Effects of Habitat Loss and Fragmentation on Population Dynamics

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Abstract: We used a spatially explicit population model that was generalized to produce nine ecological profiles of long-lived species with stable home ranges and natal dispersal to investigate the effects of habitat loss and fragmentation on population dynamics. We simulated population dynamics in landscapes composed of three habitat types (good-quality habitat ranging from 10–25%, poor-quality habitat ranging from 10–70%, and matrix). Landscape structures varied from highly fragmented to completely contiguous. The specific aims of our model were (1) to investigate under which biological circumstances the traditional approach of using two types only (habitat and matrix) failed and assess the potential impact of restoring matrix to poor-quality habitat, (2) to investigate how much of the variation in population size was explained by landscape composition alone and which key attributes of landscape structure can serve as predictors of population response, and (3) to estimate the maximum fragmentation effects expressed in equivalent pure loss of good-quality habitat. Poor-quality habitat mattered most in situations when it was generally not considered (i.e., for metapopulations or spatially structured populations when it provides dispersal habitat). Population size increased up to 3 times after restoring matrix to poor-quality habitat. Overall, habitat amount accounted for 68% of the variation in population size, whereas ecological profile and fragmentation accounted for approximately 13% each. The maximal effect of (good-quality) habitat fragmentation was equivalent to a pure loss of up to 15% of good-quality habitat, and the maximal loss of individuals resulting from maximal fragmentation reached 80%. Abundant dispersal habitat and sufficiently large dispersal potential, however, resulted in functionally connected landscapes, and maximal fragmentation had no effect at all. Our findings suggest that predicting fragmentation effects requires a good understanding of the biology and habitat use of the species in question and that the uniqueness of species and the landscapes in which they live confound simple analysis.

Key Words: ecological profiles, individual-based spatially explicit population model, landscape metrics, landscape structure, matrix heterogeneity, metapopulation, source-sink

Efectos de la Pérdida y Fragmentación del Hábitat sobre la Dinámica Poblacional

Resumen: Para investigar los efectos de la pérdida y fragmentación del hábitat sobre la dinámica poblacional utilizamos un modelo poblacional espacialmente explícito generalizado para nueve perfiles ecológicos de especies longevas con rangos de hogar estables y dispersión natal. Simulamos la dinámica poblacional en paisajes compuestos por tres tipos de hábitat (hábitat de buena calidad de 10-25%, hábitat de pobre calidad de 10-70% y matriz). La estructura del paisaje varió desde altamente fragmentado a completamente contiguo. Las metas específicas de nuestro modelo fueron (1) investigar las circunstancias biológicas en las que falla el método tradicional de usar solo dos tipos (hábitat, matriz) y evaluar el impacto potencial de restaurar la matriz a hábitat de pobre calidad, (2) investigar cuanto variación en el tamaño de la población se explicaba...
Introduction

Fragmentation and loss of habitat, which are major threats to the viability of endangered species, have become an important subject of research in ecology (Soulé 1986; Forman 1996). Reduction of the total amount of suitable habitat results in heterogeneous landscapes composed of isolated patches of suitable habitat of varying quality embedded in a hostile matrix (Noss & Csuti 1997). This process usually results in both pure habitat loss and fragmentation effects (Andrén 1994). Here we refer to pure habitat loss as changes in landscape composition that cause a proportional loss of individuals from the landscape and to fragmentation effects as additional effects resulting from the configuration of habitat (i.e., brought about through reduction in habitat patch size and isolation of habitat patches, sensu Andrén 1994). Many studies have convincingly demonstrated that the effects of this reduction on resident populations can be significant (Andrén 1994; Fahrig & Merriam 1994; Noss & Csuti 1997; Bender et al. 1998).

Most contemporary researchers studying the importance of habitat loss versus fragmentation have used simple models for hypothetical species (e.g., Andrén 1996; Bascompte & Solé 1996; Fahrig 1997; Boswell et al. 1998; Hill & Caswell 1999; Hiebeler 2000; Flather & Bevers 2002). These models generally contain strong, implicit assumptions (e.g., random-walk dispersal and only two habitat types, matrix and habitat), and because of their simplicity they do not include important processes that may affect a real population in fragmented landscapes. The results of these studies are characterized by a considerable degree of ambiguity. Some argue that habitat loss far outweighs the effects of habitat fragmentation (e.g., Fahrig 1997, 2001), whereas others argue the opposite (e.g., Hiebeler 2000).

The varying results regarding the relative importance of habitat composition and configuration are likely to be related to the variety of assumptions in the different models (Flather & Bevers 2002). Additionally, critical species attributes have not been varied systematically and therefore the results have not been put into perspective.

We argue that further progress in investigating the impact of habitat loss and fragmentation on population dynamics cannot be made without providing models with more biological realism—thus making more of the model assumptions explicit—and without putting the results in a broader perspective of varying species attributes. This can be done best with spatially explicit, individual-based models (Dunning et al. 1995; Gustafson & Gardner 1996; Wiegand et al. 1999) that allow the inclusion of behavioral rules that describe the response of individuals to the landscape and link the individual’s use of space (dispersal and habitat selection) directly to population and metapopulation phenomena.

To systematically investigate the relative effects of habitat loss and fragmentation on population dynamics, we simulated population dynamics in a range of landscapes that differ in composition and configuration, spanning the state space associated with habitat configuration from highly fragmented to completely contiguous landscapes. We focused on three specific questions. First, we used three types of habitat (good-quality habitat, poor-quality habitat, and matrix) and asked under which biological circumstances poor-quality habitat matters. This question challenges the traditional approach of using only two habitat types (habitat and matrix) but is also important for management in assessing the potential impact of restoring matrix to poor-quality habitat. Second, we asked how much of the variation in population size is explained by landscape composition alone and which key attributes of landscape structure can serve as predictors of population
response. Finally, we estimated the maximum fragmentation effects expressed in terms of equivalent pure (good-quality) habitat loss.

