The relative effects of habitat loss and fragmentation on population genetic variation in the red-cockaded woodpecker (*Picoides borealis*)

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Abstract

The relative influence of habitat loss, fragmentation and matrix heterogeneity on the viability of populations is a critical area of conservation research that remains unresolved. Using simulation modelling, we provide an analysis of the influence both patch size and patch isolation have on abundance, effective population size (N_e) and F_{ST} . An individual-based, spatially explicit population model based on 15 years of field work on the red-cockaded woodpecker (*Picoides borealis*) was applied to different landscape configurations. The variation in landscape patterns was summarized using spatial statistics based on O-ring statistics. By regressing demographic and genetics attributes that emerged across the landscape treatments against proportion of total habitat and O-ring statistics, we show that O-ring statistics provide an explicit link between population processes, habitat area, and critical thresholds of fragmentation that affect those processes. Spatial distances among land cover classes that affect biological processes translated into critical scales at which the measures of landscape structure correlated best with genetic indices. Therefore our study infers pattern from process, which contrasts with past studies of landscape genetics. We found that population genetic structure was more strongly affected by fragmentation than population size, which suggests that examining only population size may limit recognition of fragmentation effects that erode genetic variation. If effective population size is used to set recovery goals for endangered species, then habitat fragmentation effects may be sufficiently strong to prevent evaluation of recovery based on the ratio of census:effective population size alone.

Keywords: effective population size, fragmentation per se, F_{ST} , individual-based model, landscape genetics, O-ring statistics, *Picoides borealis*, spatially explicit population model

Received 7 September 2009; revision received 29 March 2010; accepted 2 April 2010

Introduction

The influence of habitat loss and fragmentation on the viability of populations is a critical area of conservation research (Soulé 1986). At issue is the extent to which loss of habitat area vs. the breaking apart of habitat (i.e. fragmentation per se) contributes to a decline in popu-

lation viability (Fahrig 2003; Lindenmayer & Fischer 2007) and the role of matrix heterogeneity on functional connectivity (Taylor et al. 2006; Revilla & Wiegand 2008). Seeking correlative relationships between landscape pattern and biological variables such as population size, patch occupancy, or species richness, but ignoring biological processes, has led to conflicting and confusing results (Lindenmayer & Fischer 2007). On the contrary, analyses of models including the link between landscape pattern and population processes indicate

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that habitat loss, fragmentation and matrix heterogeneity can critically influence the number of individuals in a landscape (Wiegand et al. 1999, 2005; Revilla & Wiegand 2008) and the occupancy of habitat patches (Hanski & Ovaskainen 2000; Hanski 2005), depending on the species' natural history.

Novel insights into linkages between biological mechanisms and landscape patterns have been generated by applying landscape genetic approaches, which integrate population genetic techniques with spatial statistics to infer how gene flow, genetic drift, and selection are affected by landscape patterns (Manel et al. 2003; Storfer et al. 2007). However, the species-specific effect of habitat loss and fragmentation (Lindenmayer & Fischer 2007) creates a significant challenge for the development of analytical tools to reveal how biological mechanisms are affected by landscape pattern. While the advent of landscape genetics provides promise, we may find that pattern–process interactions remain unique for each species.

We argue that the effects of habitat fragmentation can only be determined using a species-specific analysis capable of determining how biological mechanisms are affected by the spatial arrangement of landscape elements. Such analyses require scale-dependent metrics of landscape structure because the spatial scales at which biological processes interact with landscape patterns may vary across biological processes (Wiegand et al. 1999; Anderson et al. 2010). Scale-dependent landscape metrics can be generated by extending spatial point pattern analysis to categorical raster maps (Wiegand et al. 1999, 2006; Wiegand & Moloney 2004), which provide a moment approximation of landscape structure and are well imbedded into spatial theory (Murrell et al. 2004).

The nascent field of landscape genetics has not yet provided a method to evaluate the influence of landscape features on population processes occurring both within (i.e. drift and inbreeding) and among (i.e. gene flow) population units to understand migration–drift dynamics in complex landscapes (Storfer et al. 2007; Balkenhol et al. 2009). Inferring rates or patterns of gene flow from population genetic differences often requires an assumption of migration–drift equilibrium. However, stable environmental conditions required to achieve migration–drift equilibrium often do not exist, especially for populations of conservation concern (Nei 1986; Whitlock 1992).

In this study, we evaluate how landscape heterogeneity may affect demographic and genetic responses of fragmented populations using an individual-based, spatially explicit population model (SEPM) for the red-cockaded woodpecker (RCW; *Picoides borealis*). The strength of genetic drift and inbreeding is estimated based on the concept of effective population size, which is defined as the size of an ideal Wright–Fisher popula-

tion experiencing the same rate of genetic change, due to drift or inbreeding, as the study population (Kimura & Crow 1963). The effective population size is often a fraction of the census population size (Frankham 1995). Estimates of effective population size are critical for species of conservation concern as they indicate when drift and inbreeding will lead to the erosion of adaptive genetic variance (Palstra & Ruzzante 2008).

Our objective was to estimate the significance of habitat area, fragmentation and matrix heterogeneity by revealing pattern–process interactions involving inbreeding, genetic drift, and gene flow. For this, we evaluated how landscape heterogeneity may affect demographic and genetic responses of simulated RCW populations. We extended an existing modelling approach which has been able to reveal how landscape configuration affects population parameters in fragmented populations (Wiegand et al. 1999, 2005) by incorporating genetic processes. The RCW simulation model (Letcher et al. 1998) is ideally suited for this purpose as it integrates 15 years of field work and has been extensively validated (Schiegg et al. 2005), providing confidence that the method is capable of capturing a reasonably realistic representation of pattern–process interactions observed in nature.

