

COST-DISTANCE ANALYSIS OF CONNECTIVITY FOR AN AVIAN MIGRANT  
INHABITING A FRAGMENTED NETWORK

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COST-DISTANCE ANALYSIS OF CONNECTIVITY FOR AN AVIAN MIGRANT  
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for Calvin and Barbara Simper

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## **ABSTRACT**

### **COST-DISTANCE ANALYSIS OF CONNECTIVITY FOR AN AVIAN MIGRANT INHABITING A FRAGMENTED NETWORK**

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Dispersal is key to the persistence of metapopulations and local populations. The Black-capped Vireo (*Vireo atricapilla*, hereafter BCVI) is an endangered Neotropical migrant that breeds in discrete patches of shrubland. On the Edwards Plateau a patchwork of this habitat is maintained through periodic disturbance. I applied a cost-distance scenario based on the amount of woody cover, level of human presence, and local topography, to a series of classified landcover maps of the Balcones Canyonlands region of central Texas to determine whether a cost distance model fit observed levels of dispersal of BCVI better than simple geographic (Euclidean) distance. Pair-wise

connectivity values for a set of habitat patches on the Balcones Canyonlands Preserve (BCP) and Balcones National Wildlife Refuge (BCNWR) were evaluated for the 2008-2009 breeding seasons via a program of color-banding and resighting. Interpatch exchange rates were converted to measures of dissimilarity, entered into a pattern matrix, and confronted to model matrices containing effective distance values generated by cost-distance analysis, using simple and partial Mantel tests. Although statistical power was limited because of small sample size ( $n = 4$ ), results provide weak support for the continued use of geographic distance as a metric for interpatch connectivity.

## CHAPTER I

### INTRODUCTION

Species that inhabit early-successional landscapes pose special problems for conservation biologists. For these organisms, habitat loss is a consequence of vegetative succession as well as land-use conversion (Askins 1994). In order to maintain sufficient quantity of habitat to support viable populations, land managers may be obliged to periodically implement some type of controlled disturbance—a costly endeavor (Wilcove and Chen 1998) which can involve trade-offs with conservation of co-occurring species. Two issues warrant careful consideration for these early successional habitat specialists: 1) how best to model population dynamics so that appropriate conservation strategies can be developed (Johnson 2000; Scheiman et al. 2007) and 2) which specific sites, within the larger landscape, should be selected for habitat manipulation, i.e. disturbance (King and Byers 2002).

Stochastic patch occupancy models (SPOMs) simulate populations that inhabit discrete habitat patches. These models reduce landscapes into mosaics of two landcover types: habitat and non-habitat, referred to respectively as ‘patch’ and ‘matrix’ (Hanski and Ovaskainen 2003). Oceanic islands are the most obvious example of this type of environmental dichotomy, but the concept is applicable generally to any species which occupies a habitat type with a ‘patchy’, or discontinuous, distribution.

The important factors in SPOMs are patch size (either in terms of habitat area or number of individuals) and interpatch distance (Hanski and Gilpin 1991). Patch size affects probability of extinction (larger patches are less likely to undergo local extinction; MacArthur and Wilson 1963) and the distance between patches affects probability of colonization (probability of colonization decreases with increasing distance from neighboring patches; MacArthur and Wilson 1963). Dispersal between habitat patches influences the persistence of metapopulations as well as specific local populations via its relationship to extinction and colonization dynamics.

Fragmentation can inhibit dispersal (Doak et al. 1992). ‘Landscape’ connectivity is a measurement of how easy or difficult it is for a species to move within a landscape (Adriaensen et al. 2003; Stevens et al. 2006; Kadoya 2009). Prior researchers have partitioned landscape connectivity into ‘structural’ and ‘functional’ connectivity (Stevens et al. 2006). Structural connectivity is associated with the configuration and spatial relationships of major landscape features (e.g. nature preserves, large bodies of water, neighborhoods, etc.). From a structural perspective, the specific characteristics of matrix environments are viewed as more-or-less uniform and therefore unimportant to movement behavior (Kadoya 2009). Functional connectivity refers to an organism’s response to the specific characteristics of matrix landcover (e.g. amount of canopy cover, level of human presence, etc.). From a functional perspective, the amount and type of landcover classes making up the non-habitat matrix could have significant effects on connectivity (Stevens et al. 2006).

One means of evaluating interpatch connectivity involves applying a GIS procedure known as ‘cost-distance analysis’ (Stevens et al. 2006). In this method, a

landscape containing a set of occupied habitat patches is categorized into a set of functionally distinct land-cover classes. Each land-cover class is then assigned a 'cost' or 'friction' value according to its hypothesized or empirically demonstrated effects on movement of the species of interest. Such costs arise from the differential mortality, access to resources, and deferred costs that are inherent to each land-cover type from the perspective of the focal organism (Weins 2001; Stevens et al. 2006; Baguette and Van Dyck 2007) and are expressed through resistance to movement, habitat preference or habitat avoidance (Gonzales and Gergel 2007). Cost-distance analysis of a particular landscape yields two types of information: 1) measurement of the 'effective distance' along a least cost path (LCP) and 2) graphical delineation of that path on the landscape in question. Effective distance is the over-ground distance along a specific pathway between source and destination weighted by the cost of traversing each land-cover type encountered. It follows that a 'least cost' path is the route with the smallest effective distance between source and destination (Adriaensen et al. 2003). Both geographic distance and effective distance are point-to-point (or patch-to-patch) measures of connectivity, rather than landscape-level descriptors or indices. Effective distance along a LCP can be thought of as an alternative measure of connectivity (Weins 2001; Stevens et al. 2006), a spatially explicit version of geographic (Euclidean) distance. Cost-distance analysis uses information about functional connectivity (cost values) to calculate structural connectivity (effective distance) for a specific landscape and organism.

Ecologists have long recognized that landscape heterogeneity affects biologically important variables, such as access to cover, resource availability, microclimate, and level of human presence (Ricketts 2001; Weins 2001). Given that environments are

heterogeneous, dispersal pathways are seldom perfectly straight Euclidean lines (Weins 2001). While the influence of landscape characteristics on the movement of ground-dwelling organisms is not controversial, there is growing evidence that landscape characteristics affect avian movement behavior as well (Hass 1995; Belisle and Desrochers 2002; Harris and Reed 2002; Newton 2008). Qualitatively, the settlement pattern of many migratory avian species resembles a ‘dart-board’, wherein dispersal events plotted on a map become sparser as distance from the point of origin increases, in a manner that shows no overall directional trend (Newton 2008). Proposed explanations for this pattern include inability of second year individuals (‘SY’, i.e. birds in their first breeding year) to precisely locate their natal patch during their return to breeding grounds (Newton 2008), competitive exclusion from preferred territories within the natal patch (Hansson 1991; Newton 2008), return of SY individuals to an area that they randomly or quasi-randomly ‘diffused’ to during post-fledging dispersal (Newton 2008), or some combination of these factors. Poor navigational skills seems an unlikely explanation, since resident populations show the same pattern of younger individuals dispersing farther from natal areas that migrant populations do, and because the high level of site fidelity and natal philopatry displayed by many migrant species implies substantial homing ability (Newton 2008).