Methods

We used a previously developed spatially explicit population model (Wiegand et al. 1999), shaped in accordance to the biology of European brown bears (Ursus arctos). Because the answers to our questions critically depend on the underlying biology of the model species (e.g., dispersal abilities and habitat requirements), we generalized the critical components of the population model with respect to habitat fragmentation and created nine ecological profiles (Vos et al. 2001) that represent a spectrum of long-lived species with stable home ranges and natal dispersal.

Population Model

The model is an individual-based and spatially explicit population model that simulates the demographics, dispersal, and selection of home ranges of female bears. The model rules are described in the Appendix (for more details see Wiegand et al. 1999). Here we briefly describe how landscape structure affects population dynamics.

Individual landscapes consisted of three types of habitat: good-quality habitat (G), poor-quality habitat (P), and hostile matrix (M), and were composed of a 50 x 50 grid of cells. Demographic parameters were adjusted to produce an overall rate of population increase of $\lambda > 1.03$ ($\lambda < 0.99$) for landscapes consisting completely of good- (or poor-) quality habitat (for details see Wiegand et al. 1999, Fig. 6), and matrix was uninhabitable. A home range of maximum size occupied a $3 \times 3$ area of cells, but smaller home ranges could occur in highly suitable habitat areas (see Appendix). We included density dependence by reducing the habitat suitability of a cell if it was shared by resident females (see Appendix).

Habitat suitability linked the demographic processes to the landscape. A dispersing female (an independent female without its own home range) established a home range if the total habitat suitability of the $3 \times 3$ cell area surrounding its present location exceeded a threshold (the minimal resource requirements $Q_{min}$). Survival of resident females and dependent cubs was higher if the mean habitat suitability of the home range was higher. During 1 year, dispersal consisted of a directed random walk of up to $S_{max}$ steps through the landscape. The path taken and the risk of mortality depended on habitat suitability along the dispersal path (see Appendix). Movement continued until the dispersing female established a home range, until $S_{max}$ dispersal steps were taken, or until she died. Surviving females that did not establish a home range during a model year continued dispersing in the following year. Once a female located a suitable home range, she stayed in that location until she died. Only females occupying a home range could reproduce.

The Ecological Profiles

Dispersal and establishment of home ranges are the key processes that link demography to the landscape. Therefore, we created an array of ecological profiles that differed in the maximal number of dispersal steps ($S_{max}$) taken during 1 year and in the habitat suitability threshold ($Q_{min}$) for establishment of a home range. We selected three values for $S_{max}$ that corresponded to low, intermediate, and high dispersal abilities ($S_{max} = 4, 16, and 64$, respectively). As with $S_{max}$, we used three values for the resource requirement parameter ($Q_{min} = 24, 32, and 40$). For low ($Q_{min} = 24$) and moderate ($Q_{min} = 32$) resource requirements, home ranges could be entirely composed of poor-quality habitat, whereas a home range with high resource requirements ($Q_{min} = 40$) had to contain at least two good-quality habitat cells (see Appendix). The range of resource requirements used in different model runs corresponded to different strategies for handling the trade-off between the high risk of mortality in home ranges of low suitability home ranges and the high risk of mortality when dispersing longer distances in search of a better quality home range.

The Landscape Model

Landscape composition was determined through a set of parameters ($f_G, f_P,$ and $f_M$) that represented the proportion of cells of the three habitat types (G, P, and M) in the landscape. Wiegand et al. (1999) investigated the correlation between key variables of population dynamics and two fragmentation measures for 20 largely different landscape types. Because their results were independent of the specific landscape type used, we used five “representative” landscape types here (Fig. 1). The landscape types we used ranged from a type that was randomly structured in terms of the scale of individual home ranges (landscape type A, see Wiegand et al. 1999) to a type with one contiguous area of good-quality habitat (landscape type E). For each landscape type we generated 16 individual landscape maps (Fig. 2) with different proportions of poor-quality habitat ($f_P = 0.1, 0.3, 0.5,$ and $0.7$) and different proportions of good-quality habitat ($f_G = 0.10, 0.15, 0.20,$ and $0.25$). We varied the proportions of good-quality habitat only within a relatively small range ($\Delta f_G = 0.15$) because in situations of conservation concern, the amount of good-quality habitat in a landscape is usually quite low, and in such situations loss (or restoration) of good-quality habitat may result in levels even below 10% (e.g., McKelvey et al. 1993; Gaona et al. 1998; Vos et al. 2001). In contrast, we varied the proportion of poor-quality
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Figure 1. The five landscapes and the values of the fragmentation measures. Top row (A–E): the five landscape types that span the state space associated with configuration of good-quality habitat from highly fragmented (landscape type A) to completely contiguous (landscape type E), exemplified for landscapes with 10% good-quality habitat ($f_G = 0.1$) and 30% poor-quality habitat ($f_P = 0.3$). Middle row: landscape measure $O_{GN}(3)$ for the 20 landscapes of types A to E ($O_{GN}[3]$ is the fraction of cells of poor-quality habitat and matrix at the critical distance $r_{crit} = 3$ away from cells of good-quality habitat). The $O_{GN}(3)$ does not depend on the proportion of poor-quality habitat. Bottom row: the landscape measure $O_{GM}(3)$ for the 20 landscapes of types A to E ($O_{GM}[3]$ gives the fraction of matrix cells at the critical distance $r_{crit} = 3$ away from cells of good-quality habitat).