Rather than inferring process from patterns (e.g. Spear et al. 2005; Cushman et al. 2006; Lindsay et al. 2008), our approach infers patterns from process. This is accomplished by applying the simulation model of population processes to a large number of landscapes that vary independently in landscape composition and configuration. The approach then relates biological variables of interest to scale-dependent measures of habitat configuration. We first relate the simulated demographic and genetic variables to habitat amount based on traditional, nonspatially explicit theory, and then relate the simulated biological variables to both habitat area and scale-dependent landscape metrics. This allowed us to estimate how much of the variation in demographic and genetic variables can be explained by traditional, nonspatially explicit theory and how useful descriptors of landscape structure are for understanding biological mechanisms. The results of this pilot study applied to RCWs demonstrate that by accounting for both landscape composition and configuration, referred to in spatial statistics as first and second order effects of landscape pattern, we can simultaneously consider the influence migration and genetic drift have on the spatial apportionment of genetic variation.

Methods

We simulated population responses to landscape composition and configuration using an approach comprised

of three basic elements: first, a landscape generator that creates a high number of landscapes with independent control over landscape composition and configuration; second, an individual-based SEPM that simulates population dynamics and the spatial apportionment of genetic variation within these heterogeneous landscapes; and finally, scale-dependent landscape metrics used to correlate the emerging population and genetic indices to the corresponding measure of landscape structure (see Wiegand et al. 1999, 2005 for earlier applications of this approach in a population dynamics context).

Our null hypothesis is that habitat fragmentation, or landscape configuration, has no effect on population processes (i.e. recruitment and migration) and that the only important landscape metric is habitat amount, or landscape composition. We test this hypothesis using statistical models that relate the demographic and genetic response variables to habitat amount based on traditional, nonspatial theory. Then, we tested the alternative hypothesis that habitat fragmentation matters by relating the residuals of the nonspatial statistical models to measures of landscape configuration (i.e. second order effects).

The demographic and genetic response variables included the number of potential breeding groups (PBGs, the number of nest sites containing both an adult male and female with or without offspring), effective population size (N_e), and proportion of total genetic variation due to population subdivision (F_{ST}). F_{ST} is expected to decrease as rates of migration among breeding groups increase and as rates of genetic drift decrease, and provides an indication of the amount of relatedness among individuals within a breeding group (Whitlock 2004). Below we describe how these variables were estimated and the landscape treatments used to build the statistical models.

Red-cockaded woodpecker population model

The SEPM for the RCW simulates the species' complex mating system characterized by male philopatry (Walters et al. 1988). The SEPM was originally described in Letcher et al. (1998), and our version of the model was updated to include population genetic data (Bruggeman et al. 2009) as well as the influence landscape pattern has on dispersal behaviours and the strength of male philopatry (Bruggeman & Jones 2008).

Red-cockaded woodpeckers are a monogamous, cooperative breeding species, in which breeding groups consist of reproductively active male and female, nestlings or fledglings, and, occasionally, helpers who are usually male and full or half-sibs to the fledglings (Walters et al. 1988). Breeding groups defend territories (i.e. one cell in our simulations) that serve as reproductive and

foraging habitat. Helpers take over a territory after the male's death, and when this occurs the adult female disperses to avoid inbreeding.

To simulate male philopatry, we included the logistical regression equation derived by Pasinelli & Walters (2002), which described how the probability of male natal dispersal (or the probability of not staying as a helper) is negatively associated with adjacent habitat quality but positively associated with number of breeding vacancies within 3.5 km. All female fledglings leave their natal territory within the first year.

Dispersing individuals, or 'floaters', of both sexes are present in the region, which move continuously seeking a breeding vacancy in a territory. The model assumes that all females and first year male floaters disperse 1.4 km per season, or two cells, and older male floaters move 0.707 km per season, or one cell. To simulate foray behaviours, in which, as observed in the field (J. Walters, personal communication), birds search for breeding vacancies by embarking on multiple dispersal events while returning back the same starting location, the model assumes that fledglings, helpers, and floaters can compete for breeding vacancies within a 3.5 km radius of their current seasonal location, or five cells.

We updated the RCW SEPM to reflect recent studies on the influence landscape patterns have on dispersal. Field observations indicate that female floaters rarely cross nonforested gaps greater than 600 m (J. Walters, personal communication). Therefore, we removed females from consideration as competitors if a nonforested cell was present in between their current location and the vacant territory even if the vacancy was within 3.5 km. In contrast, there is no evidence that males exhibit gap avoidance, and the model assumes male helpers and floaters showed no gap avoidance behaviours when competing for breeding vacancies.

To update the floater movement rules, we employed a habitat-based correlated random walk model (Bruggeman & Jones 2008; Supporting Information). To reflect gap avoidance by females, the model assumed that females make directional choices based on forest cover, showing the greatest preference for high quality habitat, but when all eight adjacent cells contain the same land cover, birds tend toward straight movement. For male floaters, we assumed straight dispersal, in which birds make directional choices based on their direction of movement in the previous time step, but if high quality habitat is available in the 45° location the bird may change direction.

Landscapes

We used landscapes composed of three habitat classes that are of substantial importance for RCW population

dynamics: high quality habitat (class 1, mimicking longleaf pine savannah), low quality habitat mostly used for movement (class 2, being second growth mixed hardwood-pine forests) and nonforested areas (class 3). We generated landscapes represented by categorical raster maps that were composed of a 50 - 50 grid of cells. Each cell represented 50-ha, the average RCW territory size in old growth longleaf pine savannah (Engstrom & Sanders 1997). Each 50-ha cell could be of one of the three habitat classes. One cell of high quality habitat could contain at most one breeding group.

