THE INFLUENCE OF RIPARIAN-CANOPY STRUCTURE AND COVERAGE ON THE BREEDING DISTRIBUTION OF THE SOUTHWESTERN WILLOW FLYCATCHER

by

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TABLE OF CONTENTS

TABLE OF CONTENTS - CONTINUED

LIST OF TABLES

Table Page

LIST OF FIGURES

LIST OF FIGURES – CONTINUED

ABSTRACT

There is a long history of relating bird species diversity and distributions to heterogeneity in foliage structure as seen from within the habitat and measured from the ground up. There is also an overwhelming contribution in the literature promoting and justifying a broad-scale approach to characterizing spatial patterns, especially for the purpose of relating to, and predicting, species distributions. This study draws from the relationship between birds and habitat structure but assesses heterogeneity in structure from a broader perspective.

For this analysis, I compared the spatial distribution of a breeding population of the southwestern willow flycatcher (*Empidonax extimus traillii*) to the structure of a riparian zone with an emphasis on capturing patterns that are measured horizontally across the zone. Riparian zones are dynamic by nature and are structurally diverse in a natural, healthy system, and support a high density of breeding birds. The flycatcher prefers dense riparian habitat in close proximity to lentic water. The structural characteristics of the riparian zone where dense vegetation and water are present were hypothesized to be more structurally heterogeneous and to support a broader riparian zone.

Riparian zone structure was mapped and stand characteristics were extracted, with the intent of relating spatial patterns in stand heterogeneity and riparian extent to the spatial distribution of the southwestern willow flycatcher. A moving window function in a GIS assessed the stand characteristics, which were imported as attributes to presence/absence data points. The extent of the analysis window was varied to determine the scale at which the habitat characteristics were most highly correlated with flycatcher presence. Correlation between the structural characteristics of the stand and the presence/absence of the flycatcher was modeled with logistic regression. Results show the flycatcher is more likely to occupy habitat that is structurally heterogeneous and has more riparian vegetation. The results also show that selection is most sensitive to habitat characteristics within a relatively close proximity.

INTRODUCTION

Habitat structure is an important part of habitat selection in birds (Cody 1985; Wiens 1989). For bird species, habitat is often comprised of vegetation and much work has been done relating diversity in vegetation structure to bird species diversity (see Tews et al. 2004) and bird species' distributions (James 1971; Cody 1978; Cody 1985; Smith and Shugart 1987; Robinson and Holmes 1982; Imhoff et al. 1997). The habitat heterogeneity hypothesis says that greater structural heterogeneity within a habitat results in there being more niches to support a greater diversity of bird species (MacArthur and MacArthur 1961). Specific configurations of vegetation structure are also shown to be characteristic of a specific species' habitat (James 1971; Cody 1978; Cody 1985; Smith and Shugart 1987; Robinson and Holmes 1982).

The information resulting from work relating structural diversity to bird species diversity and distributions has not always been successful because the importance of habitat structure on avian composition is dependent on the scale of study (Wiens, Rotenberry, and Van Horne 1987; MacNally 1990; Tews et al. 2004). The 'problem of scale' in ecology (Wiens 1989; Levin 1992) has been the focus of a great deal of attention and research (Schneider 2001). How structure is perceived or quantified depends on the scale of analysis and defining heterogeneity on one scale will be perceived as homogeneity on another scale (Tews et al. 2004).

For this analysis, I aspired to determine selective factors that are important to distribution of the southwestern willow flycatcher (*Empidonax traillii extimus*), a federally listed endangered, avian species. The flycatcher breeds exclusively within riparian zones and has declined in numbers because of human-caused degradation of this important habitat. Dense riparian vegetation adjacent to surface water or saturated soils is common to all the breeding sites across the subspecies range (USFW 2002; Sogge et al. 2003). Additionally all sites supporting larger populations of the flycatcher (> 5 territories) are on broad lowland floodplains (Graf et al. 2002; Hatten and Paradzick 2003; Paradzick and Woodward 2003).

Given that structural characteristics of habitats have been shown to be predictive of the distributions of avian species, I felt that flycatcher distributions might be related to the structural characteristics of riparian zones on broad, lowland floodplains in the Southwest. Habitat selection is assumed to be adaptive (Jaenike and Holt 1991; Martin 1998) and structural preferences might reflect the habitat structure of unmodified habitat the flycatcher evolved with historically. A riparian zone is, by nature, dynamic and structurally complex because channel migration, periodic flooding, and rapid growth rates of riparian vegetation create patterns in stands of various communities and ages across the floodplain (Nilsson and Berggren 2000). The resulting canopy complexity and pattern created by structurally distinct stands across the floodplain could be important for understanding the distribution of the flycatcher.

I modeled flycatcher presence with selection parameters that characterize locations on the floodplain where slow-moving water is present, since this is a common feature of the flycatcher's habitat. The presence of lentic water indicates a location on the periphery of an active channel, near to overflow channels and seeps. Here, riparian should be structurally heterogeneous and more extensive because there is a potential to support a greater variety of seral stages within a short distance.