Conservation Biology
Volume 19, No. 1, February 2005

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Landscape Measures

Wiegand et al. (1999) introduced two scale-dependent landscape measures, $O_{GG}(r)$ and $O_{GM}(r)$, which were defined as the overall fraction of cells of good-quality habitat and matrix, respectively, at a distance $r$ from cells of good-quality habitat. These investigators found the strongest correlations between these measures and key variables of population dynamics (e.g., average number of source home ranges and mean dispersal distance) at spatial scales $r = 2–4$ (Wiegand et al. [1999], Figs. 9, 10, and 12). Therefore, we used only $O_{GG}(3)$ and $O_{GM}(3)$ at the “critical” scale $r_{crit} = 3$. Because $O_{GG}(r) = 1 - O_{GM}(r)$ if no poor-quality habitat exists (i.e., $f_P = 0$) and to give both landscape measures a consistent interpretation of a fragmentation measure, we used here the transformed measure $O_{GN}(r) = 1 - O_{GG}(r)$—the fraction of poor-quality or matrix cells at distance $r_{crit}$ from cells of good-quality habitat (i.e., $N = P$ or $M$).

The $O_{GN}(r_{crit})$ measures the fragmentation of good-quality habitat at distance $r_{crit}$ from good-quality habitat cells (Fig. 1, middle row). High values of $O_{GN}(r_{crit})$ indicate a high probability that other habitat types (i.e., $P$ or $M$) can be found at distance $r_{crit}$ from good-quality habitat cells (i.e., landscape type A). The $O_{GN}(r_{crit})$ decreases if the landscape type changes under constant composition from the highly fragmented type A to the highly contiguous type E (Fig. 1, middle row). It does not, however, reach zero as long as the proportion $f_G$ of good-quality habitat over a wider range ($\Delta f_G = 0.6$), primarily because we sought to assess the role of the third habitat type on population dynamics and the full effect of a potential restoration of matrix to poor-quality habitat.
habitat is below 1. The O_{GN}(r_{crit}) can be interpreted as a measure of patch-size effects because it was highly correlated to the log-log transformation of the mean patch area (r_{Pearson} = 0.93, n = 20) and to the number of patches (r_{Pearson} = 0.93, n = 20) if we considered only patches that could potentially serve as a home range (i.e., patches with three or more cells of good-quality habitat).

The O_{GM}(r_{crit}) measures the fragmentation of the suitable habitat (i.e., good and poor quality) at distance r_{crit} from good-quality habitat cells (Fig. 1, bottom row). High values of O_{GM}(r_{crit}) indicate a high probability that matrix cells are interspersed at scale r_{crit} from good-quality habitat cells (i.e., there are many movement barriers in the proximity of good-quality habitat cells). The O_{GM}(r_{crit}) decreases if the proportion f_p of poor-quality habitat cells increases because the proportion of matrix cells decreases (note that f_M = 1 - f_G - f_p). The O_{GM}(r_{crit}) also decreases if the landscape type changes under constant composition from highly fragmented type A to the highly contiguous type E (Fig. 1, bottom row) and reaches zero for all landscape types (except type A) if the proportion of poor-quality habitat is high.

Model Output for Analyses

As model output for an individual model simulation i, we calculated the average number of independent females (n_{i mean}), the average number of sink home ranges (n_{i sink}), and the average number of source home ranges (n_{i source}), taken for simulation years 100 through 200. Whether a home range acted as a sink or a source was determined according to its mean habitat suitability (see Wiegand et al. 1999, Fig. 6). We defined source-sink properties based on the current habitat suitability within a home range, not on a priori habitat types. Additionally, we recorded the distribution of dispersal distances (i.e., the Euclidean distance between the natal site and the own home range) between simulation years 100 and 200 and used it to calculate mean dispersal distance (d_{i mean}), maximum dispersal distance (d_{i max}), and the distance below which 95% of the observed dispersal distances fell within a model run (d_{i 95}). Within each landscape we performed 20 replicate simulations for each ecological profile and calculated the average of the variables, which we indicate with capital N and D (e.g., N_{mean} = 1/20 \Sigma_{i=1..20} n_{i mean}).
the factor change in mean population size \( N_{\text{mean}}(f_p = 0.7)/N_{\text{mean}}(f_p = 0.1) \) and the factor change in mean dispersal distance \( D_{\text{mean}}(f_p = 0.7)/(D_{\text{mean}}(f_p = 0.1) \). The habitat-matrix approximation holds if the factors of change are approximately 1.

**Variation in Population Size and the Role of Fragmentation Measures**

To address the relative importance of habitat composition and fragmentation on population size, we used an analysis of variance with the four factors: proportion of good-quality habitat, proportion of poor-quality habitat, landscape type, and ecological profile. In addition, we compared the amount of variation accounted for within each ecological profile. To determine which key attributes of landscape structure can serve as predictors of population response, we regressed mean population size \( N_{\text{mean}} \) with measures of landscape structure. This was done independently for each of the ecological profiles. Each analysis had a sample size of \( n = 80 \) because each landscape contributed 1 value. In a first step we investigated the statistical model

\[
N_{\text{mean}} = N_0 f_G + a f_p
\]

with coefficients \( N_0 \) and \( a \) that relate mean population size \( N_{\text{mean}} \) only to habitat composition. This "null model" describes the pure effect of habitat loss. For a landscape without poor-quality habitat and without matrix (i.e., \( f_G = 1 \), and \( f_p = 0 \)), \( N_{\text{mean}} = N_0 \). Thus, the coefficient \( N_0 \) is the carrying capacity of a landscape composed entirely of good-quality habitat. The null model lacks an intercept because the mean population size \( N_{\text{mean}} \) approaches 0 if \( f_G \) and \( f_p \) approach 0. We contrasted this null model to the full statistical model:

