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Modelling the negative effects of landscape fragmentation on habitat selection

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ABSTRACT

Landscape fragmentation constrains movement of animals between habitat patches. Fragmentation may, therefore, limit the possibilities to explore and select the best habitat patches, and some animals may have to cope with low-quality patches due to these movement constraints. If so, these individuals experience lower fitness than individuals in high-quality habitat. I explored this negative effect of fragmentation on habitat selection in a modelling study. Model landscapes were generated containing different amounts of habitat with differences in the degree of connectivity. In these landscapes, the behaviour of two model species was simulated with different dispersal ranges. I found that habitat selection of the species with limited dispersal range increasingly deviates from optimal selection when fragmentation increases. This effect of fragmentation on habitat selection largely limits the spatial distribution of species with limited dispersal range because constrained habitat selection is expected to result in lower mean reproductive output when more individuals occur in low-quality habitat. In addition to the often suggested causes for extinction in small, isolated patches, i.e. increased sensitivity to environmental and demographic stochasticity, constrained habitat selection may lead to an increase in extinction probability of populations when a large fraction of the individuals occur in low-quality habitat.

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1. Introduction

Landscape fragmentation is known to constrain movement of animals between habitat patches and can result in high extinction probabilities of local populations in small, isolated patches (e.g. Hanski, 1994; Prugh et al., 2008; Van Langevelde, 2000). Metapopulation theory can explain these widely observed patterns, identifying the factors affecting the spatial and temporal dynamics of populations in fragmented landscapes (Hanski, 1998, 1999). Although habitat quality determines local population densities, its role in metapopulation dynamics is highly debated (Armstrong, 2005). Several studies have assessed the role of habitat quality in metapopulation dynamics. Some have not found an additive effect of quality next to patch area and isolation (Moilanen and Hanski, 1998), others have found that habitat quality and patch isolation are both important determinants of local extinction and recolonization (Franken and Hik, 2004; Jacquiéry et al., 2008; Thomas et al., 2001), and some studies have shown that habitat quality explains the most variance in occupancy and turnover in habitat patches (Fleishman et al., 2002; Krauss et al., 2005).

In cases where habitat quality of patches has been found to determine metapopulation dynamics, habitat quality is positively related to occupancy, local densities and colonisation and negatively with extinction (Franken and Hik, 2004; Thomas et al., 2001). In one study, an interaction between local habitat quality and connectivity was found to increase the colonisation rate, and the authors interpret this interaction as the ability of the immigrants to target high-quality patches (Jacquiéry et al., 2008). This ability to target high-quality patches has also been found in an experiment (Baguette et al., 2011).

Habitat selection expresses how well an organism is able to find habitat where its fitness is maximised. Habitat selection is, however, not free of costs (Rosenzweig, 1981). Optimal foraging theory predicts that the gains that an individual achieves by selecting one patch over another must compensate for the time and energy spent travelling to the selected patch (Hengeveld et al., 2009). When movement has high costs and habitat selection is consequently constrained, the positive relation between habitat quality and population density may break down (Gilroy and Sutherland, 2007). Indeed, when fragmentation limits movement, some animals may have to cope with low-quality patches when they are not able to explore all unoccupied habitat due to these movement constraints. If so, these individuals may experience lower fitness than individuals in the best habitat patches.

In this paper, I will explore the negative effect of fragmentation on habitat selection in a modelling study. The questions addressed in this paper are: does habitat selection differ between landscapes that differ

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in degree of fragmentation, and if so, what are the effects at a population level? To address these questions, I used a spatially explicit, stochastic model to simulate the occupancy of breeding sites by a certain species in patchy landscapes. In the simulations, the amount and spatial configuration of habitat were varied.

2. Methods

2.1. Model structure

The model simulates reproduction, mortality and movement of individuals. It is based on the PCRaster Environmental Modelling language, which is a computer language for the construction of iterative spatio–temporal environmental models (http://pcraster.geo.uu.nl/, see also Van Langevelde and Grashof-Bokdam, 2011). The model landscapes for the simulations were rasters of 125 125 grid cells. In each landscape, the grid cells contained either breeding or non-breeding habitat. The amount of breeding habitat (B in % of the total amount of grid cells, 2%, 5%, 10% and 20%) varied between the model landscapes. Half of the breeding habitat was high-quality (O in number of grid cells) and the other half was low-quality (M in number of grid cells).

