Chapter 20

Habitat Fragmentation Effects Depend on Complex Interactions Between Population Size and Dispersal Ability: Modeling Influences of Roads, Agriculture and Residential Development Across a Range of Life-History Characteristics

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20.1 Introduction

Habitat loss and fragmentation are widely believed to be the most important drivers of extinction (Leakey and Lewin 1995). The habitats in which organisms live are spatially structured at a number of scales, and these patterns interact with organism perception and behavior to drive population dynamics and community structure (Johnson et al. 1992). Anthropogenic habitat loss and fragmentation disrupts these patterns and is expected to have large, negative effects on biodiversity (Flather and Bevers 2002; Haila 2002; Fahrig 2003). The majority of theoretical studies suggest that the effect of habitat fragmentation is weak relative to the effect of habitat loss (Fahrig 1997; Henein et al. 1998; Collingham and Huntley 2000; Flather and Bevers 2002; Fahrig 2003), although some studies have predicted larger fragmentation effects (Boswell et al. 1998; Burkey 1999; Hill and Caswell 1999; Urban and Keitt 2001). In addition, some theoretical studies suggest that the effects of fragmentation per se should become apparent only at low levels of habitat amount, for example below approximately 20–30% of the landscape (Fahrig 1998; Flather

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and Bevers 2002), although there is little empirical evidence available to test this prediction (Fahrig 2003).

The results of empirical studies of habitat fragmentation are often difficult to interpret because many studies fail to address habitat fragmentation at the landscape-level, and most do not distinguish between habitat loss and habitat fragmentation (McGarigal and Cushman 2002; Fahrig 2003). Fragmentation is a landscape-level process and its effects cannot be resolved through fragmentation it is necessary to experimentally or statistically control for the effects of habitat loss (McGarigal and McComb 1995; McGarigal and Cushman 2002). In order to understand the population and species level implications of these relationships it is necessary to move from site-specific inferences to assessments of how the influences of multiple factors interact across large spatial extents in influencing population size and population connectivity (Ruggiero et al. 1994; Bowne and Bowers 2004; Cushman 2006). Non-spatial studies conducted at local scales do not provide a basis for inferences at the landscape or regional level (McGarigal and Cushman 2002). There is often a gross mismatch between the scale of ecological research and population-level responses (Kareiva and Anderson 1988; Ruggiero et al. 1994). Landscape-level studies that explicitly include the spatial patterns of the environment in a representation relevant to the organisms of question, and that address species-specific movement and abundance parameters are essential to extend fine-scale species environment relationships to the level of regional populations (Cushman 2006).

In this paper we present an analysis of habitat fragmentation by roads and residential and agricultural land uses on a broad range of hypothetical vernal pool breeding animals in western Massachusetts. Our analysis models the distribution and expected densities of dispersing organisms in the terrestrial environment based on a factorial implementation of least-cost dispersal models. Our major goal is to quantify the relative influences and interaction of roads and land cover on the area and configuration of occupied terrestrial habitat for 90 different hypothetical organisms representing a factorial combination of population sizes and dispersal abilities. We test five specific hypotheses:

1. Habitat connectivity, as measured by correlation length (McGarigal et al. 2002), will increase with both population size and dispersal ability.
2. Thresholds will exist where habitat connectivity drops dramatically at low population sizes and low dispersal abilities.
3. Population size and dispersal ability will interact such that thresholds of habitat connectivity will be exacerbated at when population size and dispersal ability are both low.
4. The effects of habitat fragmentation by roads will have relatively smaller effects than habitat loss due to land cover change.
5. The effects of habitat loss and fragmentation will be disproportionately high for species with large dispersal abilities.

20.2 Methods

20.2.1 Input Data

20.2.1.1 Vernal Pool Data

We used the distribution of vernal pools in Western Massachusetts as breeding sites in the models. Vernal pools provide important habitat for a variety of species, including some amphibians that breed exclusively in vernal pools. Locations of vernal pools were obtained from the NHESP Potential Vernal Pools coverage photo-interpreted by the Commonwealth of Massachusetts Natural Heritage & Endangered Species Program (Compton et al. 2007). This data layer identifies the locations of more than 29,000 potential vernal pool habitats. These pools provide a spatially realistic pattern of source populations in a real landscape, which adds an important degree of realism to our simulations.