\[
N_{\text{mean}} = N_0 f_G + a w f_p + b w G_{\text{GM}}(3) + c w G_{\text{GM}}(3),
\]

with coefficients \( N_0 \), \( a w \), \( b w \), and \( c w \). The full model contains the addition of the two fragmentation measures \( G_{\text{GN}}(3) \) and \( G_{\text{GM}}(3) \). The full model lacks an intercept because \( G_{\text{GN}}(3) \) and \( G_{\text{GM}}(3) \) approach 0 if \( f_G \) and \( f_p \) approach 0. We used the Akaike information criterion (AIC) to decide on the inclusion of variables in the two statistical models: the final decision between alternative models was based on parsimony (lowest AIC) and simplicity (the simplest model among plausible models when \( \Delta \text{AIC} < 5 \)). To facilitate a comparison among variables and ecological profiles, we normalized all dependent and independent variables \( v \) to values between 0 and 1 (i.e., dividing them by their maximum value \( \text{max}[v] \), Table 1). This is

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<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
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<td>24</td>
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<td>4</td>
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<td>112.3</td>
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<td>2.8</td>
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\( a \) Mean, standard deviation, 95th percentile, and minimum and maximum value were estimated from the simulation results within the \( n = 80 \) landscapes and parameters \( S_{\text{max}} \) (the maximum number of dispersal steps allowed during 1 year); \( Q_{\text{min}} \) (the minimum resource requirements for home range establishment); and \( N_{\text{sink}} \) and \( N_{\text{source}} \) (the mean number of sink and source home ranges, respectively).

\( b \) Three-way analysis of variance with a \( 4 \times 4 \times 5 \) fixed-effects factorial simulation experiment (SS, sums of squares). The F of all main effects was highly significant \( (p < 0.001) \), except for the proportion of poor-quality habitat in ecological profiles 3, 7, and 8.
equivalent to a transformation of the coefficients (e.g., $N_0 = N_0^* \max [f_G]/\max [N_{\text{mean}}]$, where $N_0^*$ is the coefficient of the model with non-normalized variables).

We defined a satisfactory statistical model as one that has a prediction error not larger than the internal noise of the simulation model that results from demographic stochasticity. In this way we described the trends shown by the mean values (i.e., $N_{\text{mean}}$) irrespective of the inherent stochasticity (which may change with population size). To quantify the prediction error of a statistical model, we calculated the standard deviation, $SD_{\text{res}}$, of the residuals between predicted and observed values over all 80 landscapes. This is a suitable measure for comparing the performance of different statistical models because we normalized all dependent and independent variables to values between 0 and 1. To quantify the internal noise of the simulation model, we first calculated the standard deviation of the differences $N_{\text{mean}} - n_i'_{\text{mean}}$, taken over all 80 landscapes ($SD_{i\text{th}}$). The $n_i'_{\text{mean}}$ are the simulated population sizes for replicate $i$, and $N_{\text{mean}}$ is the average of $n_i'_{\text{mean}}$ over all 20 replicates. As a final measure of the internal noise of the simulation model ($SD_{i\text{th}}$), we used the mean of $SD_{i\text{th}}$ taken over the 20 replicate simulations (i.e., $SD_{i\text{th}} = \frac{1}{20} \sum_{i=1}^{20} SD_{i\text{th}}$).

**Maximal Fragmentation Effect**

The problem in studying the relative impact of habitat loss and fragmentation is that both are hard to tease apart in realistic landscapes because habitat loss usually increases habitat fragmentation (e.g., McGarigal & McComb 1995; Noss & Csutti 1997; Trzcinski et al. 1999). This is also reflected in our landscape measures (Fig. 1); a change in the proportion of poor- or good-quality habitat, even if the overall landscape configuration remains approximately the same (i.e., for one landscape type in Fig. 1), changes the values of our fragmentation measures. To overcome this problem we used a different approach that is unaffected by this problem and assessed the maximal effect of fragmentation by comparing the simulation results for the two extreme landscape types, A and E. For a given landscape composition, the maximal effect of fragmentation was given as the absolute loss (or gain) of individuals

$$\Delta N_{\text{frag}} = N^E_{\text{mean}} - N^A_{\text{mean}},$$

where $N^E_{\text{mean}}$ and $N^A_{\text{mean}}$ are the mean number of independent females in landscapes of type E and A, respectively. We compared the absolute loss of individuals, $\Delta N_{\text{frag}}$, to the loss of individuals caused by the pure effect of (good-quality) habitat loss:

$$\Delta N_{\text{loss}} = N_0^* \Delta f_G,$$

where $N_0^* = N_0 N_{\text{max}}/0.25$. Finally, we set $\Delta N_{\text{loss}} = \Delta N_{\text{frag}}$ and expressed the maximum effect of habitat fragmenta-

tion $\Delta N_{\text{frag}}$ as equivalent pure (good-quality) habitat loss:

$$\Delta f_G = \frac{\Delta N_{\text{frag}}}{N_0^*} = \frac{N^E_{\text{total}} - N^A_{\text{total}}}{N^E_{\text{total}} - 0.25}. \quad (5)$$

We defined the equivalent loss of good-quality habitat with respect to the entire landscape, (e.g., a loss of 20% [$\Delta f_G = 0.2$] equals a loss of 125 cells of good-quality habitat [the entire landscape is composed of 50 $\times$ 50 cells]).