The main focus of our analyses is amount vs. fragmentation of high quality habitat. We therefore generated landscapes in which the spatial configuration of high quality habitat varies from highly fragmented to highly contiguous, thus covering the entire range of interest (Fig. 1). Based on the results of Wiegand et al. (1999) and given the objective of our study we limited our analyses to five representative arrangements of breeding habitat that suffice to show the main effects.

Our second focus is the effect of matrix heterogeneity on population variables. A major question is whether structural connectivity (i.e. physical connectivity of the landscape elements provided by dispersal habitat) provides functional connectivity (i.e. movement along dispersal habitat that link patches; Taylor et al. 2006). We therefore used landscapes in which different proportions of dispersal habitat smoothly increased structural connectivity. The simplest way of doing this is arranging dispersal habitat as buffer around breeding habitat. We therefore used the landscape generator presented in Wiegand et al. (1999) to create landscapes meeting these

constraints. Details on the algorithm are provided in Supporting Information.

Figure 1 shows the five representative landscape physiognomies (i.e. arrangements of high quality habitat). The landscapes range from highly fragmented high quality habitat (left column) over intermediate states of fragmentation with increasing contiguity (middle columns) to perfectly contiguous landscape (right column). The landscape generator allowed us to generate breeding habitat with approximately the same spatial configuration, but different habitat amount ($F_1 = 0.025, 0.05, 0.07$). For a given amount of breeding habitat, we included four levels of dispersal habitat from $F_2 = 0.1$ in which dispersal habitat provided little structural connectivity to $F_2 = 0.7$ in which dispersal habitat provided high structural connectivity (Fig. 1). Therefore, five landscape physiognomies were examined each having 12 different compositions of high (three levels) and low (four levels) quality habitat. Additionally, a buffer zone of five cells of class 2 and 3 was added to the periphery of each landscape to remove edge effects that might affect directional choices during natal dispersal. Thus, population dynamics was simulated across an 180 000-ha area.

Genetic indices

We also modified the RCW SEPM to estimate effective population size (N_e) directly based on the change in genetic variation over time. Using an SEPM, we directly simulate demographic and behavioural components of the actual population that deviate from the ideal

Fig. 1 Landscapes used in the simulation with 7% high quality habitat (i.e. $F_1 = 0.07$; black). From top to bottom: proportion of low quality habitat $F_2 = 0.1, 0.3, 0.5, 0.7$ (dark grey), from left to right: landscape physiognomy changing from highly fragmented habitat (type A) to nonfragmented habitat (type E). Light grey areas are nonforested. For the values of the O-ring indices in these landscapes see Fig. A1 (Supporting Information).

Wright–Fisher population (e.g. overlapping generations, variance in reproductive success, mating system, fluctuating population size, and asymmetric immigration). N_e can be estimated to reflect the different processes that lead to the change in genetic variation [e.g. inbreeding (N_eI) and variance (N_eV) effective population size estimate the size of a genetically ideal population losing genetic variation because of inbreeding and drift, respectively].

To estimate rates of inbreeding and drift in a manner that corresponds to analytical theory (Wright 1969; Whitlock & Barton 1997; Supporting Information), each bird was given two hypothetical genetic loci. At one locus, two unique alleles were assigned to each breeder in the initial population [i.e. an infinite alleles model (IAM) of genetic variation; total alleles = 2 × number of breeders in the founding population]. Therefore, by definition offspring that inherit the same allele from both parents, assuming Mendelian inheritance including independent segregation, are identical by descent allowing a direct estimate of Wright’s inbreeding coefficient. N_eI was estimated by the rate of change in total observed heterozygosity at the infinite alleles locus in fledglings (Supporting Information). At the second locus the total number of alleles was two, and each individual was initially assumed to be heterozygous ($p_0 = q_0 = 0.5$, i.e. a diallelic locus). N_eV was estimated based on the change in allele frequency p in the diallelic locus of the fledglings, which provides a direct measure of drift (Supporting Information). N_eI and N_eV values converge at demographic equilibrium (Kimura & Crow 1963), providing a quantitative criterion for determining when a simulation has been run long enough for genetic processes to reach equilibrium with landscape structure.

Nei’s (1973) theory of gene diversity in a subdivided population was used to estimate correlation of alleles at the infinite alleles locus within and among breeding groups accumulated during the simulation. To simplify analysis, we used F_{ST} as the dependent variable (Nei 1977), which equals the proportion of total genetic variation due to population subdivision. Because of the monogamous mating system, breeding groups were treated as the ‘subpopulation’ as they represent the spatial scale at which alleles are combining at random (Sugg et al. 1996). F_{ST} is estimated as

$$F_{ST} \approx 1 - \frac{H_S}{H_T} \quad (1)$$

The IAM locus was chosen because F_{ST} is theoretically interpreted as the average co-ancestry due to population subdivision (Whitlock 2004).

We incorporated demographic–genetic feedbacks to consider inbreeding depression. Schiegg et al. (2006) estimated lethal equivalents for RCWs based on a pedigree and fledgling survival collected over 20 years in the Sandhills population. We reduced the annual mean number of fledglings per pair, I , based on the following:

$$I \approx 1 - e^{-(4.93k)^2} \quad (2)$$

where k is the kinship coefficient of the parents estimated by the average inbreeding coefficient of four hypothetical offspring.