20.2.1.2 Ecoregional Data

The US Environmental Protection Agency has delineated thirteen ecoregions in Massachusetts, based on geology, hydrology, climate, and the distribution of species. In this study we consider the ten ecoregions that comprise Western Massachusetts. We combined portions of the *Taconic Mountains* and *Western New England Marble Valleys/Berkshire Valley/Houstonic and Hoosic Valleys* ecoregions due to disjunctions, small size and irregular shape. This served to reduce edge effects, and make the areas comparable to the other ecoregions, which is important for comparability of model output. Also, given the relative ecological similarity of these two ecoregions we felt this union did not introduce appreciable subjectivity into the analysis. Thus, we implemented the analysis for eight ecoregional units in Massachusetts (Fig. 20.1).

20.2.1.3 Road and Landcover Data

The roads data were derived from USGS 1:100,000 Roads Digital Line Graphs (DLGs) with additional linework from the Massachusetts Highway Department (MHD). The road classes in this layer are listed in Table 20.1. The landcover map used in this analysis was provided by MassGIS, and contains 37 land use categories interpreted from 1:25,000 aerial photography taken in 1999. We converted the coverage to a raster grid, with a 15 m cell size. In addition, we reclassified the map into seven classes which we deemed to be most relevant to the ecologies of vernal pool breeding amphibians (Table 20.1).

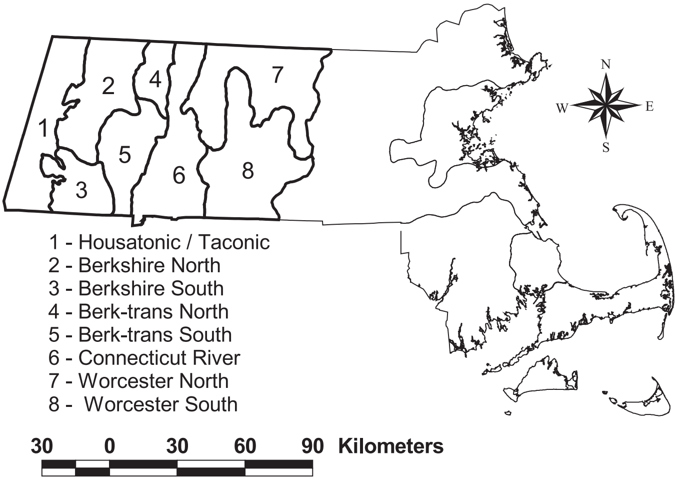

Fig. 20.1 Map of the area covered in this study. The study area consists of the eight ecoregions shown here, which cover approximately 15,000 km^2 of Western Massachusetts. These ecoregions were defined by the United States Environmental Protection Agency

Table 20.1 Road and landcover classes used in the Road and Road + Land Use scenarios. The resistance values reflect the relative cost of traveling through a cell of that class, in comparison to the minimum value of 1

Road classes	Resistance value	Landcover classes	Resistance value
Minor street	20	Forest	1
Major arterial	30	Grass/open land	10
Two-lane highway	50	Low density residential	10
Multi-lane highway	75	Row crop	20
Limited access multi-lane highway	100	High-density residential	30
		Urban	50
		Water	50

20.2.2 Model of Terrestrial Phase Amphibian Density

Our model is based on least-cost dispersal from point sources. The sources in our case are the locations of individual pools. The model calculates the probability of an organism being present in each pixel around the source, given the number of individuals which originated in the source, the dispersal ability of that species, the nature of the dispersal function, and the resistance of the landscape (Compton et al. 2007). In our analysis we use a normal probability density function as the basis of the dispersal model. In a homogeneous environment the expected density of dispersing organisms in the environment surrounding the source will be Gaussian, with the peak at the source, and the density dropping off according to the normal distribution with a standard deviation set according to the dispersal ability of the species. The standard deviation in this dispersal function represents the dispersal ability of the modeled organism. We wished to bracket the range of dispersal abilities of animal species breeding in Massachusetts vernal pools. Accordingly, we ran the models over nine levels of dispersal ability (D), corresponding to standard deviations of the normal dispersal function of 100, 200, 300, 400, 500, 600, 700, 800, and 900 m. In addition, habitat connectivity may be influenced by the population size originating at the breeding sites. Accordingly, we simulated ten levels of populations size (P), ranging from 100 to 1,000 individuals per pool, by units of 100.