Perhaps the most convincing scenario for the effect of functional connectivity on avian dispersal is the phenomenon of post-fledging dispersal. Several weeks after fledging, hatch year individuals (‘HY’s) are able to fly and forage independently and begin to move through their environment alone or in small flocks (Newton 2008). This phenomenon is sometimes referred to as ‘centrifugal’ post-fledging dispersal, to

emphasize that these individuals gradually move away from their point of origin in a manner that shows no directional preference. During this time, the young birds are foraging and accumulating fat reserves necessary to make their first migratory flight. Generally the post-fledging period ends when the HY bird completes its first prebasic moult and begins directed flight towards wintering grounds. Zimin (2001, 2002 as cited in Newton 2008) found that HY individuals who had dispersed into a particular study area during their post-fledging period returned to the same area the following year to establish territories and breed. This implies that post-fledging dispersal may equate to natal dispersal in some, perhaps most, migratory species (Newton 2008). If so, then landscape characteristics would be expected to exert an influence on dispersal patterns, since post-fledging dispersal takes place at the canopy level and involves the type of routine short flights associated with exploration or foraging.

The Black-capped Vireo (*Vireo atricapilla*, hereafter BCVI), is an endangered Neotropical migrant that breeds throughout a range extending from northern Mexico through Texas and into Oklahoma (USFWS 1991; Farquhar and Gonzales 2005). Over the last century, the amount of land containing habitat suitable for breeding BCVI has been significantly reduced as a consequence land-use conversion and secondary succession (USFWS 1991). In central Texas, BCVI breeding habitat is associated with shrubland typical of early to intermediate successional environments (Gryzybowski et al. 1994; Gryzybowski 1995; Bailey and Thompson 2007). Typically, habitat quality declines as occupied patches undergo secondary succession, a process which ultimately results in local (i.e. patch) extinction (USFWS 1991; Gryzybowski et al. 1994). Land that returns to the appropriate vegetative structure by natural processes (wildfire) or

management (mechanical clearing or prescribed burning), may be recolonized (USFWS 1991; Gryzybowski et al. 1994).

How dispersing individuals react to their environment will affect what areas they encounter in the larger landscape (Doak et al. 1992). It may be possible to model the dispersal behavior of a target species to predict locations where there will be an enhanced likelihood of individuals encountering and eventually settling in areas which have been improved. However, like most avian migrants, detailed understanding of the dispersal behavior of the Black-capped vireo is limited, especially under the conditions of fragmentation that dominate modern urban landscapes (Gryzybowski 1990; USFWS 1991).

When field data are prohibitively difficult or costly to obtain, a model which overlooks the specific mechanisms of a process (or treats them generally) may allow forecasts to be made based on the current state of a system (Turchin 1998). Such phenomenological models can provide insights into competing hypotheses, help evaluate the effects of alternative parameter values on outcomes of alternative management strategies, guide future empirical studies, and inform adaptive management (Weins 2001). The research described herein applies cost-distance analysis to the study of Black-capped Vireo dispersal. The objectives of this study are to: 1) evaluate effective distance to determine whether it predicts interpatch dispersal (in BCVI) better than geographic (Euclidean) distance, and 2) qualitatively examine the LCPs generated from cost-distance analysis in order to identify possible corridors or optimal sites for habitat restoration or land acquisition.

## CHAPTER II

### METHODS

The Balcones Canyonlands region, known locally as the Texas Hill Country, is a subsection of the larger Edwards Plateau biotic province (Figure 1a). Broadly speaking, the Edwards Plateau is an ecotonal area between the Rolling Plains to the north, the Blackland Prairie on the east, and the Stockton Plateau to the west, and is noted for high levels of biodiversity and endemism across a wide range of taxa (Riskind and Diamond 1988; Swanson 1995). The primary vegetation assemblages are juniper-oak savannah on the xeric uplands and diverse hardwood communities in the mesic valleys.

The Balcones Canyonlands National Wildlife Refuge (BCNWR) and the Balcones Canyonlands Preserve (BCP) are two neighboring preserve systems situated in western Travis and southern Burnet and Williamson Counties, Texas, USA (Figure 1b, 1c). The BCNWR and the BCP were created to preserve and manage critical habitat for two endangered neotropical migrants, the Golden-cheeked warbler (*Dendroica chrysoparia*) and the Black-capped Vireo, as well as six endemic karst-dwelling arthropods (Pease and Gryzybowski 1991; USFWS 2001). The BCP and BCNWR are patchwork collections of parcels that are situated within a rapidly developing urban landscape (Hill et al. 2009). Inside these tracts, territories of breeding Black-capped Vireos typically adjoin one another (Gryzybowski 1990; USFWS 1991), forming clusters or colonies that may be likened to the discrete ‘habitat patches’ posited by

metapopulation theory (Levins 1969; Hanski and Ovaskainen 2000, 2003). Intervening non-habitat matrix is composed of a wide variety of land-cover types, including commercial development, agricultural fields, rangeland, residential suburbs, and naturally wooded, shrubby, and open areas reflecting various levels of anthropogenic disturbance and secondary succession.

Initially, fourteen sites on the BCP and BCNWR were identified as either occupied by BCVI ( $n = 12$ ), having a history of use by BCVI ( $n = 1$ ), or having recently undergone restoration to create suitable breeding habitat for BCVI ( $n = 1$ ). In 2007, these sites were scouted to determine the number and spatial distribution of breeding territories. In 2008, adults (predominantly males) were captured and color-banded via a program of targeted mist-netting. Nests were located whenever possible and nestlings were banded with site-specific (cohort) color combinations rather than unique adult combinations since most banded juveniles will not be resighted due to mortality and off-site dispersal. In all, 79 birds were marked in 2008: 48 adults (41 males, 7 females) at ten sites, 31 juveniles at six sites. In all, ten sites held marked birds in 2008.

In 2009, the original fourteen sites were resurveyed to resight or recapture marked individuals. Singing males were located by sound, then followed and observed until their band status and identity could be ascertained. All study sites were visited at least four times throughout the breeding season. Pre-determined study routes aided in maintaining uniformity of survey effort within each plot. Recorded vocalizations were played sparingly in the latter half of the season to elicit responses from undetected individuals and to draw out BCVI inhabiting areas which were difficult to access due to dense vegetation. BCVI were detected incidentally at three previously unoccupied (or

undocumented) sites in 2009, establishing territories in at least two of these sites. Two of the original fourteen study sites were unoccupied by BCVI in both 2008 and 2009. Ultimately, fifteen occupied sites were included in the final statistical analysis. Twenty-one BCVI were resighted or recaptured in 2009.

For purposes of analysis, the spatial extent of each study site was defined to be a minimum convex polygon containing all visual or auditory observations of BCVI recorded at that site over the three year study period (2007-2009) buffered on all sides by 115m and converted to raster data format at 30 m<sup>2</sup> resolution. In order for an outlying observation to be included as part of a site, it had to be within 500 m of another observation at that site; in two cases this resulted in the omission of isolated males or pairs. A 115 m buffer size was selected because that is the approximate radius of a 10 acre circular plot, the published upper limit of a 'typical' BCVI territory (USFWS 1991).