Ring indices

Landscape ecologists have traditionally used landscape metrics that describe landscape configuration for categorical data (i.e. different landcover types) based on properties of ‘patches’ such as number of patches, edge density, shape index, or contagion (Turner 2005). However, these metrics do not usually permit calculation of the scale-dependent nature of landscape structure and are not based on deeper theoretical considerations. We therefore rely here on an alternative approach from spatial point pattern analysis (Wiegand et al. 1999, 2006; Wiegand & Moloney 2004), based on a moment approximation of landscape structure. The first moments of the spatial pattern are given by the probability that a given pixel (i.e. location r_1) is of habitat class j (i.e. landscape composition). The second moments of the spatial landscape structure are the conditional probabilities of finding habitat class j at location r_2 , conditioned on the occurrence of habitat class i at location r_1 . The second moment $O_{ij}(r)$, the O-ring statistic, is a scale-dependent measure of landscape structure (Wiegand & Moloney 2004) and for its estimation we indexed the n_i cells of habitat class 1 and divided the mean number of class h cells ($h = 1, 2$, or 3) within rings centred at the n_i cells of habitat class 1 by the mean area of these rings, but counting only habitat cells and area inside the study region:

$$O_{1,h}(r) \approx \frac{\sum_{i=1}^{n_i} \text{Points}_h[R_i(r)]}{\sum_{i=1}^{n_i} \text{Area}_h[R_i(r)]} \quad (3)$$

where $R_i(r)$ is a ring with radius r and width 1 centred in the i th class 1 cell, the operator $\text{Points}_h[X]$ counts the class h cells in a region X , and the operator $\text{Area}[X]$ determines the number of cells of the region X (Wiegand & Moloney 2004). Three ring indices were estimated, at scales (r) 1–16 cell radius, describing the correlation of high quality habitat (class 1), low quality

habitat (class 2) and nonforested (class 3) cells to high quality habitat cells. As in Wiegand et al. (1999) we used only ring indices viewing the landscape structure from the perspective of breeding habitat cells (F_1) because most population processes are centred on the cells suitable for territories.

If habitat class h is randomly distributed, the O-ring statistic approximates the value $O_{1,h}(r) = F_h$. If habitat class h tends to be clustered at scale r around class 1 we have $O_{1,h}(r) > F_h$ and if habitat class h tends to be repulsed by class 1 at scale r we have $O_{1,h}(r) < F_h$ (see Fig. A1, Supporting Information). At small scales r , the $O_{11}(r)$ provides an indication of average adjacency of potential territories regardless of other land cover classes (Wiegand et al. 1999). At large scales the univariate $O_{11}(r)$ describes average dispersion of potential territories across a landscape—in contrast, the smaller $O_{11}(r)$ (relative to F_1) the larger the cluster of potential territories (Fig. A1, Supporting Information). High values of the bivariate $O_{1*}(r)$, where $*$ indicates 2 or 3, indicate a high probability of finding one of the other land cover classes at distance r from high quality habitat, providing an estimate of the contribution land cover classes make toward fragmentation at different spatial scales r . Therefore, the O-ring statistic is capable of detecting critical spatial scales associated with fragmentation of high quality habitat.

Floater survival

To determine if the ring indices could detect differences in survival of dispersers imparted by the habitat types crossed, we modelled floater survival in two ways. Letcher et al. (1998) used a 0.62 yearly probability of floater survival for both sexes, based on data collected in the Sandhills region. We assumed that this value represents the probability of survival in high quality and low quality habitat, because the Sandhills region is heavily forested. However, we calculated an adjusted survival probability based on the number of steps per year taken in nonforested areas to simulate increased predation risk (Belisle & Desrochers 2002). The yearly probability of survival was estimated as:

$$\text{Survival}_{\text{floater}} = \frac{1}{4} sf + 0.62 \frac{p}{snf} + M; \quad \delta 4p$$

where sf equals the percent of steps taken in forested cover, snf equals per cent of steps taken in nonforested areas, and M is the probability of survival in nonforested areas. M was set equal to 0.02 and 0.62 to simulate two levels of survival in nonforested areas. Therefore, we simulated two SEPMs that varied the relationship between landscape structure and population processes.

Simulations and model output

The simulation model was run for each of the two floater survival parameters and 12 variations of landscape composition for each of the five landscape types (120 combinations in total). Each combination was run for 400 years and was replicated 100 times to account for stochasticity. Averages across the 100 replicates, and for each year, were taken for PBGs, $N_e I$, $N_e V$, and F_{ST} . The probability of extinction across the 100 replicates was also tracked—extinction occurred when only one breeding group remained. Preliminary model runs indicated that, for most landscape treatments, PBGs reached an asymptote within 20 years, or five generations (Reed et al. 1988). Therefore, we estimated $N_e I$ and $N_e V$, from years 20 to 100. For all treatments, except landscape type A and $F_1 = 0.025$, we found that equilibrium was achieved by year 100 (i.e. $N_e I = N_e V$). For landscape type A and $F_1 = 0.025$, we observed a positive probability of extinction and these treatments often did not reach equilibrium within 400 years. These treatments were excluded from further analysis.

Data analysis

Linear regression (R software package ‘stats’; R Development Core Team 2008), was conducted for both floater survival models to identify relationships between genetic indices, demographic parameters and landscape structure. Each population-level endpoint (PBG, N_e , and F_{ST} , i.e. our dependent variables) was standardized by dividing each value by the maximum value observed across all landscapes and both floater survival parameters to compare the influence habitat area and fragmentation have on the three population endpoints. To compare our results with past estimates of the ratio N_e :PBG for RCWs (Reed et al. 1993), we also performed the regression analysis for N_e without standardizing the data.