The model works by clipping an area of a given number of standard deviations around each pool and calculating the expected density within that. We calculated expected densities within 2.5 standard deviations of dispersal ability, which will include over 99% of the dispersing individuals. Within the clipped area the model calculates the expected density according to the normal dispersal function, accounting for the resistance of the surrounding landscape. A resistance value is given to each class in the land-cover and roads maps. The resistance value is in the form of the cost of crossing that cover type relative to the least cost cover type. These costs are used as weights in the dispersal function, such that the expected density in a pixel is down-weighted by the cumulative cost from the source, following the least cost route (Compton et al. 2007). Once the expected density around each pool is calculated, the values for all pools at all locations are summed to give the total expected density at each pixel. The resistance values for each land-cover class and road class are shown in Table 20.1. These resistance values are hypothetical and are not intended to optimally represent the responses of any particular species, although they are consistent with empirical data for several vernal pool breeding species in Massachusetts (Gamble unpublished data). The results of the model are surfaces of expected density of dispersing organisms in the upland environment (Fig. 20.2).

20.2.3 Modeling Scenarios

We conducted a four-way factorial modeling experiment. The four factors are (1) scenario, (2) dispersal ability, (3) abundance level, and (4) ecoregion. There were three levels of the factor scenario. These are null, roads, and roads plus land use. In the null scenario the expected density of amphibians is modeled across a null landscape where every cell has a resistance of 1. This provides a baseline prediction of distribution expected in the absence of any differential resistance in the landscape. In the roads scenario, roads were given resistance according to the definitions provided above, but the remainder of the landscape retained a resistance of 1. This scenario models the influences of roads in the absence of any differential resistance due to landcover, and provides a measure of the relative influence of roads. The third scenario includes the resistance of both roads and land use. The differences between the second and third scenario provide a measure of the relative influence of land use, and the third scenario itself gives a measure of the combined influences of

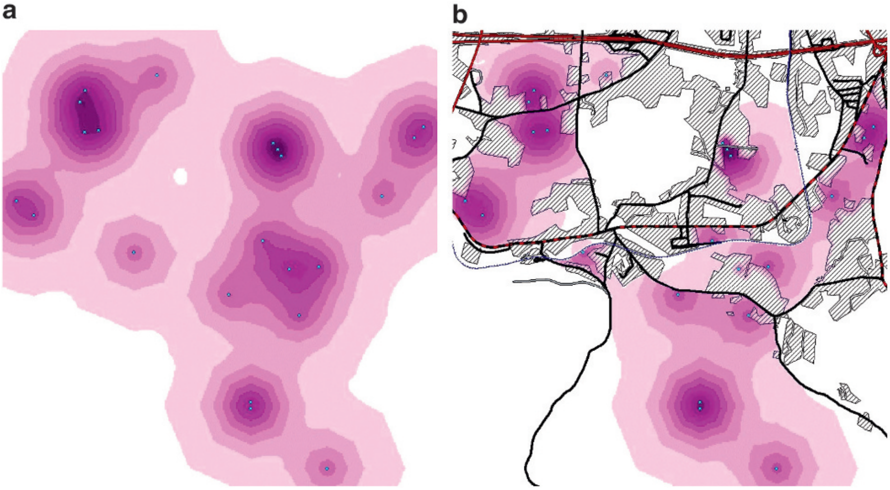

Fig. 20.2 Example of changes in population connectivity predicted for a small area of one ecoregion between the Null (**a**) and Roads + Land Use scenario (**b**). The relative darkness of the filled area indicates the expected density of dispersing juveniles in the uplands based on the least-cost kernel dispersal model. In the Roads + Land Use scenario roads are represented by solid lines and residential areas by cross-hatched polygons. These features reduce both the predicted area of dispersal habitat and the expected density of amphibians within it

roads and land use, and provides a measure of the full effect of human development on habitat connectivity (Fig. 20.3).

The factor dispersal ability had ten levels, abundance nine levels and ecoregion eight levels, as discussed above. We ran the model over the 1920 combinations of these four factors. For each combination we created an output grid showing the expected density of the organisms in each cell of the landscape. These grids have a 15 m cell size and the cell value is equal to the expected density in that cell.

20.2.4 Fragstats Analysis of Resulting Maps

The 1920 output grids were reclassified into binary maps for analysis in FRAGSTATS. We recoded the output grids into binary maps showing the areas predicted to have 5 or more adults per hectare We used FRAGSTATS (McGarigal et al. 2002) to calculate the correlation length of predicted habitat for each cover map. The correlation length is the area weighted mean radius of gyration, and provides a measure of the average distance an organism can move within a patch before encountering the patch boundary from a random starting point. When aggregated at the class or landscape level, the correlation length represents the average traversability of the landscape for an organism that is confined to remain within a single