**Results**

**Descriptive Statistics of Simulation Results**

For all ecological profiles, differences in mean population size among landscapes were marked (Table 1). Mean population size ($N_{\text{mean}}$) varied by a ratio of 1:10, and the coefficient of variation for $N_{\text{mean}}$ yielded approximate values of 0.4. Variation in mean population size among ecological profiles was less than among different landscape structures, ranging from 139 independent females (ecological profile 3) to 85 (ecological profile 7). In contrast, dispersal distances varied little among landscapes but changed considerably among the ecological profiles.

Ecological profiles with low and intermediate resource requirements ($Q_{\text{min}} = 24$ and 32) produced marked source-sink dynamics and the number of sink home ranges exceeded that of source home ranges. In this case a home range could be composed entirely of poor-quality habitat cells. For ecological profiles with high resource requirements ($Q_{\text{min}} = 40$), sink home ranges occurred mostly because of a density-dependent decline in habitat suitability when home ranges overlapped. Consequently, there were more source home ranges than sink home ranges.

**Habitat-Matrix Approximation**

In fragmented landscapes (type A), mean population size responded strongly to an increase in poor-quality habitat from $f_p = 0.1$ to $f_p = 0.7$ (Fig. 3). Mean population size increased up to 2.7 times for ecological profile 9 and more than 2 times for ecological profiles 4, 5, 8, and 9 (Fig. 3). For all other landscape types, however, the maximal increase was relatively moderate and reached factors of 1.47 (B), 1.35 (C), and 1.27 (D and E).

The changes in population size resulting from the addition of poor-quality habitat were accompanied by distinct changes in mean dispersal distances. In one case population size increased and mean dispersal distance decreased (ecological profiles 1, 5, and 6 in landscape type A). This is because new sink home ranges were created and dispersing individuals had to cover less distance to encounter a vacant home range. In a second case we observed the opposite effect: population size increased and dispersal distance increased (ecological profiles 4, 7, 8 and 9 in
landscape type A). In this case poor-quality habitat predominantly played the role of dispersal habitat (the probability to move to a neighboring cell of poor-quality habitat was 4 times the probability to move to a neighboring cell of matrix; see Appendix). Consequently, the addition of poor-quality habitat in a fragmented landscape facilitated movement between patches and more rapid occupation of vacant home ranges.

Variation in Population Size and the Role of Fragmentation Measures

When analyzed separately for the different ecological profiles, the proportion of good-quality habitat accounted for 71–89% of the variation in mean population sizes, the landscape type accounted for 5–26%, and the proportion of poor-quality habitat accounted for 0.2–6.1% (Table 1). When analyzed across the full complement of landscape treatments and ecological profiles, the proportion of good-quality habitat accounted for 68.3% of the total variation in population size, fragmentation for 12.3%, and the ecological profile for 13.8%. The direct impact of the proportion of poor-quality habitat remained weak.

Knowledge of landscape structure alone was insufficient to satisfyingly predict mean population size, \(N_{\text{mean}}\), the prediction error \(SD_{\text{res}}\) of the null models (Eq. 1) ranged between 0.084 and 0.141, which was above the internal stochasticity \(SD_{\text{th}}\) of the simulation model (Table 2,
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Table 2. Results of the two statistical models (Eqs. 1 & 2) that describe the results of the simulation model, reported separately for the nine ecological profiles.

<table>
<thead>
<tr>
<th>Ecological profile</th>
<th>Internal model noise, SD_{ib}</th>
<th>Null model, Eq. 1</th>
<th>Full statistical model, Eq. 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N_{mean} = N_{0} f_{G} + a_{p}</td>
<td></td>
<td>N_{mean} = N_{0} f_{G} + a_{w} + b_{w} O_{GN} + c_{w} O_{GM}</td>
</tr>
<tr>
<td></td>
<td>N_{0}</td>
<td>a_{p}</td>
<td>SD_{res}</td>
</tr>
<tr>
<td>1</td>
<td>0.063</td>
<td>0.789</td>
<td>—</td>
</tr>
<tr>
<td>2</td>
<td>0.080</td>
<td>0.803</td>
<td>—</td>
</tr>
<tr>
<td>3</td>
<td>0.064</td>
<td>0.803</td>
<td>—</td>
</tr>
<tr>
<td>4</td>
<td>0.063</td>
<td>0.785</td>
<td>—</td>
</tr>
<tr>
<td>5</td>
<td>0.082</td>
<td>0.751</td>
<td>0.084*</td>
</tr>
<tr>
<td>6</td>
<td>0.069</td>
<td>0.729</td>
<td>0.100</td>
</tr>
<tr>
<td>7</td>
<td>0.067</td>
<td>0.746</td>
<td>—</td>
</tr>
<tr>
<td>8</td>
<td>0.081</td>
<td>0.840</td>
<td>—</td>
</tr>
<tr>
<td>9</td>
<td>0.058</td>
<td>0.875</td>
<td>—</td>
</tr>
</tbody>
</table>

*Definitions: N_{mean}, mean number of independent females between simulation years 100–200, averaged over the 20 replicate simulations; f_{G}, proportion of good-quality habitat; f_{p}, proportion of poor-quality habitat; O_{GN} and O_{GM}, fragmentation measures; N_{0}, a, a_{w}, b_{w}, c_{w}, coefficients of the statistical models; all dependent and independent variables were scaled to values between 0 and 1 to make the regression coefficients comparable between ecological profiles; SD_{ib}, internal noise of simulation model due to demographic stochasticity; SD_{res}, prediction error of statistical model (a statistical model described the results of the simulation satisfyingly if SD_{res} < SD_{ib}).