A ‘null model’ was developed for each dependent variable to confirm existing analytical spatially implicit theory that relates population size and genetic structure only to habitat area. Therefore, null models approximated the variation in population endpoints due to landscape composition without accounting for landscape physiognomy.

Null model for PBG and N_e . Spatially implicit models that do not account for second order effects of landscape structure (i.e. fragmentation) relate population size linearly to total area of habitat, based on the concept of carrying capacity (e.g. Simberloff 1988; Fahrig 2003). Thus, the null model for PBG is (Wiegand et al. 1999, 2005):

$$PBG \propto F_1; \quad \delta 5b$$

where F_1 is the proportion of high quality habitat (class 1). N_e is not traditionally related to habitat area, but rather demographic variables such as number of breeding groups or demes (Nunney 1993; Whitlock & Barton 1997). Therefore, the null model for N_e (i.e. ignoring the spatial arrangement of breeding groups) is:

$$N_e \propto PBG \quad \delta 6b$$

Null model for F_{ST} . F_{ST} is traditionally related to effective population size of breeding groups (N_{es}) to gain insight into the competing influence genetic drift and gene flow. However, influences of genetic drift and gene flow will vary greatly at local scales in natural populations, because of differences in habitat quality, the spatial arrangement of breeding groups, and the adjacency of breeding groups to land cover types that may facilitate or impeded migration. Population geneticists account for these effects analytically by assuming a spatially homogeneous dispersal process (but see McRae 2006) and equal rates of drift across groups (Whitlock 1992). Rather than ignoring these second order effects, we first related F_{ST} to the first order effects of drift and inbreeding at the total population scale:

$$F_{ST} \propto \log N_e \quad \delta 7b$$

Then, we built fragmentation models using ring indices to determine if variation in rates of drift and migration at local scales could be detected by the ring indices. The log transformation of N_e was appropriate for our data and corresponds to past results. For example, loss of neutral variation because of drift in continuous populations approximates a negative exponential process based on effective population size (N_e , Frankham 1996). Under an Infinite Island Model, F_{ST} decreases exponentially as a function of N_m , effective number of immigrants per generation (Whitlock & McCauley 1999). Expectations from a Finite Island Model indicate that F_{ST} increases exponentially with number of breeding groups (Wang 2004).

Fragmentation models. In a second step, several alternative regression models including second order effects of landscape structure were constructed by including the three ring indices. These models evaluate the ability of the ring indices to capture spatially explicit effects not accounted for by spatially implicit theory. We applied hierarchical model construction and AIC model selection criteria (Fernández et al. 2003). We first regressed

one ring index at one scale against the residuals from the null model regression. This procedure was then completed for each of the three ring indices and all 16 scales independently. Results from these models revealed for each ring index $O_1(r)$ a critical scale r that accounted for the most variance remaining from the null model.

A ‘fragmentation model’ was then assembled by including the independent variable of the null model and the independent ring indices at the critical spatial scales. AIC model selection criteria were then applied, selecting the most parsimonious model with $DAIC < 3$. Spearman correlation analysis of the fragmentation variables [i.e. $O_{11}(r)$, $O_{12}(r)$, and $O_{13}(r)$] included in the final fragmentation model was also preformed (Supporting Information).

Results

For all treatments achieving demographic equilibrium by year 100, the observed frequency of heterozygous genotypes did not deviate significantly from expectations under Hardy–Weinberg equilibrium based on a chi-squared test (Li & Horvitz 1953).

Potential breeding groups

The null model regression indicated that 99% of the variance in PBGs could be accounted for by the composition index fraction of high quality habitat (F_1 ; Table 1). The fitted coefficients and adjusted R^2 values were very similar across the floater survival parameters, but the best null model was observed with the highest disperser survival.

Despite the strong effect of total area of high quality habitat on population size, we examined if inclusion of spatial correlation of land cover classes could improve model fit. Regression of individual O_1 indices against the residuals from the null model indicated that the remaining variance could be accounted for by each of the three ring indices at different spatial scales (Fig. 2a–c). We found two critical spatial scales for the univariate O_{11} and bivariate O_{12} ring indices (Fig. 2a, b), but only one critical scale for O_{13} (Fig. 2c). The probability of finding high quality habitat 1–5 cells away from high quality habitat (O_{11}) accounted for, on average, 55% of variance in the residuals and was positively correlated with the residuals of the null model. When floater survival was low ($M = 0.02$), the probability $O_{12}(9)$ of finding low quality habitat nine cells away from high quality habitat was positively correlated with the residuals and explained as much as 31% of the remaining variance from the null model (Fig. 2b). In contrast, when floater survival was high ($M = 0.62$), the probability $O_{12}(1)$

Table 1 Comparison of null models, rooted in past theories that ignore spatial complexity, to fragmentation models, which incorporate landscape complexity using O-ring index approach (e.g. $O_{11}(r)$ = probability of finding high quality habitat (class 1) at distance r from high quality habitat)