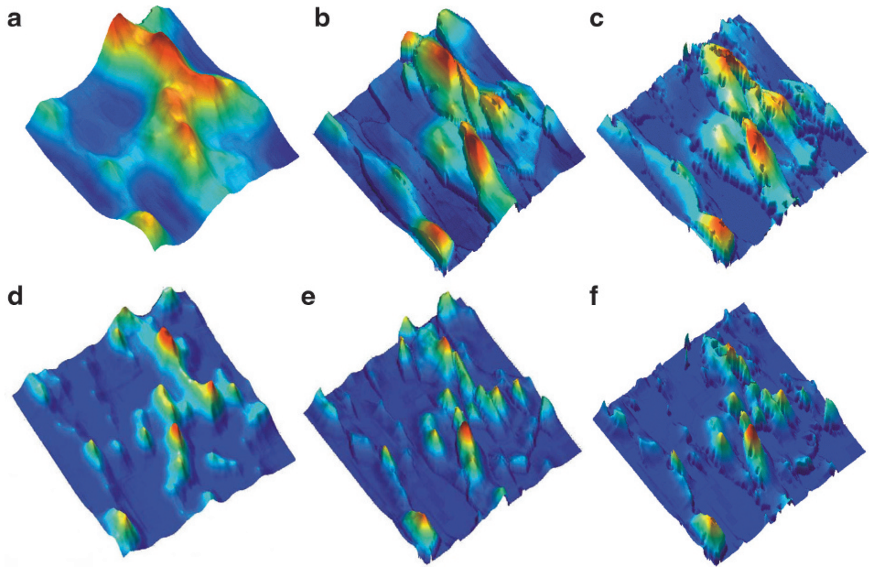

Fig. 20.3 Visual depiction of predicted density of organisms in the terrestrial environment in one small section of one ecoregion, across two levels of dispersal ability and three scenarios: (**a–c**) 400 dispersing individuals; (**d**–**f**) 800 dispersing individuals; (**b** and **d**) Null scenario; (**b** and **e**) Roads Scenario; (**c** and **f**) Roads + Land Use scenario. The height of the surface is proportional to expected density of organisms in the landscape

patch. It gives a global measure of the habitat connectivity in the landscape and is a more relevant functional measure of habitat availability for vernal pool breeding amphibians than more basic measures such as patch size, nearest neighbor distance and percentage of the landscape in occupied habitat (McGarigal et al. 2002).

20.2.5 Analysis of Habitat Correlation Length Across Life-History Space

To visualize the relationships between dispersal ability, population size and habitat connectivity, we formed matrices of the correlation-lengths of dispersal habitat predicted by the model across the factorial of dispersal ability and population size, for each of the three scenarios. We computed the average response surface for each scenario across the eight ecoregions. Then we computed the proportion of decrease in predicted correlation length of dispersal habitat from the null scenario to the roads and Roads + Land Use scenarios. These difference surfaces measure the relative impact of roads and land use on the correlation length of occupied terrestrial habitat across the life-history space.

20.3 Results

20.3.1 Null Scenario

Correlation length of predicted occupied habitat in the null model was strongly related to both population size and dispersal ability (Fig. 20.4). Not surprisingly, correlation was highest for large populations of animals with large dispersal ability, and lowest for those with limited dispersal ability and small population size. There were strongly non-linear, threshold-like relationships with both population size and dispersal ability. There are three distinct zones which are of interest in the correlation length surface across life-history space surface. The first is a zone of highly interconnected occupied habitat. This roughly corresponds to a zone of Fig. 20.4 above 10,000 m of correlation length. Species occupying this zone are able to occupy large interconnected portions of the landscape. The second zone of interest corresponds to the opposite set of conditions, those where populations occupy relatively small and disjunct patches. This corresponds roughly to the zone below 3,000 m in Fig. 20.4. In this zone, unoccupied habitat is the matrix,