Cost-distance analysis assumes that landcover properties influence movement behavior through effects on preference, avoidance, survivorship, and deferred costs (Conroy et al. 1995; Travis and French 2000; Stevens et al. 2006; Wang et al. 2008). Natural (i.e. undeveloped) landscapes were assigned to landcover categories according to amount of woody cover present (Table 1): little or no cover (0-5%, 'field'), moderate cover (>5-30%, 'savannah'), and substantial cover (>30-100%, 'forest'). The other landscape characteristic believed to influence landcover cost was level of human presence. Three levels were originally designated: little or no presence (the 'natural' landcover types), a moderate level which included some vegetation cover ('residential'), and frequent and intensive presence with little or no vegetative cover ('developed').

Adding a category for open water (Lake Travis is a major landscape feature within the study region) resulted in a total of six broadly defined landcover categories.

The selection of an appropriate spatial resolution, or minimal mapping unit, for cost-distance analysis is not trivial (Lillesand et al. 2008). Rae et al. (2007) found that cell size was the most significant source of uncertainty in their dispersal models. The 'grain' of a landscape is determined by the perceptual range of the organism under examination (Bauguette and Van Dyck 2007) and so the resolution of any spatially explicit model should be individualized to the species under study (Weins 2001; Adriaensen et al. 2003). A spatial resolution of 30 m<sup>2</sup> was selected for this study because 1) thirty meters is roughly similar to the 25 m behavioral threshold noted by Belisle and Desrochers (2002), 2) a 30 m resolution allows composite or 'mixed' landcover types such as 'savannah' and 'residential' to be represented as distinct categories, and 3) thirty meters is a common resolution for remotely sensed data, such as Landsat imagery.

Landcover classification initially proceeded through visual interpretation of recent (2006) high resolution (ca. 15 - 61 cm) aerial photography (Sanborn Map Company 2006). Digitization took place at 1:4000 scale, which allowed an area of approximately 1 km<sup>2</sup> to be viewed on a desktop monitor-- at this scale, details of the landscape on the order of 30 m<sup>2</sup> were easily discernable. Approximately 120 km<sup>2</sup> was digitized by visual interpretation. This dataset became the training area for a maximum likelihood supervised classification (Lillesand et al. 2008) implemented in ERDAS Imagine ® 9.3. The maximum likelihood algorithm assumes that the set of reflectance values for a particular spectral category (defined by the training area) are distributed normally in each spectral band of the dataset undergoing classification (Lillesand et al. 2008).

The supervised classification procedure was performed on recent Landsat 7 imagery collected during three distinct times of year: spring (19 April 2008 overlaid on 21 March 2003), summer (27 July 2009 overlaid on 21 July 2001) and winter (27 November 2007 overlaid on 15 December 2002). A malfunction in the “Scan Line Corrector” on Landsat 7 took place in 2003 (Lillesand et al. 2008), resulting in a series of linear data gaps in all subsequent imagery. Cost-distance analysis is critically affected by large contiguous linear features (Adriansen et al. 2003), therefore the data gaps were corrected by applying a ‘gap-filling’ algorithm (Scaramuzza et al. 2003). Six of the eight spectral bands recorded by Landsat 7 were used in the classification process—the thermal and panchromatic bands were omitted because of their differing image resolutions (60 m<sup>2</sup> and 15 m<sup>2</sup> respectively). Since the training set (the area of photo interpretation) was created to represent information categories (i.e. landcover classes) rather than true spectral classes (Lillesand et al. 2008), a certain amount of misclassification in the ‘mixed’ landcover types such as ‘residential’ (which contained both impervious cover and trees) and ‘savannah’ (which contained both trees and open areas) was inevitable. To compensate for this misclassification, ‘residential’ and ‘developed’ landcover types were aggregated into one cost category (Table 1). This reclassification also helped fill incidental pixel gaps in potentially important linear barriers such as multilane highways (Adriaensen et al. 2003). The ‘water’ category was assigned subsequently to the classification process by identifying pixels with very low reflectance values ( $DN \leq 25$ ) in Band 4 (near infrared) of an unmodified pre-2003 scene recorded during a period when lake level was ‘full’ (i.e. non-drought, large islands not present).

Once generated, cost maps were cropped to the geographical extent of a rectangle bounding a minimum convex polygon containing all seventeen study sites (including the two unoccupied sites) buffered on all sides by 5 km. This resulted in a rectangular study region 38.9 km x 55.9 km (2,176 km<sup>2</sup>). The largest individual study site represented ca. 1/5000 of the full study region.

Each landcover category can, in the absence of empirical data, be assigned an *a priori* cost value based on expert opinion of how an organism will react to a given habitat type (Ferrerias 2001; Adriaensen et al. 2003; Gonzales & Gergel 2007). The relative ranking of these cost values is the most important factor governing the resulting least cost pathways, although higher absolute differences between categories allow for greater deviation from Euclidean straight-lines (Adriaensen et al. 2003; Gonzales & Gergel 2007). Low costs should be associated with high behavioral preference, low mortality, or easily negotiated environments, while high costs should coincide with avoidance behavior, high mortality, and resistance to movement (Ferrerias 2001). The rationale for the cost assignment employed in this study was as follows:

1.) cost should increase as amount of woody cover decreases

$$\text{cost}(\text{forest}) < \text{cost}(\text{savannah}) < \text{cost}(\text{field}),$$

2.) open water should have similar or equal cost to open land

$$\text{cost}(\text{water}) = \text{cost}(\text{field}),$$

3.) and human occupied areas should be associated with significantly higher cost so that they function as barriers to movement

$$\text{cost}(\text{developed}) = \text{cost}(\text{residential}) \gg \text{cost}(\text{all other categories}).$$

Actual cost values assigned to each category are given in Table 1. In order to account for possible classification errors between the savannah and field landcover types, COST-MAP 5 and COST-MAP 6 aggregated these two categories (Table 1, Table 2).

In addition to the classified landcover map of the region created specifically for this study, two other publicly available landcover maps were evaluated in order to allow comparison of effective distance values and least-cost pathways. The National Land-Cover Database (NLCD) of 2001 is a widely used land-cover map covering the coterminous United States (Homer et al. 2004). It is comprised of 29 land cover classes and is derived from data produced by Landsat 5 and 7. The Texas Ecological Systems Project (TESP) is a recently created land-cover map spanning the state of Texas (German et al. 2009). Both land-cover maps divide vegetation classes into narrower categories than my model required, therefore in both cases structurally similar landcover classes corresponding to the broad classes used in my own model were aggregated together. For example, in the TESP schema, categories labeled ‘grassland’, ‘herbaceous’ and ‘barren’ would correspond to the ‘field’ category, categories labeled ‘forest’ and ‘woodland’ would correspond to ‘forest’, and ‘urban high density’ and ‘urban low density’ would correspond to ‘developed’.

To account for possible effects of topography on dispersive movements in Black-capped Vireos, a GIS layer was created using elevation data obtained from the Shuttle Radar Topography Mission (Farr et al. 2007). The elevation data layer was converted to a slope layer using the Slope tool of ArcView 9.3. The resulting raster data was divided into nine categories using the Jenks Natural Breaks system in ArcView. The goal was to classify the set of slope values into three categories—areas of ‘low’, ‘medium’ and ‘high’

slope. I used 5.6 ° and 16.6 ° as cut-off values for the slope categories. High slope was assigned the highest cost value, medium slope was given an intermediate value, and low slope areas were assigned the lowest cost (Table 1). To avoid LCPs which merely followed canyon bottoms, curvature of each raster cell was calculated using the Curvature tool of ArcView 9.3, which assigned each grid cell a value representing either positive (convex, value = 1) or negative (concave, value = 0) curvature. This value was subtracted from the slope value for each raster cell, resulting in a reduction in the cost of all slope classes when curvature was positive. Thus the cost value of level upraised portions of the terrain (i.e. plateaus) was made lower than level areas in low lying parts of the terrain (i.e. canyon bottoms).