Disperser survival (M)	Null model Y = C + b Q				Fragmentation model Y = C + b Q + a O ₁₁ (r) + b O ₁₂ (r) + c O ₁₃ (r)									
	C	b	Adj. R ²	AIC	C	b	a	r	b	r	c	r	Adj. R ²	AIC (¹ DAIC)
Y = PBG'; Q = F ₁														
0.02		12.6	0.992	310		13.4	+	1	+	9	0.257	3	0.998	392
P-value		< 0.001				< 0.001					< 0.001			(82)
0.62		12.7	0.995	339		13.5	+	1	0.046	1	0.158	4	0.999	402
P-value		< 0.001				< 0.001			0.018		< 0.001			(63)
Y = N _e '; Q = PBG'														
0.02		0.353	0.690	203		0.153	0.437	2	0.204	1	–	4	0.860	245
P-value		< 0.001				0.014	< 0.001		0.004					(42)
0.62		0.356	0.620	183		0.144	0.431	1	0.296	1	0.163	5	0.806	218
P-value		< 0.001				0.083	< 0.001		0.005		0.091			(35)
² Y = N _e '; Q = PBG														
0.02		2.78	0.690	609		1.20	614	2	287	1	–	4	0.860	567
0.62		2.80	0.620	629		1.13	606	1	416	1	229	5	0.806	594
Y = F _{ST} '; Q = log(N _e)'														
0.02	1.26	0.546	0.635	350	1.12	0.407	0.524	13	–	6	0.106	3	0.787	378
p-value	< 0.001	<0.001			< 0.001	<0.001	0.003				< 0.001			(28)
0.62	1.26	0.540	0.629	352	1.11	0.393	0.477	13	–	6	0.099	4	0.768	377
P-value	< 0.001	<0.001			< 0.001	<0.001	0.009				0.001			(25)

Spatial scales (r) for all O-ring indices were identified by regressing the residuals from the null models ($Y = C + bQ$) against each spatial scale independently. AIC model selection was used to determine the most informative O-ring indices for inclusion in the fragmentation models. If AIC model selection led to dropping an O-ring index, (+) or (–) is included to indicate its relationship with the dependent variable. All variables were standardized to 0 to 1 (e.g. $PBG^* = PBG/\max(PBG)$). Results for N_e without standardization are included to facilitate comparison of the N_e :PBG reported in past studies. (sample size = 56 landscape treatments).

¹DAIC = AIC for null model—AIC for fragmentation model.

²P-values not presented as they are identical to those observed for normalized data.

Fig. 2 Adjusted R^2 values from the regression of O-ring indices at scales 1–16 (r) against the residuals from the null models for all endpoints. Closed circle: $M = 0.02$. Open circle: $M = 0.62$.

explained the majority of the residual variance (29%) and was negatively correlated with the residuals. The most important ring index was the probability of find-

ing nonforested areas 3–4 cells away from high quality habitat ($O_{13}(3-4)$), accounting for 72% and 58% of the residual variance for low and high floater survival,

respectively. The spatial scale associated with O_{13} for high floater survival increased by one unit relative to low floater survival to 4.

Based on AIC model selection criteria, the fragmentation model for low floater survival included only $O_{13}(3)$. The AIC values of this fragmentation model decreased considerably compared with the null model (Table 1). For high floater survival, both $O_{12}(1)$ and $O_{13}(4)$ were selected.

Effective population size

The null model for N_e indicated that only 62–69% of total variance in N_e was explained by the number of PBGs (Table 1). In contrast, 81–86% of total variance in N_e was explained when including ring indices in the fragmentation model. N_e was positively correlated with PBGs. The intercept term was dropped out because it was not significantly different from zero for both floater survival assumptions.

The critical scales accounting for the majority of residual variance from the null model were similar to those observed for PBGs (Fig. 2d–f). We observed two peaks in adjusted R^2 for O_{11} at lag distances 1–2 and 16 (Fig. 2d). At small lag distances the relationship between N_e and O_{11} is positive, but the relationship is negative at longer lag distances (Table 1). For the ring indices O_{12} , the biggest peak was observed at a lag distance of one cell (Fig. 2e), which was negatively correlated with N_e . For O_{13} the lag distances at four or five units contributed most to variance in N_e (Fig. 2f). The fragmentation model for low floater survival ($M = 0.02$) included $O_{11}(2)$ and $O_{12}(1)$. The fragmentation model for high floater survival included all possible ring indices [$O_{11}(2)$, $O_{12}(1)$, and $O_{13}(5)$].

Proportion of total genetic diversity because of population subdivision

The null model for F_{ST} indicated that 63–64% of total variance in F_{ST} was explained by $\log(N_e)$ (Table 1). In contrast, 77–79% of total variance in F_{ST} was explained when including ring indices in the fragmentation model. F_{ST} was negatively correlated with $\log(N_e)$.

Critical scales observed for O_{11} and O_{12} were roughly the inverse of those observed for PBGs and N_e (Fig. 2g–h). Regression of ring indices against the residuals indicated that $O_{11}(13)$ explained the majority of the remaining variance from the null model (Fig. 2g). The probability $O_{12}(6)$ was negatively correlated with F_{ST} and was more important for low floater survival (Fig. 2h). In contrast, $O_{11}(13)$ and $O_{13}(3–4)$ were positively correlated with F_{ST} . AIC model selection indi-

cated the best fitting models for both floater survival assumptions included $O_{11}(13)$ and $O_{13}(3–4)$.

Discussion

Using an ecologically realistic model, we have been able to contrast the effects of habitat area vs. fragmentation on multiple characteristics of population structure. In our system, the sole analysis of demographic variables would lead one to conclude that habitat fragmentation does not affect population viability. Holding habitat area constant, second order effects of landscape configuration accounted for only an additional 0.6–0.4% of the variance in PBGs. In contrast, second order effects (i.e. landscape configuration) contribute more substantially to the prediction of N_e , accounting for, on average, an additional 18% of the residual variance from the null model. Further, the fitted coefficients for each O-ring index (a–c) are larger than the fitted coefficient for PBGs. Therefore, although the null model explained 62–69% of the variance in N_e , when both first and second order statistics are incorporated into a single equation, we found that second order effects are more important. We found an additional 14–15% of the variance in F_{ST} was due to second order effects not already accounted for by second order effects reflected in N_e . Inclusion of second order effects contributed less to prediction of population endpoints when floater survival was not decreased by crossing nonforested areas. Therefore, demographic stochasticity contributes more to the observed variation in these cases.