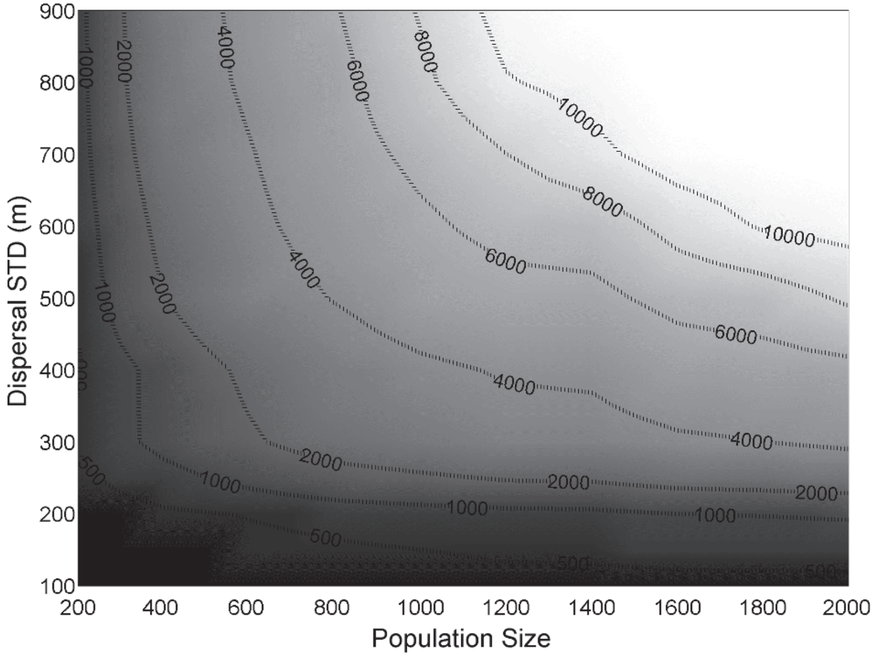

Fig. 20.4 Correlation length of habitat occupied by a minimum of five individuals per hectare across a factorial combination of dispersal ability and population size for the Null scenario. The dashed contours and indicate correlation length of occupied habitat. The surface shows strong non-linear interactions between population size and dispersal ability

with occupied habitat accounting for less than 30% of the landscape in disjunct patches. The third zone corresponds to where correlation length rapidly increases, and where small, disjunct patches of occupied habitat rapidly coalesce into large interconnected blocks. This zone roughly corresponds to the area between 4,000 and 8,000 m in Fig. 20.4. The proportion of the landscape covered by occupied habitat in this zone is between 35 and 55%.

20.3.2 Roads Scenario

The average correlation length among the eight ecoregions decreased dramatically when the resistance of roads was included in the model (Fig. 20.5). This large reduction occurred across nearly all of the life-history space. Well over half of the life-history space experienced at least a 75% reduction in expected correlation length of occupied terrestrial habitat (Fig. 20.5). The largest reductions occurred

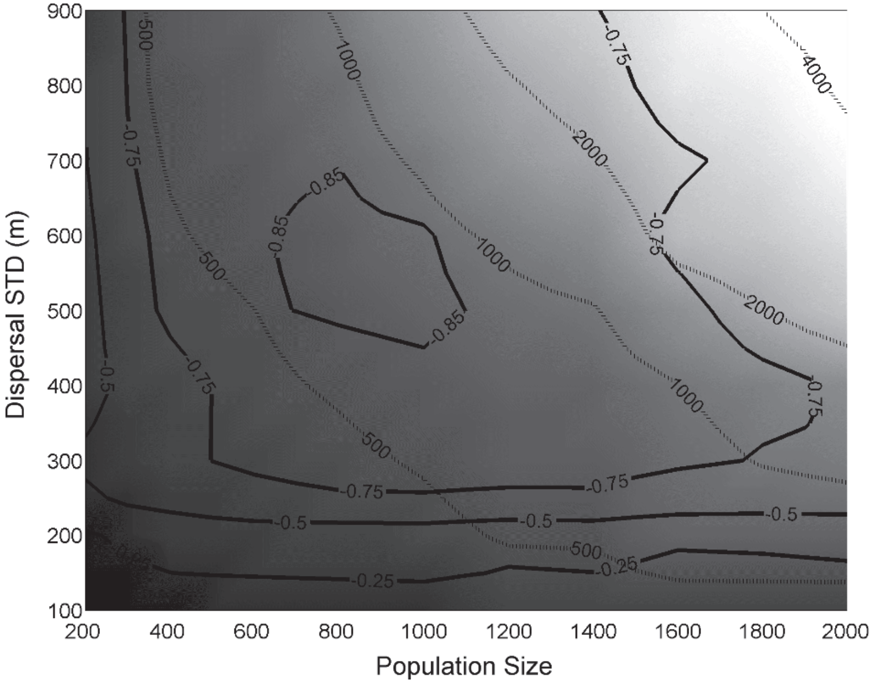

Fig. 20.5 Correlation length of habitat occupied by a minimum of five individuals per hectare for the Roads scenario. The dashed contours and indicate correlation length of dispersal habitat. The solid contours indicate the proportional decrease in correlation length in the Roads scenario from that of the Null scenario. Over 60% of the life-history space is predicted to experience at least a 75% reduction of occupied habitat correlation length due to roads in comparison with the null scenario, and approximately 10% of the life-history space experiences over 85% reduction in habitat connectivity

in the center of the life-history space. Organisms with between 400 and 600 m dispersal standard deviations and population sizes between 700 and 1,200 individuals were expected to experience decreases in correlation length of dispersal habitat of over 85%. Because of its position near this threshold, the center of the life-history space appears to be particularly vulnerable to habitat fragmentation due to roads.