*aModel selection was based on parsimony (lowest AIC) and simplicity (the simplest model among plausible models with ΔAIC < 3).

*bProbability: * 0.005 < p < 0.05; in all other cases p < 0.005.

Fig. 4a). The most parsimonious full statistical models (Eq. 2) contained at least one fragmentation measure (Table 2) and yielded satisfactory statistical models that explained all variation in population size resulting from landscape structure within the limits set by demographic stochasticity (Table 2, Fig. 4b).

The coefficient a_{w} of poor-quality habitat remained low (|a_{w}| ≤ 0.17), indicating a weak direct effect on mean population size, similar to that obtained with the analysis of variance (Table 1). The significant coefficients of the landscape measures O_{GN}(3) and O_{GM}(3) described a negative effect of fragmentation on population size. Interestingly, the coefficients b_{w} and c_{w} were negatively correlated (Table 2, r_{p} = −0.88, p = 0.002, n = 9), which suggests that O_{GN}(3) and O_{GM}(3) describe “competing” aspects of habitat fragmentation that dominate under different biological circumstances.

Maximal Fragmentation Effect

The maximal fragmentation effect was marked (Fig. 5) and when averaged over all ecological profiles and 16 different landscape compositions, yielded a loss of half the population (N_{t} \text{mean}/N_{t}^{E} \text{mean} = 0.45 ± 0.21) (± SD). The equivalent pure loss of (good-quality) habitat was equal to an area of 7% (± 2.6%) of the total landscape. In general, the maximal fragmentation effect was stronger for landscapes with lower proportion of poor-quality habitat (gray circles in Fig. 5) and for ecological profiles with lower mean dispersal distance.

Ecological profiles 7 and 4 were most sensitive to maximal habitat fragmentation, yielding an average equivalent loss of 10.0% (± 2.6%) and 9.2% (± 2.0), respectively. The largest effects occurred when the proportion of poor-quality habitat was low (gray circles in Fig. 5). In

Figure 4. The two (a and b) statistical models for ecological profile 9 with high dispersal ability (S_{max} = 64) and scarce breeding habitat (Q_{min}). The graphs show predicted values over observed values (the average population sizes of the simulation model, bars, range of ± 1 SD taken from the 20 replicate simulations). Solid lines show the expected line for a perfect statistical model, and dotted lines indicate the uncertainty of the simulation model due to internal stochasticity (i.e., SD_{ib} = 0.058).

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these cases the dispersal ability was low and the habitat suitable for home ranges was scarce, with females unable to reach vacant, but distant, home ranges. The maximal fragmentation effect occurred for ecological profile 7: a fragmented landscape with \( f_G = 0.25 \) and \( f_p = 0.1 \) sustained approximately the same population size as a nonfragmented landscape with \( f_G = 0.1 \) and \( f_p = 0.1 \) (i.e., an equivalent pure loss of 15% good-quality habitat). Expressed as maximal decline in population size, the factor change in population size \( \frac{N_{\text{A mean}}}{N_{\text{E mean}}} \) reached a value of 0.16 for ecological profile 7 in the landscapes with \( f_G = 0.1 \) and \( f_p = 0.1 \).

Ecological profiles 8 and 9, with the highest mean dispersal distances, showed a response to maximal fragmentation that ranged from no effect at all (landscapes with abundant dispersal habitat, \( f_p = 0.7 \)) to a maximal decrease in mean population size to approximately one-fourth of the population size in the nonfragmented landscape with the same composition \( (f_p = 0.1, f_G = 0.1) \) or an equivalent pure loss of 10% of good-quality habitat \( (f_p = 0.1, f_G = 0.25) \). This result shows that abundant dispersal habitat can completely mitigate the effect of good-quality habitat fragmentation if the dispersal potential of the species is sufficiently large (cf. ecological profiles 8 and 9 in Fig. 5). In this case the landscape is functionally connected and population dynamics are that of a spatially structured population.

**Discussion**

**Habitat-Matrix Approximation**

Our study is among the first investigations that use three habitat types (good-quality habitat, poor-quality habitat,
and matrix) to assess the traditional approach of using two habitat types only (habitat and matrix). The traditional habitat–matrix approximation did not hold when poor-quality habitat provided sink habitat in the neighborhood of highly fragmented good-quality habitat or when poor-quality habitat provided dispersal habitat, enhancing movement between patches of highly fragmented breeding habitat. In both cases, the “error” of not considering poor-quality habitat could have the effect of more than doubling the predicted population size (Fig. 3). The first case is well conceptualized and follows directly from source-sink theory (Pulliam 1988; Pulliam & Danielson 1991). The second case, however, has important implications for conservation because increasing the amount of poor-quality habitat in a landscape can be interpreted as a successful conservation measure to improve matrix quality—dispersal mortality decreased and the restored habitat enhanced dispersal between patches of fragmented breeding habitat. Restoring larger portions of the matrix (e.g., by restoring landscape structures that increase the survival of dispersers by providing shelter from predators or food sources) might be economically cheaper and ecologically easier than restoring breeding habitat.

The second case also has important implications for theoretical studies on fragmentation. It suggests that dispersal habitat matters most for species with intermediate-dispersal abilities living in landscapes composed of small patches of breeding habitat in which dispersal habitat can enhance the occasional exchange of individuals between patches (i.e., a metapopulation or a spatially structured population). Thus, theoretical metapopulation studies need to explicitly consider dispersal habitat instead of using the more traditional binary habitat–matrix approximation. The effect of landscape heterogeneity on dispersal, however, is complex and difficult to analyze and measure because the uniqueness of each landscape and the complex interactions of effects will always confound simple analysis (Gustafson & Gardner 1996; Moilanen & Hanski 1998). Dispersal habitat introduces an additional degree of freedom in possible landscape configurations that may lead to completely different structural connectivity values for landscapes with the same configuration of good-quality habitat patches but different configurations and proportions of dispersal habitat. This has resulted in metapopulation studies generally ignoring matrix heterogeneity (Wiens et al. 1993; Gustafson & Gardner 1996; Wiegand et al. 1999).

