but to disperse through the matrix, with all the dangers that that entails (plus the possibility of leaving the study area). Despite the large overall increase in breeding quality habitat, the structure of the landscape therefore prevented the nuthatch population from becoming self-sustaining over the long-term under this option.

The results of increasing the area of breeding quality habitat in Monks Wood alone are given in Figure 7. The results showed a lower threshold at

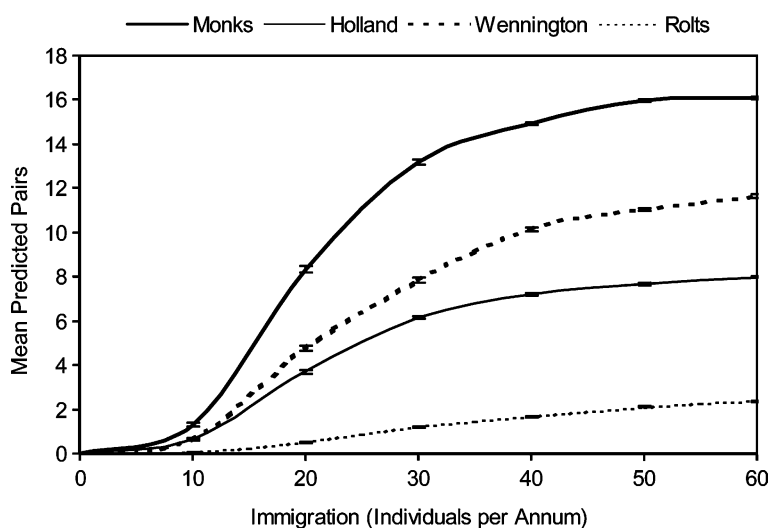


Figure 5. Predicted population size (mean number of pairs) in Monks, Holland, Wennington and Rolts Woods, as a function of immigration into the study area. Perceptual range was set at 2 km. The error bars give 95% confidence levels.

Table 2. Woodland area and nuthatch breeding habitat in the whole study area for each of the numbered woods identified in Figure 4b.

Option	Existing total area (ha)	Existing breeding area (ha)	Increased breeding habitat area (ha)	Cumulative breeding habitat area (ha)
Current, all woods	1660	298	0	298
Wood 1	72	30	42	340
Wood 2	35	20	15	355
Wood 3	50	20	30	385
Wood 4	85	32	53	438
Wood 5	32	14	18	456
Wood 6	157	40	117	573

The ‘increase in breeding habitat area’ column gives the increase in breeding area for each identified wood. The ‘cumulative breeding habitat area’ column gives the total amount of breeding habitat in the whole study area as habitat quality in each wood is increased. The ‘Current’ option represents the baseline areas of all woodland and breeding quality habitat, as shown in Figure 4.

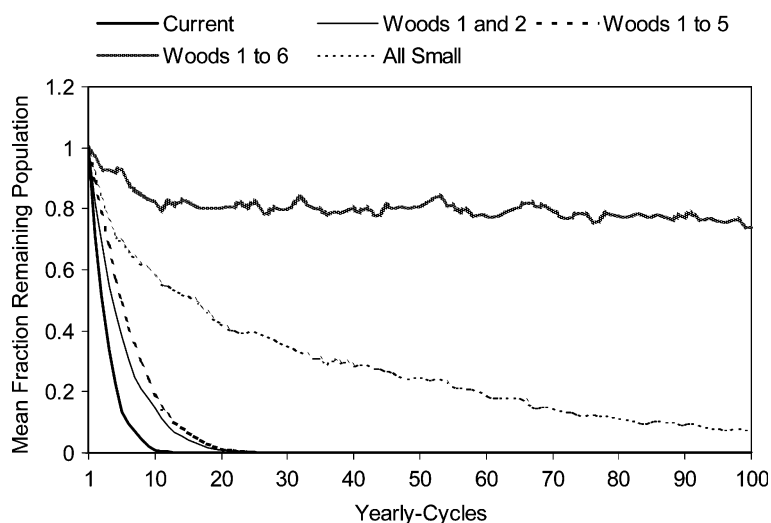


Figure 6. The mean fraction of remaining population in the study area, resulting from increasing the area of breeding quality habitat in selected woods (Figure 4b), as per the legend. Perceptual range was set at 2 km.