20.3.3 Roads and Land Use Scenario

The average correlation length among the eight ecoregions decreased substantially when the resistance of land use categories was added to that of roads (Fig. 20.6). Interestingly, this reduction was somewhat smaller than that due to road effects. Approximately 20% of the life-history space experienced decreases in correlation

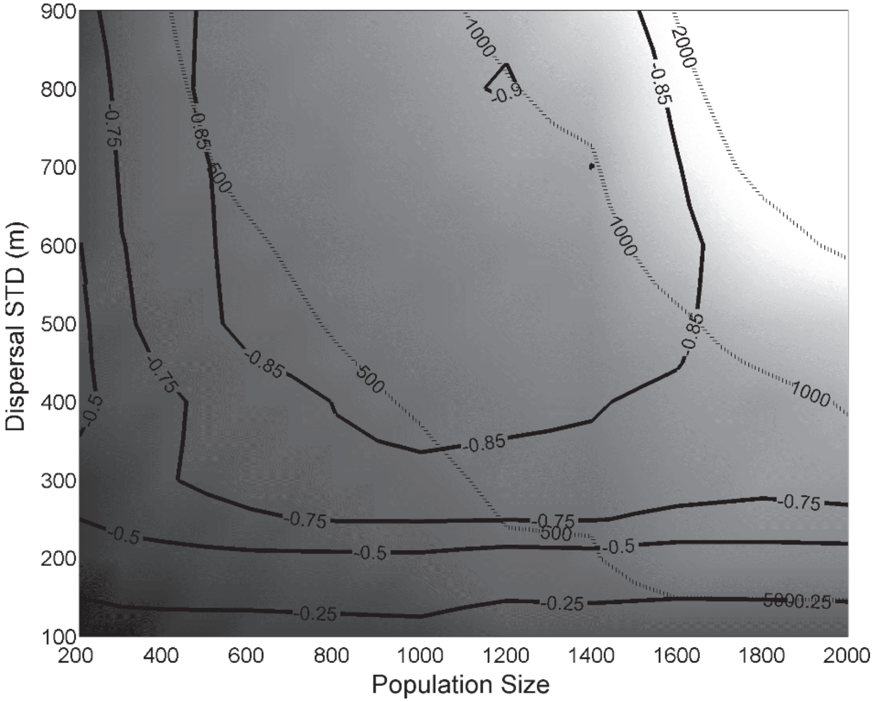

Fig. 20.6 Correlation length of habitat occupied by a minimum of five individuals per hectare for the Roads + Land Use scenario. The dashed contours indicate correlation length of occupied habitat. The solid contours indicate the proportional decrease in correlation length in the Roads + Land Use scenario from that of the Null scenario. Over 40% of the life-history space is predicted to experience at least an 85% reduction of dispersal habitat correlation length due to roads in comparison with the null scenario

length of over 40% beyond those of the roads scenario. With the combined effects of roads and residential/urban development, the proportion of the life-history space predicted to experience over 85% reduction in habitat connectivity increased from less than 10% to nearly 50% (Fig. 20.6).

20.4 Discussion

20.4.1 Hypothesis 1: Habitat Connectivity Will Increase with Both Population Size and Dispersal Ability

Holding dispersal ability constant, increasing population size will result in increased height of the surface at all points in the landscape, resulting in larger areas that have expected densities above the lower limit of one animal per hectare. Holding population size constant and increasing dispersal ability will result in the surface spreading out. Peaks in local abundance will lower, but the area occupied will increase.

As expected, the simulations suggest that there is a strong interaction between population size and dispersal ability in influencing habitat connectivity. Animals with large population sizes and high dispersal abilities are predicted to have high levels of population connectivity (Fig. 20.4). Conversely, those with low population sizes and low dispersal abilities are predicted to have low levels of population connectivity. The predicted correlation length of occupied habitat spanned over an order of magnitude in the null model, from less than 500 to over 10,000 m.

The structure of the correlation length surface implies potential life-history tradeoffs between animals with high dispersal and those with high population sizes. Specifically, assuming that there are fitness costs to increasing either dispersal ability or population size through adaptation, an isocline of correlation length could reflect an evolutionary stable strategy (Martin 1995; Charnov 1997). If actual organisms were distributed along the isloclines in Fig. 20.4, this would be consistent with life-history tradeoffs. However, this is presently untestable given lack of knowledge of the population sizes and dispersal abilities of actual organisms.