The model simulates the occupancy of breeding sites by pairs. The model species represent animals that have territories and the juveniles disperse looking for unoccupied habitat (many birds and mammals). Each grid cell with habitat in the model landscapes represents a site that can be occupied by the model species. During simulations, I assumed that the number, size and habitat quality of the sites remained constant. I differentiated between cells that were occupied by a breeding pair and cells with only one individual (unpaired individuals or "floaters"). The sum of all cells occupied by a pair is a measure of the population density that can reproduce during the next year. Each simulation started with 25% randomly-selected occupied sites with pairs. I did not find an effect of different starting values on the outcomes. Each time step (one year) starts with all sites occupied by a pair, N_t. The model then determines which pairs produce juveniles, followed by the redistribution of these juveniles over unoccupied sites. Finally, it is determined whether animals will experience a severe or normal winter, which determines their survival. The surviving pairs can reproduce in the next time step.

During the breeding season, each pair has a probability P_r that J juveniles are produced. Both P_r and J depend on habitat quality, but are independent of density. After reproduction, the juveniles move away from their natal site and search for unoccupied sites. Individuals that do not find an unoccupied site are not explicitly further followed. The model landscapes were considered as closed systems, no immigration occurred. When they occupy a territory, adults and juveniles have an independent survival probability, P_a and P_j, which depends on habitat quality and the character of the winter (normal or severe). During winter (especially severe winters), low-quality habitat is assumed to provide low food availability to ensure survival. Due to these differences, high-quality habitat acts as a source and low-quality habitat as a sink.

After winter, the remaining population with size N_{t+1} can reproduce during the next year. The population size at the beginning of the next year will be:

$$N_{t+1} = P_a N_t + P_j P_r J N_t \tag{1}$$

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

2.2. Connectivity of the model landscapes

For variation in habitat geometry, I distinguished two spatial scales at which the habitat was either clumped or randomly arranged

Table 1
Parameters and values used for the simulation study.

Spatial pattern of the model landscapes		
Landscape size	125×125 cells	
Fraction breeding habitat B	Varied (2, 5, 10 or 20%)	
Fraction high-quality habitat	0.5	
Demographics of the model species		
Probability of a severe winter	0.2	
	High-quality O	Low-quality M
Reproduction probability P_r	0.6	0.3
Size of offspring J	3	2
Survival probability of adults P_a		
In normal winters	0.8	0.6
In severe winters	0.7	0.45
Survival probability of juveniles P_j		
In normal winters	0.6	0.4
In severe winters	0.3	0.2
Movement of the model species		
Landscape resistance for movement		
Breeding habitat	1	
Non-breeding habitat	2	
	Model species 1	Model species 2
Dispersal range of juveniles R_d	15 cells	50 cells
Resettlement range of adults R_s	3 cells	15 cells

(Fig. 1). The algorithm to generate the model landscapes is explained in Appendix A. To quantify the connectivity of each model landscape, I first measured the position of each habitat site i relative to all other sites j in a landscape. The relative position of each site i was approximated as the reciprocal of the shortest effective distances d_{ij} to all other sites j (distance from centre to centre, Van Langevelde et al., 1998, 2002; Van Langevelde, 2000):

$$c_i = \sum_{j=1}^{n} \frac{1}{d_{ij}} \quad \forall i \text{ and } i \neq j$$

where n is the total number of breeding sites within the landscape. The calculation of the distance d_{ij} was weighed using values for the resistance for movement (see below). Low values of c_i imply that site i has a low connectivity to all other sites, i.e. it has a long distance to other sites. The connectivity of landscape k was then calculated by summing the values for the relative position of all sites and corrected for the amount of breeding habitat as:

$$C_k = \frac{\sum_{i=1}^{n} c_i}{O_k + M_k}. \tag{2}$$

Low values of C_k indicate highly fragmented habitat. C_k can be used for comparison between the landscapes that differ in amount of habitat (Van Langevelde and Grashof-Bokdam, 2011; Van Langevelde et al., 1998).

2.3. Movement of the model species

After reproduction, the juveniles and the unpaired individuals search for unoccupied sites within a certain radius, i.e. the maximum movement distance D. This distance is defined as the maximum number of grid cells an individual can move from its natal site. I assumed that the further an unoccupied site is located from occupied ones, the lower the probability that it will be selected. This probability decreases exponentially with the distance to an occupied site (Hanski, 1999), as $P_m = 0.1^{d_{ij}/D}$. For the maximum movement distance D, the probability to be selected is arbitrarily set to 0.1, and the probability for distances larger than D equals 0. The probability that an unoccupied site within this radius will be selected depends on the distance to this site and the costs of