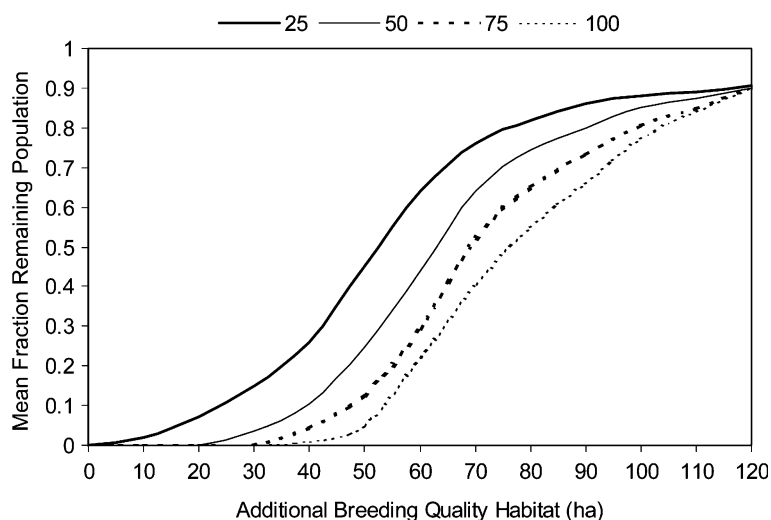


Figure 7. The mean fraction of remaining population in the study area, at 25, 50, 75 and 100 years (as per the legend), resulting from increasing the area of breeding habitat in Monks Wood. Perceptual range was set at 2 km.

an addition of approximately 40–50 ha, with an upper threshold of approximately 65–75 ha.

Discussion

The model comparison tests demonstrated that, as suspected, the fragmented structure of the existing suitable habitat in the study area was incapable of supporting a nuthatch population without external

immigration. The current landscape is effectively acting as a sink. Information on nuthatch distribution in eastern England obtained from local county bird reports and atlas data (Gibbons et al. 1993; Bircham et al. 1994; Clark 1996) revealed two likely sources of immigrant nuthatches. The main source is probably South Rockingham Forest, which lies some 12 km to the west of the study area, the other is a more wooded area to the northwest of Peterborough and of the study area

(Smith and Gilbert 2002). With immigration rate affecting the predicted population sizes in target woods (Figure 5), identification of these sources and their likely emigration rates are necessary to increase the accuracy of PatchMapper's predictions.

PatchMapper's predictions, using a presumed nuthatch perceptual range of 2 km and a range of westerly immigration rates (from Rockingham Forest), over-estimated the mean population sizes for Monks, Wennington and Rolts Woods at the higher immigration rates (Figure 5). To match the observed numbers of nuthatches in the study area, the model required an annual immigration rate of about 10–15 birds, which seems not unrealistic. These results showed that PatchMapper was capable of producing a close match to observed population sizes, although the work was based on feasible, but unvalidated, parameters.

The results from the model were based on a static landscape. In reality, the current population may be a result of historical changes in land-cover. Historically, deforestation was widespread in the UK by the 14th century and the county of Cambridgeshire was poorly wooded (c. 1.5% cover) until the mid 20th century (Smith and Gilbert 2002). Recent increases (up to about 4%) in woodland cover are unlikely to have altered the distribution of breeding habitat for nuthatches, especially since much of this increase is recent and the trees have yet to mature. This was thought to eliminate changes in amount or configuration of suitable habitat as a possible cause of the current patch occupancy levels. However, an increase in unsuitable woodland patches may make it easier for nuthatches to disperse but more difficult to find a suitable breeding site, reducing the chance of dispersers settling to breed.