Topographically derived cost values were added to cost maps generated from landcover categories for each landcover map generated (Table 2). Multiple versions of these cost maps using various versions of absolute cost values were not evaluated to avoid over-fitting the data (Turchin 1998).

Model matrices were populated with effective distance values produced by the Cost Distance tool in ArcGIS 9.3. Effective distance, in this study, represents costs accrued along an LCP, rather than the over-ground distance of the LCP (Ferreras 2001, Stevens et al. 2006). Each classified landcover map produced one associated model matrix.

The data matrix used to evaluate the model matrices was calculated from the band-resight data. Interpatch connectivity  $C_{ij}$  between each pair of study sites  $i$  and  $j$  was defined as:

$$C_{ij} = \frac{D_{ij} + D_{ji}}{(M_i + M_j) - (R_i + R_j)}$$

where  $D_{ij}$  equaled the number of individuals that relocated from patch  $i$  to patch  $j$  (aggregating sexes and instances of natal and breeding dispersal),  $M_i$  equaled the number of individuals marked in 2008 on patch  $i$ , and  $R_i$  equaled the number of birds marked in 2008 on patch  $i$  that returned to patch  $i$  in 2009.

BCVI were not detected at two study sites (Sites 16 and 17) in either 2008 or 2009, therefore these sites were excluded from data and model matrices. Interpatch connectivity values between each pair of the remaining fifteen study sites were entered into 15 x 15 square-symmetric data matrix. Four study sites that were not occupied in 2008 but were occupied in 2009 were included in the model evaluation, but because no marked individuals could be exchanged between pairs of such sites, connectivity values for such pairings were assigned the value 'NA.'

Models were evaluated by confronting the empirically-derived data matrix to a series of model-derived matrices containing effective distance values. Simple and partial Mantel tests were used to assess correlation between the two independent matrices (Sokal and Rohlf 1995). Since Mantel tests compare matrices of dissimilarity values (Legendre and Legendre 1998), measures of connectivity or similarity in the banding data matrix were converted into dissimilarity values ( $DS_{ij}$ ) by subtraction from 1 (Sokal and Rohlf 1995).

$$DS_{ij} = 1 - C_{ij}$$

A simple Mantel test was used to compare the banding-dispersal data matrix to a model matrix containing Euclidean distance values. Because effective distance is often highly correlated with Euclidean distance, partial Mantel tests were performed to determine the

partial correlation of data and model matrices while controlling for the effect of Euclidean distance (Stevens et al. 2006).

The ‘qcf’ package (Bjornstad 2009) in the program R (R Development Core Team 2009) was used to perform the simple Mantel and partial Mantel tests. This package applied pairwise deletion whenever ‘NA’ values were encountered in the data matrix. Model evaluations involved 100,000 permutations per test. Biologists recognize a difference between natal dispersal, which is movement from the patch of origin to the patch where an individual breeds for the first time, and breeding dispersal, which is the movement of an adult from one patch to another (Paradis et al. 1998). Although dispersing adults and juveniles may respond differently to landscape cues (Baguette and Van Dyck 2007), I aggregated all interpatch movements in order to increase sample size. Because of the small number of documented dispersal events ( $n = 4$ ), significance criteria was set at a level of  $\alpha = 0.1$ .

## CHAPTER III

### RESULTS

#### *Dispersal Distances and Return Rates*

Between the 2008 and 2009 breeding seasons, four marked BCVI dispersed between habitat patches. One event represented breeding dispersal; the three others were instances of natal dispersal. The three dispersing SY individuals all originated from SITE 10. Figure 2 shows the dispersal profile for the 2008-2009 interval. Dispersal distances were measured as the minimum linear distance between study sites and ranged from 2.79 to 22.04 km. The mean natal dispersal distance was 11.02 km (SD = 9.92 km), and the mean distance for all dispersal events was 9.13 km (SD = 8.95 km). Return rates for marked adult males between 2008 and 2009 were 58.3% (7/12) on the BCP and 27.6% (8/29) on the BCNWR. Two of thirty-one marked SYs returned to their natal patch (6.4%) and no returning adult females were resighted.

#### *Model Evaluation*

The correlation of the model matrix containing Euclidean interpatch distances to the pattern matrix containing dissimilarity values based on dispersal events was statistically significant ( $p < 0.1$ , Table 2). All other models were likewise supported, according to this relaxed criterion (Wang 2008). However, if there is a significant correlation between Euclidean distance matrix and a model derived matrix (all models,

$r = 1$ ,  $p < 0.01$ , Table 2), geographic distance is assumed to be the explanatory variable (Legendre and Legendre 1998). When partial Mantel tests were employed to control for the effect of geographic distance, none of the cost-distance models showed a statistically supported partial correlation (Table 2). However, COST-MAP 4, which combined information about topography with data from the most recent and locally derived land-cover map, was the only cost-based model examined in this study that wasn't logically disqualified due to a negatively signed Mantel correlation which would indicate, nonsensically, that dispersal probability is positively correlated with effective distance (Stevens et al. 2006).

#### *Proportional Increase in Effective Distance/Geographic Distance*

Figure 3 shows the distribution of the proportional increase in effective distance (derived from COST-MAP 4) over geographic distance for the full set of study sites. This value was calculated for each site by summing the effective distance values between that site and every other site (either a row or column of a model matrix) and dividing that quantity by the sum of the geographic distances between that site and every other site (the corresponding row or column of pattern matrix) then subtracting 1. Thus, this value is a measurement of the predicted difference in connectivity between geographic and cost models for each site relative to all other sites.

## CHAPTER IV

### DISCUSSION

The results of this study provide weak support for the continued use of geographic distance as a representation of connectivity in patch occupancy models of Black-capped Vireos. This finding is in accordance with the concept of structural connectivity, which deemphasizes the role of matrix land-cover on dispersal (Kadoya 2009). However, the determination of ‘no effect’ should be judged with a degree of skepticism and applied cautiously. The number of dispersal events documented during the study period was small ( $n = 4$ ) and represents a single annual interval. The lack of statistical power associated with a sample size this small undermines the credibility of any inferences made. In addition, two incidental spatial patterns uncovered during this study could be interpreted as indirect evidence of the effect of functional connectivity on BCVI dispersal: 1) the spatial coincidence of a LCP node on SITE 10, the largest extant BCVI colony on the BCP, and 2) a substantial difference between the BCP and BCNWR in return rates of marked males.