The ratio of effective population size to PBGs was very sensitive to second order effects. The null model, ignoring these effects, indicated that the ratio was 2.8 for the most ecologically plausible dispersal assumption (i.e. for $M = 0.62$, $b = 2.80$ in Table 1; or $N_e:N_b = 1.4$, where $N_b = 2\text{PBG}$). Therefore, inclusion of only first order effects (i.e. the pure effect of habitat availability) indicates that the simulated population is losing genetic variation due to drift and inbreeding more slowly than a genetically ideal population of the same size. Given the complex mating system, including inbreeding avoidance behaviour, this result is perhaps not surprising, as other species have demonstrated an ability to retain more genetic variation than expected in a randomly mating population (Sugg et al. 1996). However, when second order (i.e. configuration) effects are included, we found that the ratio of N_e :PBG to be 1.13 for $M = 0.62$ (Table 1; or $N_e:N_b = 0.57$). Previous estimates of N_e for RCWs were based on demographic methods, which account for departures from a genetically ideal population, found $N_e:N_b$ ratios from 0.65 to 0.8 (Reed et al. 1993). Our estimate, which is a direct estimate of N_e based on the erosion of genetic variation

over time and accounts for both first and second order effects, corresponds more closely to theoretical estimates by Nunney (1993) who found $N_e:N_b \sim 0.5$ under a variety of mating systems in continuously distributed populations (i.e. second-order effects were excluded from the analysis).

The sensitivity of N_e to habitat fragmentation per se indicates that the spatial association of habitat can have a significant effect on a population's adaptive potential (Palstra & Ruzzante 2008). This finding is a strong argument against the viewpoint that spatial configuration makes little or no difference for population viability compared with the total amount of suitable habitat in the landscape (i.e. Fahrig 2003). The conservation implication is that increases in habitat adjacency could more effectively ameliorate the erosion of genetic variation than increases in habitat area alone. Further, our results suggest that conservation planning based solely on demographic criteria could lead to fragmented landscapes in which populations expected to be demographically stable maintain a much smaller effective population size than would be possible if landscape and genetic factors were recognized. Bruggeman et al. (2009) demonstrated how both demographic and genetic criteria could be used to inform tradeoffs between habitat area and connectivity while accounting for nonequilibrium conditions common to conservation planning.

Inferring pattern from process

All simulation models included feedback mechanisms between adjacency of breeding territories, which leads to retaining more helpers (Pasinelli & Walters 2002), and the increased production of fledglings (Letcher et al. 1998). Landscapes with high quality habitat adjacent to high quality habitat [i.e. high values of $O_{11}(1-2)$] were associated with larger effective population sizes. In fact, we found this was the most important factor explaining N_e . When nonforested areas decreased floater survival ($M = 0.02$), the scale associated with O_{11} was 1 unit greater than observed for $M = 0.62$. Therefore, the scale that explained most of the residual variance from the null model increased in the presence of matrix friction, indicating the importance of larger patches (Fig. 2d). Similarly, we found that fragmentation of breeding habitat by low quality habitat (class 2) adjacent to high quality habitat decreased N_e (Table 1).

A possible reason for the discrepancy in $N_e:N_b$ ratios between our study and that of Reed et al. (1993) could be the indirect influence the second moments of landscape structure may have on the demographic variables they used to estimate N_e . For example, individual survival and variance in reproductive success among

groups, critical demographic variables used to indirectly estimate N_e , could be influenced by the second moment structure of the landscape. Our SEPM includes one such feedback mechanism (i.e. number of fledglings < number of helpers < spatial autocorrelation of breeding habitat). Therefore, landscapes with high values of $O_{11}(1-2)$ will also be expected to have lower variance in reproductive success among groups, and therefore greater N_e , as these groups will have a similar number of helpers.

Another important spatial scale is the perceptual range at which fledglings and floaters can compete for breeding vacancies (i.e. within five cells). The negative relationship between PBG and the ring index O_{13} at critical scales 3 or 4 indicated that the presence of nonforested areas at the edge of the bird's perceptual range decreased population size. Similarly, the presence of nonforested areas at the edge of the bird's perceptual range increased F_{ST} , or the average co-ancestry within groups. The index O_{13} at critical scales 4 or 5 was negatively associated with N_e , indicating that the presence of nonforested habitat at the edge of a bird's perceptual range increased the erosion of genetic variation. It is interesting to note that the coefficient associated with O_{13} was strongest, and the critical scale of fragmentation was smaller, when floaters were penalized for crossing nonforested gaps (Fig. 2c,i). So the importance of O_{13} may reflect the presence of landscape friction (Ricketts 2001; Spear et al. this volume).

Landscape friction was also likely detected with O_{12} . Recall that two peaks were observed at lag distance 1 and 9 for PBG (Fig. 2b). The regression coefficients switch from negative at $O_{12}(1)$ to positive at $O_{12}(9)$. Therefore, fragmentation of high quality habitat by adjacent low quality habitat decreased PBG, but the presence of poor quality habitat far from good quality habitat increased PBG. Assuming $M = 0.02$, $O_{12}(9)$ was more important than $O_{12}(1)$. Therefore, the presence low quality forested habitat, which does not contribute to a reduction in disperser survival, far from breeding habitat, increased rates of dispersal.