Comparative analyses of patch occupancy and spatial structure have shown that the distribution of patch occupancy is not only a function of patch heterogeneity, but also depends on a species' degree of habitat specialisation. Biedermann (2004), for example, found that for two hemipterans sharing the same host plant (*Brachypodium pinnatum* L.), the habitat specialist *Neophilaenus albipennis* was present in 20% fewer patches than the habitat generalist *Adarrus multinotatus* (Boheman). A similar effect was also found for butterfly species with specialist and generalist host plant requirements (Steffan-Dewenter and Tschamtker

2000). With its dependence on mature deciduous woodland, the nuthatch can be considered a habitat specialist. Patch occupancy levels for the nuthatch were low in the highly fragmented woodland habitat of the study area, suggesting both patch heterogeneity and habitat specialisation as causes of the existing patchy distribution. The results of increasing the quality of existing habitat, analogous to increasing the availability of the species specialist requirements, supported this conclusion.

In this study, to reduce the dependence of the resident nuthatch population on immigration, three 'habitat management' plans were tested by increasing woodland habitat quality rather than total woodland area. The first two plans had little effect until Monks Wood was included (Figure 6). Without changing Monks Wood, the population still declined, even when all woods except the largest three (the 'All Small' option) were improved. This suggested that the largest suitable wood in the area (Monks Wood) was a key feature and that, for this study area, improving the quality of core woods would be more effective than improving that of smaller, more dispersed ones. The third plan (Figure 7) revealed that a lower threshold of approximately 40–50 ha of the unsuitable habitat in Monks Wood was required to mature and/or be managed to increase quality, to enable the study area nuthatch population to become largely self-sustaining. Increasing the amount of breeding quality habitat above this threshold increased emigration from Monks Wood to the surrounding woods, thereby increasing the 'self-sustainability' of the whole study area population. This continued until the whole wood was converted to breeding quality habitat, with saturation starting to occur at an upper threshold of 65–75 ha. The area of existing habitat being below a critical persistence threshold is therefore suggested as one cause of the low occupancy levels and patchy distribution of the nuthatch in the study area. The population in Monks Wood is predicted to be self-sustaining with an area of suitable habitat much smaller than when all small woods converted to suitable habitat failed to create a sustainable population. This suggests that both the total amount of suitable habitat and the configuration of the habitat are important in determining the viability of the population.

Species with greater dispersal abilities are more likely to have higher population sizes, and to

occupy more patches, in fragmented landscapes than those with restricted dispersal abilities (Laurance 1991). Landscapes have, as an example, been found to be more connected for the habitat generalist white-footed mouse (*Peromyscus leucopus* Rafinesque) than for the habitat specialist eastern chipmunk (*Tamias striatus* L.) (Henein et al. 1998). As a further example, Wang et al. (2004) in a butterfly study, found that the highly mobile *Melitaea phoebe* (Denis and Schiffmuller) had a higher number of local populations than the less mobile *Euphydryas aurina* (Rottemburg). Dispersal ability is another possible cause of patch occupancy levels which can also be investigated with PatchMapper. Perceptual range as well as landscape configuration and mobility may affect connectivity or dispersal ability within fragmented habitat by enabling individuals to find more isolated habitat patches. The results of the tests in this study were based on a perceptual range of 2 km; the effect of perceptual range on population viability is the subject of a separate study (Alderman in prep.).

The identification of the true causes of population distribution within a fragmented landscape by empirical experimentation presents considerable challenges (Walsh and Harris 1996; Ormerod and Watkinson 2000), but the possibility of experimentation by computer simulation presents a practical alternative (Turner 1989). As distribution maps are used widely to assess species' status, an understanding of the reasons behind the distribution of species is essential (Cowley et al. 2000). The results of the tests in this study showed that an individual-based SEPM, such as PatchMapper, which models the movement of individuals is one type of model that can be used for this purpose.