#### *Nodes*

Cost-distance analyses conducted for this study uncovered ‘nodes,’ points where a set of LCPs connecting multiple source populations, but derived from a single cost map, intersect or converge (Gonzales and Gergel 2007). Although COST-MAP 4 showed no

improvement over geographic distance in predicting dispersal, it was the sole cost-distance model that was not logically disqualified due to incorrect sign of the correlation. In Figure 1c the complete set of LCPs generated by the COST-MAP 4 is overlaid on a map of the full study region. A node ('1' in Figure 1c) is apparent where LCPs originating from the BCP converge before proceeding northwest towards the BCNWR. The convergence point is spatially coincident with SITE 10, which has been the most populous BCVI colony on the BCP since its inception (Travis County 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009). This suggests the possibility that BCVI may be aggregating at this site because it represents a funnel for dispersing individuals traversing the larger landscape. If so this supports the *a priori* assumptions of COST-MAP 4: that connectivity is enhanced by 1) increased woody cover, 2) relative isolation from human-dominated environments, and 3) minimal elevational change along dispersal pathways. Delineation of LCPs and their associated nodes could provide the basis for future model validation and adaptive management (Conroy et al. 1995; Baguette and Van Dyck 2007; Rae et al. 2007). A second node ('2' in Figure 1c) is apparent, as LCPs originating from sites on the BCNWR proceed to the southeast towards the BCP. The area surrounding this node, as well as the entire shared LCP connecting the two nodes, would be a logical zone for BCVI monitoring and habitat evaluation.

#### *Return Rates and Matrix Structure*

Populations displaying a high degree of natal philopatry and site fidelity have been associated with isolated locales such as islands (Weatherhead and Forbes 1994). As the amount of suitable habitat available becomes more limited, individuals may be more

likely to return to a familiar site due simply to a general lack of options. This principle may underlie the difference in return rates for adult males on the BCP and BCNWR. On the BCP, the percent of returning males was nearly twice as high as on the BCNWR (58.3% and 28.6% respectively). Within the boundaries of the BCP, both BCVI abundance and the quantity of suitable habitat are relatively limited, and matrix landscapes tend to include substantial human presence. In contrast, the BCNWR is situated in an area of relatively sparse urban development and is likely to adjoin a greater amount of suitable BCVI habitat and more numerous off-site territories. Thus, there are key differences in both the demographic context and the non-habitat matrix within which these two preserves are embedded. The net result of these differences could be greater interchange of individuals between on-site and off-site habitat patches on the BCNWR than takes place on the BCP. In other words, a population which is patchy (*sensu* Harrison 1991) on the BCNWR becomes even patchier (*i.e.* more isolated and concentrated) on the BCP, creating a situation which more closely resembles a ‘classical’ metapopulation (Levins 1969; Hanski and Gilpin 1991; Harrison 1991; Stith et al. 1996). Prescribed burning was conducted on portions of three BCNWR tracts containing BCVI populations in 2008 and 2009, and this may have contributed to the lower return rates observed through the temporary reduction in the amount suitable habitat contained within these study sites.

#### *Encirclement and Fragmentation Threshold*

The matrix landscape that surrounds patches of habitat can potentially have an important impact on persistence of metapopulations and local populations (Rodewald

2003). Weins (2001) speculated that a ‘fragmentation threshold’ could be exceeded if effective interpatch distances become too great to allow sufficient immigration for the rescue (sensu Brown and Kodric-Brown 1977) of occupied habitat patches. If matrix landscapes become less and less suitable for dispersal, fragmentation could be effectively ongoing despite the fact that adjacent patches haven’t physically changed location with respect to each other. An extreme form of this phenomenon occurs when areas of high quality habitat become completely inaccessible to dispersing individuals because of the inhibiting effect of barrier landcover types, a phenomenon referred to as ‘encirclement’ (Hill et al. 2009).

Encirclement is a problem to contend with when planning a reserve system in an urbanizing area. This process may have contributed to the local extinction of the BCVI population at SITE 16. In the decades preceding the formation of the BCP, SITE 16 was the largest known BCVI colony in Travis County, holding 33 territories in 1985 (Gryzybowski 1990). However, BCVI abundance at this site declined at annual rates as high as 30% until the population finally went to zero in 1998 ((DLS Associates 1990; Gryzybowski 1990; USFWS 2001; Abbruzzese and Koehler 2002).

The dwindling population at SITE 16 has been attributed to the detrimental edge-effects of adjacent development, such as increased exposure to feral cats and avian nest predators, in conjunction with a decline in habitat suitability due to vegetative succession (Abbruzzese and Koehler 2002). However, development of adjacent and surrounding properties may have effectively isolated this colony. As shown in Figure 3, SITE 16 exceeds all other sites in the ratio of effective distance (derived from COST MAP 4) to geographic distance, except SITE 17, which has no history of BCVI occupancy. This

suggests that the difference between geographic and effective distance is more dramatic for SITE 16 than for any occupied patch in the BCP-BCNWR system. More substantial differences between effective distance estimates and geographic distance measurements between sites would be expected to create a stronger signal for the effects of functional connectivity on colonization and rescue— thus, the particular history of this mid-sized colony may be a testament to the effect of matrix landscapes on BCVI dispersal. If patch connectivity has been adversely affected, this should manifest preferentially on younger, more recent immigrants—older, site-faithful individuals presumably have a better chance of relocating to the territory that they have occupied year after year. Accordingly, the last individual to inhabit the site had been banded ten years earlier, making it one of the oldest surviving BCVI on record (Abbruzzese and Koehler 2002). SITE 16 is also located on the southern edge of the BCP-BCNWR BCVI metapopulation. Lande (1987) pointed out that patches of habitat situated near the boundary of metapopulations are at greater risk of extinction due to reduced proximity to other source patches. Although there have been occasional records of small groupings (2-3 territories) on tracts to the south of SITE 16, no large or mid-size colonies (>10 territories) have been recorded in recent decades within the spatial extent of the current study.

*Applications to Preserve Design (Selection of Sites for Habitat Restoration)*

The BCP-BCNWR system presents an interesting case study in conservation trade-offs: both preserves are charged with the protection of two co-existing endangered species with conflicting habitat requirements: the Black-capped vireo, which breeds in deciduous shrubland and the Golden-cheeked warbler (hereafter GCWA), which utilizes

closed-canopy woodlands. Although there is considerable overlap in the realized niche of both species, especially where foraging and post-fledging movement of juveniles is concerned (Houston 2008), the requirements of their respective breeding habitats are distinct—thus, an area is suitable for either one or the other. Given the limited amount of available habitat within preserve acquisition boundaries, managers must determine how to manipulate the landscape to maximize benefit for BCVI while minimizing losses for GCWA.

Practical application of the empirical results of dispersal studies to preserve design is more complicated than it may appear. Many studies have evaluated landscapes by computing various indices (e.g. nearest neighbor, incidence function, buffer measure) to quantify landscape conditions which are expected to impact structural connectivity (Vos et al. 2001; Moilanen and Nieminen 2002; Winfree et al. 2005; Kadoya 2009). However, because these indices are landscape-scale descriptors, the information generated is difficult to translate into specific recommendations for selecting sites for the creation of new habitat patches. One possible spatially-explicit approach would be to buffer (in the GIS analysis sense) occupied patches using a distance value obtained from the dispersal kernel of the focal species, then selecting and evaluating areas of buffer overlap. Selecting the appropriate distance to use for this purpose is not a straightforward process, especially for species that show a fat-tailed dispersal function that demonstrates considerable dispersal capability. Stith et al. (1996) selected the maximum ‘typical’ dispersal distance (by their terminology the ‘inner’ dispersal distance) to be 3.5 km for Florida scrub-jays (*Aphelocoma coerulescens*) based on several criteria, such as percent of individuals dispersing that distance or less, observed gap crossing behavior, and

distance driven declines in colonization rates. This method is sound, but requires a fairly comprehensive dispersal kernel in order to improve upon simple metrics, such as mean, median, or root-mean-squared dispersal distance. Comparable values for BCVI derived from this study are the mean dispersal distance, 9.13 km (SD=8.95 km), and 8.2 km as a cut-off for capturing 75% of dispersers. However, these values are tentative, because the dispersal–distance function generated by this study (Figure 2) is limited due to small sample size and pools sexes as well as natal and breeding dispersal. Long distance dispersal events have been documented in Black-capped Vireos, although they are believed to be relatively infrequent (Cimprich et al. 2009).