Nonetheless, a few theoretical studies address the effect of matrix heterogeneity (e.g., Gustafson & Gardner 1996; Moilanen & Hanski 1998) or matrix quality (e.g., Fahrig 2001; Vandermeer & Carvalj 2001) on (meta)population dynamics. Our finding that the overall effects of fragmentation and matrix heterogeneity on population size can be well described by two fragmentation measures with clear biological interpretations is an important step for obtaining a more general understanding of this issue. One fragmentation measure, \( O_{GN}(r_{crit}) \), captures patch-size effects of good-quality habitat patches at a critical scale, \( r_{crit} \), and contributes significantly to the ability to predict population sizes for species with low dispersal ability: in landscapes with lower values of \( O_{GN}(r_{crit}) \), more home ranges are situated at the edge of good-quality habitat patches. Consequently, the mean habitat suitability of such “edge” home ranges is lower and the risk of mortality higher. This patch-size effect is usually not considered in theoretical studies.

The second fragmentation measure, \( O_{GM}(r_{crit}) \), captures patch isolation effects at a critical scale \( r_{crit} \) and contributes significantly to predict population sizes for species with intermediate dispersal ability. The \( O_{GM}(r_{crit}) \) differs substantially from other measures of patch isolation (e.g., Vos et al. 2001) because it considers the structure of dispersal habitat and uses a critical scale, \( r_{crit} \), that is independent of maximal (or average) dispersal distance (Wiegand et al. 1999, Eq. 8 and Fig. 12). The \( O_{GM}(r_{crit}) \) correctly described fragmentation effects for landscapes with three types of habitat and species with intermediate dispersal ability (ecological profiles 8 and 9). This finding is a promising starting point for future investigation into generalizing different dispersal rules and landscape structures. The need for this is documented in a growing body of empirical studies that provide evidence for the importance of matrix heterogeneity during dispersal (e.g., Delin & Andrén 1999; Palomares et al. 2000; Reunanen et al. 2000; Ricketts 2001; Revilla et al. 2004).

**Variation in Population Size and the Role of Fragmentation Measures**

As expected, the proportion \( f_G \) of good-quality habitat was the strongest predictor of population size (e.g., Andrén 1994, 1996), but figures were notably below the \( >96 \% \) found by Flather and Bevers (2002) in a similar study. The main reason for this difference is the different range of habitat proportion considered (0.1–0.9 in Flather & Bevers [2002]). Flather and Bevers (2002), however, analyzed a “below threshold condition” (defined through a persistence threshold of habitat amount) that involved a narrower range of habitat amounts. For this subset of landscapes, they found that habitat amount accounted for between 30% and 52% of the variation in population size. This figure is in better agreement with our results, which suggest that the overpowering effect of habitat amount is considerably reduced if habitat loss is placed in a perspective of realistic habitat proportions and losses and in a broader perspective of varying species attributes. We argue that the response of a population to habitat fragmentation may in general not be straightforward but strongly dependent on species-specific properties.

An additional reason for stronger impacts of habitat fragmentation in our study compared with the results of other studies (e.g., McGarigal & McComb 1995; Fahrig...
1997, 1998, 2001; Trzcinski et al. 1999; Flather & Bevers 2002) are differences in the species groups considered. Long-lived species with stable home ranges and natal dispersal may be more vulnerable to effects of habitat fragmentation. A recent study on the habitat quality of brown bears in northern Spain (Naves et al. 2003) suggests that habitat suitability varies considerably at a spatial scale slightly smaller than a home range. Home ranges at the edge of good-quality habitat patches could comprise poor-quality habitat areas that decrease the overall suitability of the home range and may increase the risk of mortality. This fragmentation effect was important in our simulation model but not included in more simple models for hypothetical species (e.g., Fahrig 1997; Flather & Bevers 2002).

Earlier attempts to explain variation in response variables of population dynamics (mostly dispersal success) with measures of landscape composition and structure have not been particularly successful (e.g., Gustafson & Gardner 1996; Schumaker 1996; Tischendorf 2001). Even when considering a fully realized deterministic population model, Flather and Bevers (2002) failed to find descriptors of landscape structure that satisfactorily accounted for the variation in population size introduced by altering landscape structure. They attributed the unexpected high magnitude of unexplained variation in population response to the absence of appropriate variables that captured patch isolation effects. Notably, our full statistical model (Eq. 2) yielded for all ecological profiles a satisfying statistical model with a prediction error not larger than the limit set by demographic stochasticity. This result increases our confidence in our approach of landscape measures, which differs from that usually taken (e.g., McGarigal & Marks 1995; Gustafson 1998; Flather & Bevers 2002).

The Maximal Fragmentation Effect

Maximal fragmentation effects were strong, yielding on average a population decline to half of its size compared with population sizes in the unfragmented landscape with the same composition. Maximal effects were equivalent to a pure loss of 15% good-quality habitat and a drop in population size to 16% of the population size in the corresponding unfragmented landscape. In a metapopulation situation (when breeding habitat was scarce, ecological profiles 8 and 9), we found large variations in the maximal fragmentation effect caused by variation in the proportion of poor-quality habitat. If the landscapes were functionally connected (i.e., abundant poor-quality habitat facilitated the exchange of individuals between patches of fragmented breeding habitat), fragmentation had no effect at all, whereas the maximal fragmentation effects were large in functionally disconnected landscapes with little poor-quality habitat.