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References

- Adler R.A. and Nuernberger B. 1994. Persistence in patchy irregular landscapes. *Theor. Popul. Biol.* 45: 41–75.
- Alderman J., McCollin D., Hinsley S., Bellamy P., Picton P. and Crockett R. 2004. Simulating population viability in fragmented woodland: nuthatch (*Sitta europaea* L.) population survival in a poorly wooded landscape in eastern England. In: Smithers R. (ed.), *Landscape Ecology of Trees and Forests*. Proceedings 12th Annual IALE(UK) Conference. 21st–24th June 2004. IALE(UK). Royal Agricultural College, Cirencester pp. 76–83.
- Andr n H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71: 355–366.
- Bellamy P.E., Brown N.J., Enoksson B., Firkbank L.G., Fuller R.J., Hinsley S.A. and Schotman A.G.M. 1998. The influences of habitat, landscape structure and climate on local distribution patterns of the nuthatch (*Sitta europaea* L.). *Oecologia* 115: 127–136.
- Biedermann R. 2004. Patch occupancy of two hemipterans sharing a common host plant. *J. Biogeogr.* 31: 1179–1184.
- Bircham P.M.M., Rathmell J.C.A. and Jordan W.J. 1994. *An Atlas of the Breeding Birds of Cambridgeshire* (vice county 29). Cambridge Bird Club.
- Cain M.L. 1985. Random search by herbivorous insects: a simulation model. *Ecology* 66: 876–888.
- Clark J.S. 1996. *The Birds of Huntingdon and Peterborough*. J.S. Clark, Hilton.
- Cowley M.J.R., Wilson R.J., Leon-Cortes J.L., Gutierrez D., Bulman C.R. and Thomas C.D. 2000. Habitat-based statistical models for predicting the spatial distribution of butterflies and day-flying moths in a fragmented landscape. *J. Appl. Ecol.* 37: 60–72.
- Currie D. and Matthysen E. 1998. Nuthatches *Sitta europaea* do not delay postfledging dispersal in isolated forest fragments. *Belg. J. Zool.* 128: 49–54.
- Dunning J., Stewart D., Danielson B., Noon B., Root T., Lamberson R. and Stevens E. 1995. Spatially explicit population models: current forms and future uses. *Ecol. Appl.* 5: 3–11.
- Enoksson B., Angelstam P. and Larsson K. 1995. Deciduous forest and resident birds: the problem of fragmentation in a coniferous forest landscape. *Lands. Ecol.* 10: 267–275.
- Fahrig L. 1988. A general model of populations in patchy habitats. *Appl. Math. Comput.* 27: 53–66.
- Forman R. 1995. *Land Mosaics: The Ecology of Landscapes and Regions*, 1st ed. Cambridge University Press, The Edinburgh Building, Cambridge, UK.
- Gibbons D.W., Reid J.B. and Chapman R.A. 1993. *The New Atlas of Breeding Birds in Britain and Ireland: 1988–1991*: T. & A.D. Poyser.
- Halstead A.J. 2004. Berberis sawfly, *Arge berberidis* Schrank (hymenoptera: argidae), a pest new to Britain. *Br. J. Entomol. Nat. Hist.* 17: 131–135.
- Hanski L. 1998. Metapopulation dynamics. *Nature* 396: 41–49.
- Henein K., Wegner J. and Merriam G. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. *Oikos* 81: 168–186.
- Hinsley S.A., Bellamy P.E., Newton I. and Sparks T.H. 1995. Habitat and landscape factors influencing the presence of individual bird species in woodland fragments. *J. Avian Biol.* 26: 94–104.
- Hinsley S.A., Pakeman R.J., Bellamy P.E. and Newton I. 1996. Influence of habitat fragmentation on bird species distributions and regional population sizes. *Proc. Roy. Soc. Lond B* 263: 307–313.