Another option for addressing the site selection problem is the use of least cost pathways. Plotting LCPs on real landscapes allows the visualization of idealized corridors between active colonies (Adriaensen et al. 2003). This could facilitate the identification of areas harboring undocumented sub-populations or sites which could support future colonies. However, despite the graphical suggestiveness of LCPs plotted on a landscape, these pathways, nodes and convergences are theoretical optima—actual organisms may never traverse them (Weins 2001; Rae et al. 2007). Even if they do, a phenomenological study such as this can only infer patterns, not prove the behavioral basis for these patterns (Turchin 1998). A strong criticism of cost-distance analysis is that it assumes that a dispersing individual possesses complete fore-knowledge of the landscape between source and destination (Baguette and Van Dyck 2007). One way to address this problem would be to implement stochastic individual-based models, such as ‘random walk’ or one of its variants (self-avoiding, correlated, etc.) to model dispersal in a way that incorporates known population sources but does not prescribe destinations (Gustafson

and Gardner 1996; Schippers et al. 1996; Zollner and Lima 1999). Ultimately, the selection of any site for restoration or potential acquisition should be contingent on direct observation and evaluation of its particular environmental and biotic characteristics.

### *Spatial Structure of BCVI Populations in the Balcones Canyonlands*

The question of whether the BCVI population in the Balcones Canyonlands region is best described as a metapopulation, a ‘spatially structured’ population, a patchy population, or simply a ‘population’ showing no spatial structure is unresolved. If the population is well mixed in the sense that the yearly inhabitants of each patch are effectively drawn from a common pool, with an equal chance of settling in any patch of available habitat, then perhaps the matrix landscape plays only a small role in settlement probability and habitat created anywhere within the substantial flight capabilities of the organism contributes equally to population persistence (Scheiman et al. 2007). However, if distance (whether geometric or effective) influences dispersal, then connectivity matters. It follows that the particular location of a patch is significant, not merely its footprint, and the spatial configuration of patches will have consequences for the metapopulation capacity of the network beyond the total acreage of potential habitat contained by that network (Hanski and Ovaskainen 2000).

Species or populations that are adapted to ‘unstable’ (sensu Thomas 2000) habitat types have presumably evolved dispersal strategies that cause them to seek new patches as old ones become less and less suitable (Weins 2001). Most (3/4) of the dispersing individuals documented in this study were observed to have paired and/or bred successfully, indicating perhaps that the dispersal component of this population is not

composed of 'inferior' competitors (Hansson 1991). Gryzybowski (1990) observed an interesting relationship between large and small BCVI colonies: large aggregations are generally more productive per-capita than small colonies, yet small, marginal groupings are the necessary seed stage of what may eventually become large, productive colonies. Thus, population sources could begin and end as population sinks (*sensu* Pulliam 1988). This is consistent with the observation that immigration is proportionately higher in the growth phase of a colony and lower in its waning years (Newton 2008). Stith et al. (1996) proposed a nomenclature to describe different classes of 'local' populations: 'mainlands' are large, highly populated, and effectively extinction-proof; 'islands' are small populations with yearly extinction probabilities greater than 50%; and 'mid-lands' are intermediately-sized populations associated with longer time-to-extinction than 'islands'. BCVI breeding in the Balcones Canyonlands region seem to be distributed among several 'mid-lands' (containing 4-30 territories) and a number of 'islands' consisting of 1-2 territories that typically persist for 1-3 years (Abbruzzese and Koehler 2002, 2003; Travis County 2002, 2003, 2004, 2005, 2006, 2007, 2008, 2009; Becker and Koehler 2004, 2005; City of Austin 2006, 2008; O'Donnell et al. 2007). Species that display 'intermediate' levels of dispersal may be impacted by habitat loss more acutely than those with very low or very high levels of dispersal because they do not disperse sufficiently to locate all available habitat, while at the same time losing the benefit of remaining within the favorable environment of the natal patch (Thomas 2000). Although productivity may be lower in the 'islands' due to sub-optimal habitat quality or difficulties in locating and securing mates, offspring produced by these satellite

populations may actually play a critical role in the demographic rescue of ‘mid-land’ populations if dispersal is an integral part of the life cycle of most individuals.