20.4.2 Hypothesis 2: Thresholds will Exist where Habitat Connectivity Drops Dramatically at Low Population Sizes and Low Dispersal Abilities

A critical threshold is an abrupt, nonlinear change that occurs in an organism's response across a small range of habitat loss and fragmentation (With and King 1999). Both empirical data (Carlson and Stenberg 1995; Doncaster et al. 1996; Jansson and Angelstam 1999) and theoretical models predict critical thresholds of habitat where ecological relationships change abruptly (O'Neill et al. 1988; Turner and Gardner 1991; With and Crist 1995; Bascompte and Sole 1996; Flather and Bevers 2002). For example, some theoretical and empirical work suggests that major population declines will occur when habitat area drops below 10–30% (With and Crist 1995; Hill and Caswell 1999; Jansson and Angelstam 1999; Fahrig 2001; Flather and Bevers 2002).

As anticipated by our hypothesis, habitat connectivity changes non-linearly with dispersal ability and population size. Correlation length of occupied habitat was predicted to be uniformly low at either low population sizes or low dispersal abilities. Of these two factors, dispersal ability seems to have a larger influence, with correlation length decreasing sharply below dispersal abilities of 300 m (Fig. 20.4). Below a dispersal distance standard deviation of 300–400 m, increasing population size cannot compensate for decreased dispersal ability. Organisms with less than 400 m dispersal standard deviation are predicted to exist in naturally fragmented populations regardless of their population sizes. This has potentially important ecological implications, as most invertebrate species inhabiting vernal pools have dispersal abilities at or below this level. Similarly, when populations are reduced below 600–400 individuals, increasing dispersal ability cannot compensate for decreasing population size. Populations less than approximately 400 individuals are predicted to exist in disconnected fragments of habitat regardless of dispersal ability.

20.4.3 Hypothesis 3: Population Size and Dispersal Ability will Interact such that Thresholds of Habitat Connectivity will be Exacerbated when Population Size and Dispersal Ability are both Low

Several simulation studies have suggested that habitat fragmentation effects become important to population viability when habitat areas are small (Fahrig 1997; Flather and Bevers 2002). Our hypothesis, in contrast, centers on relationships between habitat connectivity, population size and dispersal ability. The hypothesis that population size and dispersal ability will interact non-additively to reduce habitat connectivity at low population sizes and dispersal abilities is not supported. At low levels population size and dispersal ability act largely independently over large ranges of each factor (Fig. 20.4). While there are thresholds along dispersal ability and along population size where habitat connectivity decreases dramatically, these parameters do not appear to interact negatively at low levels. Thus there is no evidence of habitat fragmentation due to low dispersal ability being exacerbated by low population size. In contrast, in the roads and Roads + Land Use scenarios, the correlation length isoclines angle from upper left to lower right throughout the life-history space (Figs. 20.5 and 20.6). This indicates that they interact throughout the life history space, with no evidence of decreasing interaction when population size and dispersal abilities become small or become large. Thus, our third hypothesis is not supported.

While dispersal ability and population size interact in the Roads and Roads + Land Use scenarios, this interaction does not increase as population size and dispersal ability decrease.

20.4.4 Hypothesis 4: The Effects of Habitat Fragmentation by Roads will Have Relatively Smaller Effects Than Habitat Loss Due to Land Cover Change

A number of theoretical (Fahrig 1997, 2003) and empirical (Villard et al. 1999; Trzcinski et al. 1999; Cushman and McGarigal 2004) studies suggest that the effects of habitat loss are generally greater than those of habitat fragmentation (Fahrig 2003). Also, effects of habitat fragmentation are predicted to increase below some level of habitat loss. Some theoretical studies suggest that the effects of fragmentation per se should become apparent only when habitat area drops below approximately 20–30% of the landscape (Fahrig 1998, 2003; Flather and Bevers 2002). Threshold studies considering only a single factor at a single scale are limited in their applicability to real-world systems, because habitat loss and fragmentation in real landscapes typically involve multiple factors operating at several scales.

