CHAPTER 1 - INTRODUCTION

Habitat fragmentation, or the subdivision of once-continuous tracts of habitat into discontinuous patches, has been implicated as a primary factor in the loss of species (Harris 1984; Myers 1986; Wilcove et al. 1986). Habitat fragmentation isolates and reduces sizes of habitat patches, increasing the vulnerability of local populations of plants and animals to environmental and demographic threats (Shaffer 1981; Lovejoy et al. 1986; Wilcove et al. 1986; Goodman 1987; Lande 1988). In metapopulations, habitat fragmentation can reduce migration rates among habitat patches, increasing extinction rates in local populations and decreasing rates of recolonization of vacant patches (Levins 1970; Hanski and Gilpin 1991).

Habitat fragmentation has genetic consequences as well; reduced local population sizes and connectivity among populations can lead to increased levels of inbreeding (Wright 1943), increased differentiation among subpopulations (Slatkin 1985), and reduced effective population sizes in metapopulations (Hedrick and Gilpin 1996). The loss of genetic diversity due to the increased influence of genetic drift can reduce the ability of a population to adapt to environmental changes (Lande and Barrowclough 1987), and inbreeding in local populations can lead to reduced individual viability and fecundity (Charlesworth and Charlesworth 1987; Wildt et al. 1987; O'Brien and Evermann 1988; Saccheri et al. 1998; Couvet 2002). Taken together, the environmental, demographic and genetic effects of habitat fragmentation can accelerate the decline and extinction of species and populations (Gilpin and Soulé 1986; Gilpin 1987; Lande 1988).

Because dispersal is a prerequisite for gene flow, understanding how habitat fragmentation affects genetic structuring of populations first requires understanding how landscape characteristics affect the movement of organisms. To quantify this relationship, Merriam (1984) introduced the concept of landscape connectivity, which he defined as the degree to which the landscape facilitates or impedes movement among resource patches. Baudry and Merriam (1988) note that landscape connectivity can encompass processes other than individual movement, and here I use the term to refer to both the movement of organisms within individual lifespans and the movement of genes over many generations, the latter process resulting from the former. Although the effect of spatial heterogeneity is often the focus of studies concerned with natural populations in fragmented habitats, few tools exist that can predict the consequences of landscape characteristics on genetic structuring of natural populations (Michels et al. 2001).

In this dissertation I examine how landscape connectivity affects the genetic structuring of natural populations using both conventional tools and a new model of landscape connectivity and gene flow. I begin in Chapter 2 by using traditional molecular tools and data analysis techniques to examine population structuring of pumas (*Puma concolor*) in the southwestern USA. Pumas are a useful model species for studying the effects of landscape pattern on interpopulation connectivity because the scales of their movements and habitat use are large enough to be captured by existing GIS maps of vegetation and other features that may facilitate or impede their movements. The naturally patchy distribution of puma habitat in the region provides an excellent laboratory for investigating how habitat pattern affects gene flow using genetic data.

Although the traditional methods used in Chapter 2 shed a good deal of light on processes affecting genetic structuring within the study region, this dataset also illustrates the inadequacy of traditional models of isolation by distance when they are applied to heterogeneous landscapes. Such models assume unbounded populations with homogeneous migration rates and deme sizes or population densities. Although the models can be somewhat crudely modified to include habitat barriers (King 1987), no general models of genetic structuring that can truly accommodate heterogeneous and bounded habitat have been developed to date. As a consequence, studies of genetic structuring across landscapes ("landscape genetics," Manel et al. 2003) often describe patterns rather than test hypotheses.

The remainder of the dissertation focuses on the development and testing of a new model of gene flow in heterogeneous landscapes that attempts to overcome these limitations. The "conductance model" is based on electronic circuit theory, and its mathematical basis is described in Chapter 3. The model exploits similarities between gene flow in natural populations and conductance in electronic circuits; as more connections are added among demes, gene flow is increased among demes connected directly by migration or indirectly by gene flow via intervening demes. Likewise, as more connections are added among nodes, conductance is increased across electronic networks.

The conductance model can be used to efficiently solve very large networks, which allows it to be applied to large GIS maps. Furthermore, when demographic parameters are not known with certainty (as is the case with most studies of natural populations), the conductance model can be used as an index of connectivity without the need to model population densities and migration rates explicitly.

In Chapter 4 I test the conductance model with two previously published datasets, one consisting of North American wolverine (*Gulo gulo*) populations and one of

Mesoamerican mahogany (*Swietenia macrophylla*) populations. Although the model could be tested using the puma dataset described in Chapter 2, I wanted to first apply the model at a coarser scale, i.e., that of a species' range. This obviated the need to model habitat because I was able to use a more parsimonious approach of mapping species ranges using published range maps or obvious geographic constraints, e.g., the limited extent of the Mesoamerican landmass. In this chapter I use the conductance model as a simple index of landscape connectivity, i.e., a measure of relative connectivity or isolation of pairs of points on a landscape.

For both wolverines and mahogany populations, the conductance model substantially improves over traditional models of isolation by distance. The next step will be to apply the model at the scale of a species' habitat, rather than the coarser scale of its range. In the last chapter, I discuss the promise and difficulties of applying the model at finer scales.

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