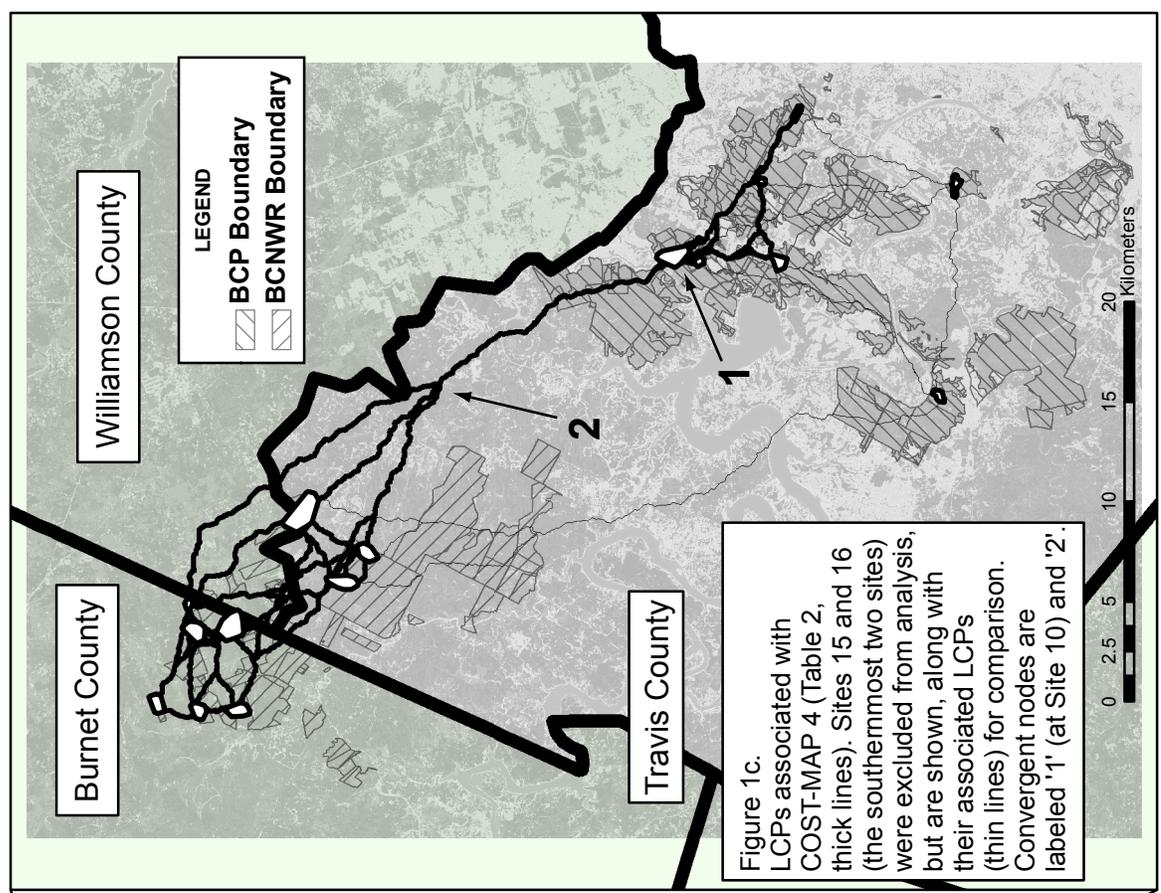
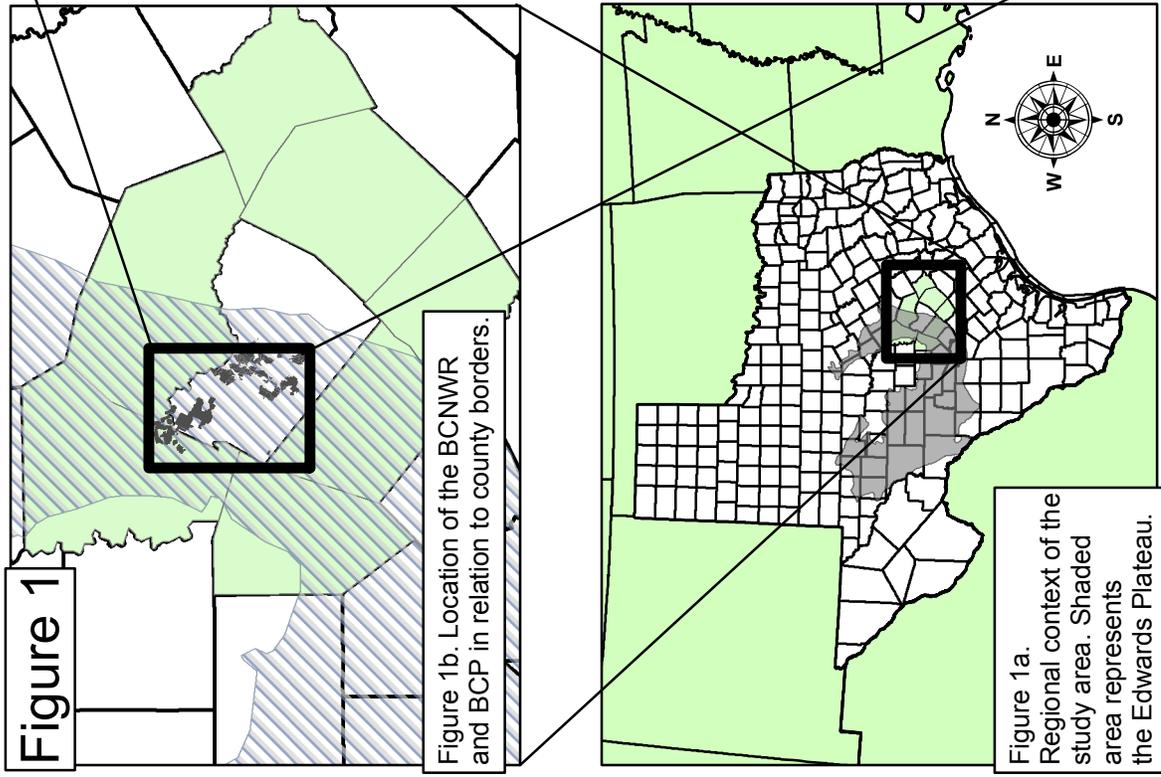
Stewardship of threatened populations requires the creation and safeguarding of a sufficient amount of habitat, appropriately configured for the species in question. However one chooses to classify the BCVI population on the BCP-BCNWR, consideration should be given to maintaining connectivity between and among these preserve systems. Interpreting too literally the conclusion that there is no effect of matrix landcover on connectivity may create an overly optimistic expectation for population persistence than is warranted, especially if landcover conversion of existing non-habitat matrix continues at a rapid pace. Although identification, acquisition, and creation of high quality habitat will continue to be a primary concern for conservation biologists, the issue of landscape connectivity has, until recently, received less attention (Doak et al. 1992). The expansion of the dispersal-distance function for BCVI across a variety of landscapes and spatial scales should be a research priority. Houston (2008) observed Black-capped vireo fledglings utilizing relatively dense woodland areas composed of mature Ashe juniper and tall canopy trees, presumably taking advantage of increased cover as a means of predator avoidance. Similar behavior was noted in the course of this study. A detailed examination of multi-habitat use in this species, and by fledglings in particular, should be pursued. Finally, further research on interpatch dispersal in migratory species generally is sorely needed.

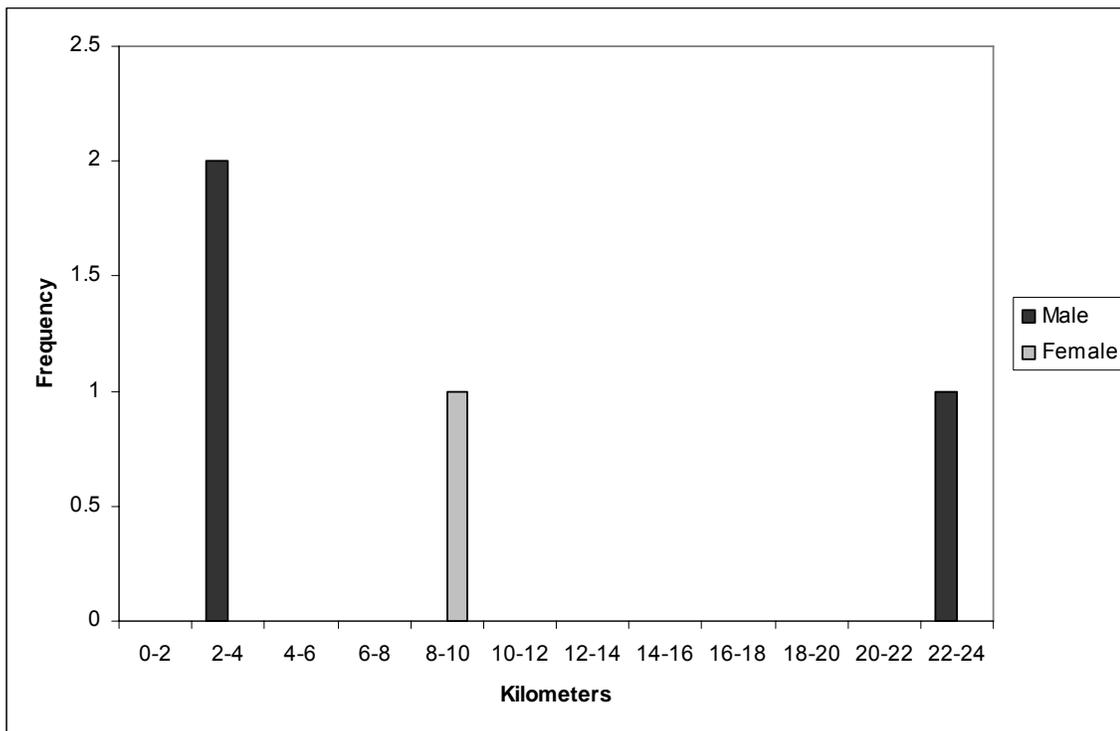
**Table 1.** Landcover categories and associated cost values for cost-distance dispersal models of Black-capped Vireos on the BCP and BCNWR.