Our fourth hypothesis addresses these issues by evaluating the relative impacts of fragmentation by roads and habitat-loss due to land use changes. We expect that habitat fragmentation due to roads will have relatively smaller effects on habitat connectivity than habitat loss and fragmentation due to agricultural, residential and urban development. Contrary to our expectation, roads had a substantially greater impact on habitat connectivity than did Land Use (Figs. 20.5 and 20.6). These results show that the road network in western Massachusetts may result in substantial reductions in habitat connectivity for species that have difficulty or avoid crossing roads. Roads may subdivide habitat for these species into patches and attenuate migration, reducing the area of occupied habitat. The western Massachusetts landscape is very heavily roaded but is forest dominated. Thus the predominance of road impacts probably reflects the nature of this study area, which is highly dissected by roads but only moderately perforated by agricultural, residential and urban development. While land use effects are quantitatively less than road effects in our study area, their impacts are synergistic. Habitat fragmentation due to residential and urban development are proportionally greatest in the zones of life history space that were least severely impacted by roads alone. Thus, the relative importance of roads vs. land use may be different than in other landscapes that differ in the density of roads and the degree of habitat loss due to agricultural, residential or other land uses.

The observed importance of road effects is consistent with results reported for pond breeding amphibians (Cushman 2006). Roads can have substantial negative effects on species that avoid or experience high mortality risk when crossing roads (Vos and Chardon 1998, Carr and Fahrig 2001). Habitat fragmentation by roads and other barriers decreases dispersal (Gibbs 1998, deMaynadier and Hunter 2000), increases mortality (Fahrig et al. 1995; Carr and Fahrig 2001) and reduces genetic diversity (Reh and Seitz 1990). Habitat fragmentation can increase extinction risk by reducing demographic and genetic input from immigrants and reducing the chance of recolonization after extinction (Lande 1988; Sjögren-Gulve 1994). The relative importance of habitat loss due to land use and fragmentation by roads will depend on interactions between the habitat requirements and dispersal ability of the organisms and the pattern of roads and land uses in the subject landscape.

20.4.5 Hypothesis 5: The effects of Habitat Loss and Fragmentation will Be Disproportionately High for Species with Large Dispersal Abilities

A number of recent empirical studies have found that the negative effects of habitat fragmentation increase with increasing dispersal ability (Carr and Fahrig 2001; Cushman 2006). Carr et al. (2002) suggest that highly vagile organisms may be at a disadvantage in landscapes with roads because of increased likelihood of mortality. In a fragmented landscape individuals of species with large dispersal abilities will generally encounter roads and other anthropogenic barriers at higher rates than less vagile species. This will tend to increase mortality risk and decrease habitat connectivity.

Our model results largely match these predictions. Consistent with the expectation of our hypothesis, as population sizes and dispersal abilities increase in fragmented landscapes, the relative impact of habitat fragmentation increases (Figs. 20.5 and 20.6). In the Roads scenario, the proportional reduction in correlation length from the null scenario increased with increasing dispersal ability, to a maximum decrease at dispersal abilities between approximately 500 and 600 m (Fig. 20.5). Similarly, in the Roads + land Use scenario the largest decrease in correlation length from the null scenario occurred at a dispersal distance standard deviation of approximately 800 m. In both cases, there is a clear pattern of increasing impacts of fragmentation on habitat connectivity with increasing dispersal abilities, particularly as dispersal distance standard deviation increases from 200 to 500 m. Our results suggest that in western Massachusetts current patterns of roads, agriculture and residential development have a disproportionate impact on species with mid-sized populations and relatively large dispersal abilities.

20.4.6 Validating and Extending Results

There are several ways that one could empirically test the predictions of these models for particular species. First, one could conduct large-scale, mark-recapture studies (e.g. Gamble et al. submitted) of dispersing juveniles of several species, and quantify the similarity of actual movement rates and patterns to those predicted by the model. The challenge in these studies is one of cost and sample sizes. Large-scale mark-recapture metapopulation studies are exceptionally expensive to implement, take a number of years to produce reliable results, and generally do not provide large landscape-level sample sizes due to financial and logistical constraints. An alternative to mark-recapture movement studies is to use molecular genetic methods to empirically derive rates of gene flow among ponds and effective population sizes (Schwartz et al. 1998; Manel et al. 2003; Funk et al. 2005; Cushman et al. 2006). Molecular genetic methods offer a particularly attractive approach to quantifying gene flow across heterogeneous landscapes, as the logistical and financial costs of extensive mark-recapture study grids are obviated, and the genetic characteristics of subpopulations at each sampled pond can provide both information on its effective population size and the degree to which it differs genetically from other ponds (Funk et al. 2005). Such methods allow one to quantify rates of gene flow between ponds, and quantify resistance to movement due to gradients of landscape conditions (Cushman et al. 2006).

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