- Jones R.A. 2004. *Brachycarenum tigrinus* (Schilling) (hemiptera: rhopalidae) new to Britain. *Br. J. Entomol. Nat. Hist.* 17: 137–141.
- Lande R., Engen S. and Saether B.E. 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *Am. Nat.* 154: 271–281.
- Laurance W.F. 1991. Ecological correlates of extinction proneness in Australian tropical rain forest mammals. *Conserv. Biol.* 5: 79–89.
- Lennon J.J., Kunin W.E., Corne S., Carver S. and van Hees W.W.S. 2002. Are Alaskan trees found in more favourable sites in marginal areas? *Global Ecol. Biogeogr.* 11: 103–114.
- Lima S.L. and Zollner P.A. 1996. Towards a behavioural ecology of ecological landscapes. *TREE* 11: 131–134.
- Liu J., Dunning J.B. and Pulliam H.R. 1995. Potential effects of a forest management plan on Bachman's sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. *Conserv. Biol.* 9: 62–75.
- Lurz P.W.W., Rushton S.P., Wauters L.A., Bertolino S., Currado I., Mazzoglio P. and Shirley M.D.F. 2001. Predicting grey squirrel expansion in north Italy: a spatially explicit modelling approach. *Lands. Ecol.* 16: 407–420.
- Matthysen E. 1986. Some observations on sex-specific territoriality in the nuthatch. *Ardea* 74: 117–183.
- Matthysen E. 1989a. Nuthatch *Sitta europaea* demography, beech mast and territoriality. *Ornis Scand.* 20: 278–282.
- Matthysen E. 1989b. Territorial and nonterritorial settling in juvenile eurasian nuthatches (*Sitta europaea* L.) in summer. *Auk* 106: 560–567.
- Matthysen E. 1990. Behavioural and ecological correlates of territory quality in the eurasian nuthatch (*Sitta europaea*). *Auk* 107: 86–95.
- Matthysen E. 1998. *The Nuthatches*. T & AD Poyser Ltd., London.
- Matthysen E. and Adriaensens F. 1998. Forest size and isolation have no effect on reproductive success of eurasian nuthatches (*Sitta europaea*). *Auk* 115: 955–963.
- Matthysen E., Adriaensens F. and Dhondt A.A. 1995. Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos* 72: 375–381.
- Newton I. 1986. *The Sparrowhawk*. T & AD Poyser Ltd, Calton.
- Nilsson S.G. 1976. Habitat, territory size and reproductive success in the nuthatch *Sitta europaea*. *Ornis Scand.* 7: 179–184.
- Nilsson S. 1987. Limitation and regulation of population density in the nuthatch *Sitta europaea* (Aves) breeding in natural cavities. *J. Anim. Ecol.* 56: 921–937.
- Oostermeijer J.G.B., Luijten S.H., Ellis-Adam A.C. and den Nijs J.C.M. 2002. Future prospects for the rare, late-flowering *Gentianella germanica* and *Gentianopsis ciliate* in Dutch nutrient-poor calcareous grasslands. *Biol. Conserv.* 104: 339–350.
- Opdam P., Rijdsdijk G. and Hustings F. 1985. Bird communities in small woods in an agricultural landscape: effects of area and isolation. *Biol. Conserv.* 34: 333–352.
- Ormerod S.J. and Watkinson A.R. 2000. Editors' introduction: birds and agriculture. *J. Appl. Ecol.* 37: 1–5.
- Pravosudov V.V. 1993a. Breeding biology of the eurasian nuthatch in northeastern Siberia. *Wilson Bull.* 105: 475–482.
- Pravosudov V.V. 1993b. Social organisation of the nuthatch (*Sitta europaea*). *Ornis Scand.* 24: 290–296.
- Pulliam H., Dunning J. and Liu J. 1992. Population dynamics in complex landscapes: a case study. *Ecol. Appl.* 2: 165–177.
- Ricketts T. 2001. The matrix matters: effective isolation in fragmented landscapes. *Am. Nat.* 158: 87–99.