The contribution low quality habitat makes to dispersal was also detected in F_{ST} values. The probability $O_{12}(6)$ was negatively related to F_{ST} , indicating increased rates of dispersal among breeding groups. While this index dropped out during AIC model selection, it was more strongly correlated with the residuals in the presence of landscape friction (Fig. 2h). The most important ring index for predicting F_{ST} was $O_{11}(13)$. When $O_{11}(13) = F_1$ indicates that breeding habitat is randomly distributed at lag 13 cells, indicating high fragmentation of breeding habitat in our landscapes (see Fig. A1, Supporting Information). Conversely, landscapes where breeding habitat was clustered showed

values of $O_{11}(13) = 0$ (Fig. A1, Supporting Information). Thus, $O_{11}(13)$ depicts a large-scale isolation effect of good quality habitat. The positive relationship between $O_{11}(13)$ and F_{ST} indicates that when patch size is small, and high quality habitat is scattered, loss of genetic variation because of drift will be higher and rates of migration lower. In a review of empirical genetic studies, Keyghobadi (2007) found that the great majority of studies found the same link between landscape pattern and spatial apportionment of genetic variation. The scale-dependent measures of habitat fragmentation offered here provide an analytical construct for evaluating these effects that, if adopted, would lend consistency necessary for comparing studies of fragmentation.

Contribution to landscape genetics

We found that the complex spatial population genetic structure arising in fragmented landscapes can be described by relatively simple and theoretically well justified landscape indices. To our knowledge, this study represents the first approach to relate genetic structure to physical structure of the landscape incorporating multiple land cover classes and critical spatial scales that describe habitat fragmentation. By accounting for both first and second order effects of landscape pattern we can consider the influence migration and genetic drift have on the spatial apportionment of genetic variation simultaneously. In contrast, spatially implicit models in population genetics such as Wright's Island Model hold second order effects constant by assuming equal rates of drift and homogeneous dispersal. Our approach also contrasts with studies using Mantel tests that establish correlative relationships between landscape attributes between two points (e.g. distance or habitat type) and genetic divergence also observed between these two points (Spear et al. 2010). The Mantel test provides a very useful approach for inferring how the second moments of landscape structure affects dispersal within a single landscape, but requires testing post-hoc hypotheses regarding the relationship between land cover and dispersal behaviours and an assumption of migration–drift equilibrium.

Analysis of genetic variation incorporating both first and second order effects, not requiring an assumption of migration–drift equilibrium, led to novel results. We observed the response of residuals from the null models for N_e and F_{ST} across scales for O_{11} display an inverse relationship. This scale-dependent relationship has never been characterized before in a heterogeneous landscape. While the shape of this relationship across scales may result from RCWs particular life history traits, the inverse relationship for N_e and F_{ST} observed

with O-ring indices maybe common across species and warrants further investigation. The similarity in shape for the response of all O-ring indices across scales for PBGs and N_e , although fragmentation had very little effect on PBGs, is also interesting. These inter-relationships could reveal unique aspects of natural history. For example, the contrasting sensitivity between PBG and N_e maybe indicative of competition for breeding vacancies that leads to high occupancy rates but few successful long distance dispersal events. A strong competition for space has been previously recognized for this species and results from the time needed to excavate nesting cavities in live pines (i.e. 6–10 years; Conner et al. 2001).

We believe landscape indices theoretically rooted in point pattern analysis will have wide application in landscape genetics as summary statistics useful for identifying important second order effects. Point pattern analysis can be applied in a variety of environmental systems (Wiegand & Moloney 2004). Certainly, SEPMs have also been developed for a great diversity of populations (Grimm et al. 2005). Despite the potential broad applicability, some important limitations should be mentioned. Our approach is designed to compare different landscapes and not to make inference within a given landscape as is performed with Mantel tests. Use of a territorial species, a well specified SEPM (Schiegg et al. 2005), and computer simulations, which permitted a large sample size across a variety of landscape treatments, likely helped to generate the strong relationships between pattern and process we observed. Our use of computer simulations to infer pattern from process is one example of the contribution individual-based SEPMs can make toward development of new statistical approaches capable of distilling the relationship between landscape heterogeneity and population genetic processes (Epperson et al. 2010). The next step in development is application with empirical genetic data to determine how well we can infer process from patterns. Field application must contend with issues of sampling from very few landscapes and only a subsample of the true genetic population.

Acknowledgements

We thank Lisette Waits and four anonymous reviewers whose comments significantly improved this paper. We also thank Pat Zollner for suggesting this collaboration, Michael Blum for his review and discussions, and Kim Scribner for informing us about this special issue. DJB was supported by a Guest Scientist Grant from Helmholtz UFZ Department of Ecological Modelling and by the U.S. Department of Defense, through the Strategic Environmental Research and Development Program (SERDP). NF was supported by a Marie Curie Fellowship by the European Commission (HPMD-CT-2001-00109).

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DJB focuses on development of demographic-genetic models for use in endangered species management and the extension of spatial ecology to environmental policy. TW’s research entails the extension of point pattern analysis to ecological systems and the use of individual-based models. NF focuses on the application of spatial ecology to understand vertebrate habitat relationships and population dynamics, including wildlife epidemiology.

Supporting information

Additional supporting information may be found in the online version of this article.

Appendix A. Generation of landscapes and figures of O-ring statistics.

Appendix B. Details of RCW SEPM.

Appendix C. Results of Spearman rank correlation analysis of O-ring statistics included in fragmentation model.

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