Our findings suggest that predicting fragmentation effects (and thus designing appropriate conservation measures) requires a good understanding of the biology and habitat use of the species in question. A change in critical species-specific characteristics, such as dispersal ability or use of dispersal habitat, altered the response of model species to fragmentation completely, from no change at all to a loss of 80% of the individuals. The uniqueness of species and landscapes in which they live will always confound simple analysis. Therefore, it is not surprising that current theoretical studies in which simple models for hypothetical species were applied have been characterized by a considerable degree of ambiguity (e.g., Fahrig 1997, 1998, 2001; Hill & Caswell 1999; Hiebeler 2000; Flather & Bevers 2002).

Phenomenological models are often effective in helping to discern whether or not a particular type of effect is occurring in a system. Ecological systems, however, especially those involving habitat loss and fragmentation, are complex and such models may not help elucidate the causal chains by which the effect operates. Our approach of carefully providing more biological realism has the advantage that it makes more model assumptions explicit. The concept of ecological profiles allowed us to track and explain the differences in model outcome over a range of species characteristics, whereas such a comparison between simple models with different assumptions and formulations is difficult. The comparison of our results among differing species characteristics should make our study useful as a starting point for future investigations. There is no reason to expect that the response of other species groups to fragmentation may be less critically influenced by species-specific characteristics. The variability in outcome we found, however, should not be taken as a source of frustration over the failure to generalize, but as a motivation for further research.

Acknowledgments

Funding provided by the UFZ-Centre for Environmental Research, Leipzig, and Iowa State University enabled the authors to travel between Germany, the United States, and Spain for cooperative work. E. R. was supported by a Marie Curie Fellowship provided by the European Community (Contract EVK2-CT-1999-50001). We thank J. Bascombe, E. Knauer, J. Naves, K. Wiegand, C. Wissel, H. Possingham, and especially two anonymous reviewers for assistance during the development of ideas or for comments on drafts of this manuscript.

Literature Cited


Appendix

The demographic submodel is a simplified version of a nonspatial demographic model for brown bears in northern Spain (Wiegand et al. 1998). We did not include subadult and adult males because we were interested in the aspects of population dynamics that are primarily determined by females. The parameters of the demographic submodel are listed in Wiegand et al. (1999, Table 1), but mortality rates are modified by local habitat quality. Mortality rates were adjusted to produce an overall rate of population increase of λ > 1.03 (λ < 0.99) for landscapes consisting completely of good (poor)- quality habitat (Wiegand et al. 1999, Fig. 6).

We distinguished between habitat quality Z and habitat suitability Q. Habitat quality was defined by the landscape maps (good-quality habitat, Z = 7; poor-quality habitat, Z = 4; and matrix, Z = 1). Habitat suitability Q was reduced when a cell was shared by several females as home range, and was Q = Q otherwise. The habitat suitability of a cell of good or poor-quality habitat dropped to 0.5, 2, 0, or 3, 2, 1, respectively, if two, three, or four females shared the cell as home range. Independent, nonresident females dispersed and searched for a home range. We modeled sequential dispersal from multiple natal sites with competition between residents and dispersers by first selecting the oldest female and continuing in order of decreasing age. During 1 year, dispersing females were allowed to perform Smax site-sampling steps. They moved one grid cell per step, and the cell to which they moved was selected with a probability that was directly proportional to the habitat quality.
suitability $Q$ of the cell, relative to that of the other eight cells of the $3 \times 3$ cell area surrounding the present location. Movement continued until the dispersing female found a home range, until the maximal number of dispersal steps was reached, or until she died.

Mortality during dispersal was considered in addition to age-dependent mortality (see below) as a per-step probability of dying, defined as $(1 - Q_m/9)/R_{\text{max}}$, where $Q_m$ was the mean habitat suitability of the $3 \times 3$ cell neighborhood, determined after accounting for density effects, and $R_{\text{max}} = 400$ was a scaling constant (see Wiegand et al. 1999).

A dispersing female established a home range if the total habitat suitability of the $3 \times 3$ cell area surrounding its present location exceeded the minimal resource requirements $Q_{\text{min}}$. The home range was the collection of the highest quality cells that, as a whole, exceeded the threshold $Q_{\text{min}}$. Resident females stayed in their home range until death, even if the total habitat suitability of the home range temporarily dropped below the threshold $Q_{\text{min}}$ after a newcomer settled nearby.

Only females occupying an own home range could reproduce. We did not consider different probabilities for litter production in home ranges with different habitat qualities; instead, we varied cub mortality in accordance with the habitat quality of the mother’s home range. Similarly, we did not consider variability in reproduction as a function of habitat quality because the rate of increase of a brown bear population is much more sensitive to mortality rates than to reproduction (Wiegand et al. 1998).

We multiplied the age-dependent mortality rates (given in Wiegand et al. 1999, Table 1) with the factor $[1 - c_m(1 - Q_{\text{HR}}/4)]$, where $Q_{\text{HR}}$ is the mean habitat quality of the home range and $c_m = 0.35$, a scaling constant (Wiegand et al. 1999) that determined the magnitude of the impact of habitat suitability on mortality. Mortality applied to each individual independently. For dependent cubs we used the mean habitat quality $Q_{\text{HR}}$ of their mother’s home range; for resident females (including successful dispersers of the year), we used the $Q_{\text{HR}}$ of their own home range; and for dispersers that did not find a home range, we applied a mortality rate that corresponds to $Q_{\text{HR}} = 4$. 

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