- Ruckelshaus M., Hartway C. and Kareiva P. 1996. Assessing the data requirements of spatially explicit dispersal models. *Conserv. Biol.* 11: 1298–1306.
- Samways M.J. 1989. Insect conservation and landscape ecology: a case-history of bush crickets Tettigoniidae in Southern France. *Environ. Conserv.* 16: 217–226.
- Saunders D.A., Hobbs R.J. and Margules C.R. 1991. Biological consequences of ecosystem fragmentation: a review. *Biol. Conserv.* 1: 18–30.
- Schippers P., Verboom J., Knaapen J.P. and Apeldoorn R.C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography* 19: 97–106.
- Schooley R.L. and Wiens J.A. 2003. Finding habitat patches and directional connectivity. *Oikos* 102: 559–570.
- Simberloff D.S. 1995. Habitat fragmentation and the extinction of bird populations. *Ibis* 137([Suppl] 1): 105–111.
- Smith S. and Gilbert J. 2002. National Inventory of woodland and trees – county report for Cambridgeshire. Woodland Surveys Branch of Forestry Research, Forestry Commission, 231 Corstorphine Road, Edinburgh. EH12 7AT.
- Steffan-Dewenter I. and Tschamntke T. 2000. Butterfly community structure in fragmented habitats. *Ecol. Lett.* 3: 449–456.
- Sutcliffe O. and Thomas C.D. 1996. Open corridors appear to facilitate dispersal by ringlet butterflies (*Aphantopus hyperantus*) between woodland clearings. *Conserv. Biol.* 10: 1359–1365.
- Travis J. and French D. 2000. Dispersal functions and spatial models: expanding our dispersal toolbox. *Ecol. Lett.* 3: 163–165.
- Turner M.G. 1989. Landscape ecology: the effect of pattern on process. *Annu. Rev. Ecol. Syst.* 20: 171–197.
- Villard M., Trzcinski M.K. and Merriam G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv. Biol.* 13: 774–783.
- Walsh A.L. and Harris S. 1996. Factors determining the abundance of vespertilionid bats in Britain: geographical, land class and local habitat relationships. *J. Appl. Ecol.* 33: 519–529.
- Wang R., Wang Y., Chen J., Lei G. and Xu R. 2004. Contrasting movement patterns in two species of chequerspot butterflies, *Euphydryas aurina* and *Melitaea phoebe*, in the same patch network. *Ecol. Entomol.* 29: 367–374.
- Wennergren U., Ruckelshaus M. and Kareiva P. 1995. The promise and limitations of spatial models in conservation biology. *Oikos* 74: 349–356.
- Wesolowski T. and Stawarczyk T. 1991. Survival and population dynamics of nuthatches *Sitta europaea* breeding in natural cavities in a primeval temperate forest. *Ornis Scand.* 22: 143–154.
- Wiens J.A. 1994. Habitat fragmentation: island v landscape perspectives on bird conservation. *Ibis* 137: 97–104.
- Wiens J.A., Schooley R.L. and Weeks R.D. 1997. Patchy landscapes and animal movements: do beetles percolate? *Oikos* 78: 257–264.
- With K. 1997. The application of neutral landscape models in conservation biology. *Conserv. Biol.* 11: 1069–1080.

- With K.A. and King A.W. 1999. Extinction thresholds for species in fractal landscapes. *Conserv. Biol.* 13: 314–326.
- Zollner P.A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented landscapes. *Lands. Ecol.* 15: 523–533.
- Zollner P.A. and Lima S.L. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. *Oikos* 80: 51–60.
- Zollner P.A. and Lima S.L. 1999. Search strategies for landscape-level interpatch movements. *Ecology* 80: 1019–1030.