LANDCOVER CATEGORY	DESCRIPTION	COST VALUE	
		SAVANNAH and FIELD not aggregated	SAVANNAH and FIELD aggregated
Forest	35 – 100% woody cover, very restricted visibility at 1.5 m	1	1
Savannah	5 – 35% woody cover, horizontal visibility at least 30 m at 1.5m	2	3
Field	0 – 5% woody cover	4	3
Water	open water	4	3
Residential	residential level of human presence; woody cover > 5%	8	8
Developed	heavy human presence	8	8
Flat	0 - 5.6 degrees (NLCD: 0 - 6.3 degrees)	1	1
Low slope	5.6 - 16.6 degrees (NLCD: 6.3 - 19.7 degrees)	2	2
High slope	16.6 - 90 degrees (NLCD: 19.7 - 90 degrees)	3	3
Top	Positive curvature	-1	-1
Bottom	Negative curvature	0	0

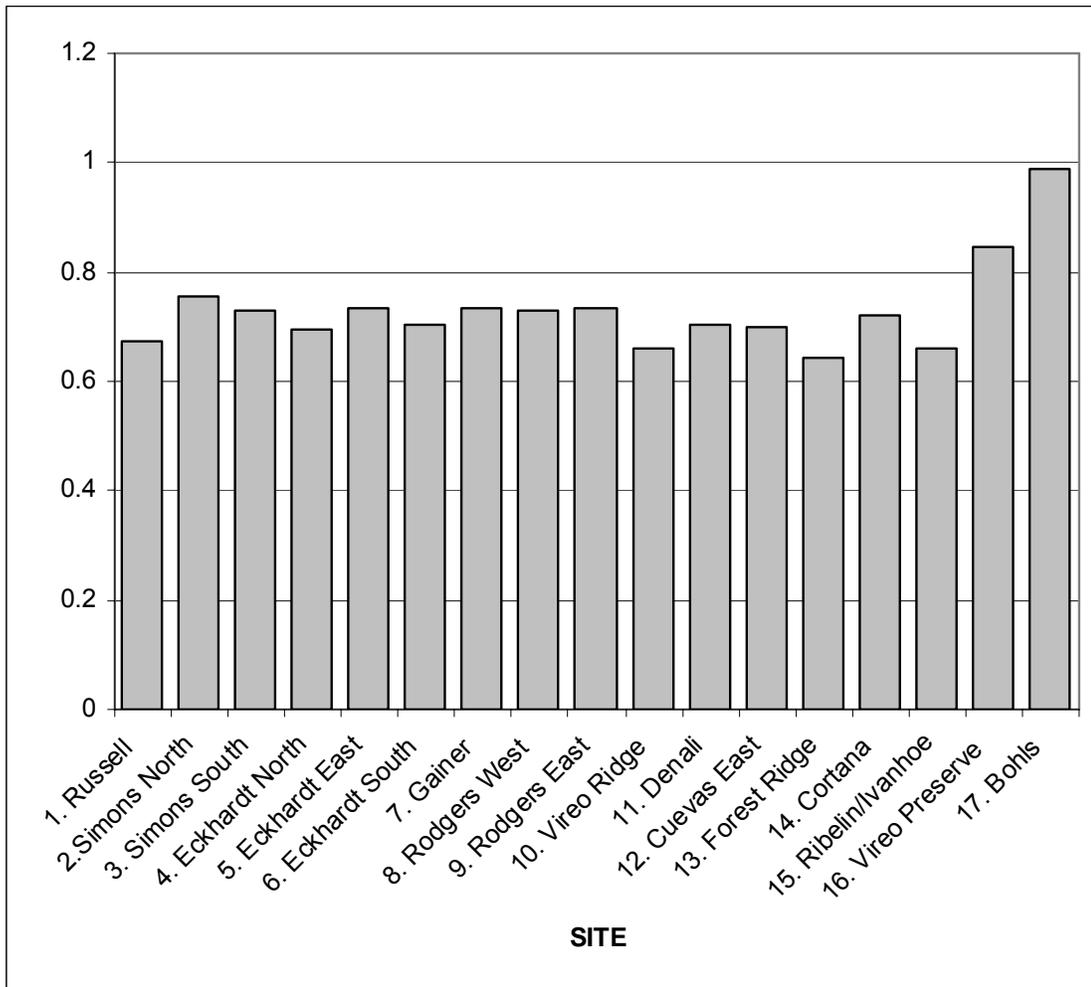
**Table 2.** Results of cost-distance model comparisons for Black-capped Vireo dispersal in the Balcones Canyonlands region, Texas, USA.

Cost Model / Landcover Map	Partial Mantel with Euclidean		Simple Mantel with Data Matrix		Simple Mantel with Euclidean	
	r	p	r	p	r	p
COST-MAP 1: Euclidean	na	na	0.1500	0.0675	na	na
COST-MAP 2: Topography	-0.0437	0.3565	0.1473	0.0709	0.9985	2.00E-05
COST-MAP 3: Study Generated	-0.0022	0.4913	0.1495	0.0691	0.9980	2.00E-05
COST-MAP 4: Study Generated + Topography	0.0160	0.4473	0.1506	0.0679	0.9987	2.00E-05
COST-MAP 5: Study Generated Combined Field and Savannah	-0.0480	0.3451	0.1457	0.0767	0.9967	2.00E-05
COST-MAP 6: Study Generated Combined Field and Savannah + Topography	-0.0071	0.4729	0.1492	0.0701	0.9979	2.00E-05
COST-MAP 7: NLCD2001	-0.0489	0.3375	0.1481	0.0716	0.9993	2.00E-05
COST-MAP 8: NLCD2001 + Topography	-0.0493	0.3357	0.1474	0.0693	0.9988	2.00E-05
COST-MAP 9: TESP	-0.0428	0.3600	0.1483	0.0720	0.9993	2.00E-05
COST-MAP 10: TESP + Topography	-0.0196	0.4347	0.1487	0.0692	0.9985	2.00E-05





**Figure 2.** Dispersal profile of Black-capped Vireos for the 2008-2009 interval at the Balcones Canyonlands National Wildlife Refuge (BCNWR) and the Balcones Canyonlands Preserve (BCP), Texas, USA.



**Figure 3.** Proportional increase in effective distance values over geographic distances between habitat patches on the Balcones Canyonlands National Wildlife Refuge (BCNWR) and the Balcones Canyonlands Preserve (BCP), Texas, USA. Effective distance was derived from COST MAP 4 Although Sites 16 and 17 were excluded from Mantel tests because they were unoccupied by BCVI in 2008 and 2009, they are included for comparison.

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## VITA

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