As stated, the main objective of this study was to relate habitat structure to the distribution of the southwestern willow flycatcher. I took advantage of the tools afforded by GIS (1) to map the stand structure of a lowland riparian zone within a broad valley that supports a large population of the flycatcher, (2) to analyze the amount of variation in stand structure (stand heterogeneity) within a given extent, (3) to quantify dense riparian vegetation within the given extent, and (4) to relate the stand characteristics to the distribution of the flycatcher.

Mapping the vegetation structure required determining the best scale for analysis. Lowland riparian areas have a great deal of structural complexity and yet they are naturally narrow and limited in size, making for unambiguous delineation of its boundaries, but requiring high resolution to capture structural heterogeneity. A landcover map discards unnecessary detail by integrating lower-level patterns and grouping regions with similar characteristics. Eliminating excessive detail of vegetation structure within the riparian zone, I integrated lower-level patterns by delineating "stands", which I define as relatively homogeneous in age and vegetation community (A "patch" in contrast, is defined as contiguous woody riparian vegetation with distinct boundaries with non-woody landcover). Riparian zone community structure is relatively consistent within a given reach where patterns in community structure are defined by distance to the river and are relatively predictable (Muldavin et al. 2000). I defined seven stand types that were characterized by structure using the height of the canopy and the presence or absence of additional foliage layers under the canopy. This effectively partitioned the system into homogeneous units that were applied to the entire system, and created a meaningful basis for describing heterogeneity.

Mapping riparian is a difficult task because of its dynamic nature and limited extent, and it requires an understanding of the vegetation patterns as they are related to landscape features and disturbance (Muller 1997). To better understand these patterns, I sampled vegetation along transects running perpendicularly to the river. I projected vegetation variables obtained by vegetation sampling and from a data set of vegetation measurements at willow flycatcher nest sites and non-nest sites over digitized air photos. I used the spatially projected data, additional color-infrared air photos and digital orthophoto composite interpretation to delineate riparian stands based on canopy height and the presence or absence of subcanopy and understory layers, and produced a landcover map that was used to derive variables for analysis.

I used neighborhood functions in a GIS to quantify riparian vegetation and structural heterogeneity. Neighborhood functions total the amount of each stand type within a moving window that is passed over the landcover map. Stand proportions were used to calculate stand diversity, and the quantity of riparian vegetation within a given extent. The size of the analysis window, or analysis extent needed to be biologically relevant to the flycatcher, and to capture characteristics of the riparian zone that varied across the floodplain. Rather than selecting a single scale of analysis, I varied the extent in four phases. Analysis of a digitized map in a GIS provides the opportunity to repeat analyses on varying scales. Varying-scale analyses have been shown to be successful for other studies characterizing stream networks (Schuft et al. 1999) and avian-habitat relationships (Thompson and McGarigal 2002; Hatten and Paradzick 2003).

Logistic regression was used to model flycatcher habitat preferences where presence/absence was the modeled response and stand characteristics within progressively increasing distances, patch area, patch perimeter, and patch perimeter-area ratio were the explanatory variables. Emphasis was placed on understanding the importance of stand heterogeneity and the amount of riparian vegetation to flycatcher distribution. To evaluate scale-dependent relationships between flycatcher presence and the quantity and diversity of the canopy layers, each analysis extent was used independently in tests for association and output from each extent was compared to one another.

This research clarifies fundamental characteristics of flycatcher habitat. The results of this analysis provide support for the proposed hypothesis, and suggest that the estimated probability of flycatcher presence is greater where there is a greater amount of structural heterogeneity, in patches with greater area and more core area, and where riparian vegetation is more extensive. This knowledge can be applied to planning for habitat restoration for this endangered species. The result of varying the analysis extent shows that habitat characteristics within a relatively close proximity are more correlated to flycatcher presence than those within a greater extent. The success of the approach I used to model a species' distribution advocate incorporating quality field-based data, and using predictors that directly influence species' distributions.

OBJECTIVES

The main objectives of this investigation are (1) to identify stand characteristics of a riparian zone with an emphasis on capturing patterns that are measured horizontally across the zone, and (2) to relate the structure to the breeding distribution of the southwestern willow flycatcher, an endangered, riparian-obligate avian species.

The flycatcher prefers dense vegetation near stagnant water and seems to be partial to broad lowland floodplains. Given this and the established relationship between birds and the structure of their habitat, I asked what stand structure was characteristic to wet areas on broad lowland floodplains and if these are vital characteristics of flycatcher breeding habitat. I predict that: (1) flycatchers will be present in areas that have more riparian cover, and (2) that structural complexity of the vegetation as measured horizontally across the floodplain will significantly predict flycatcher presence.

BACKGROUND

The Southwestern Willow Flycatcher

The southwestern willow flycatcher is a small bird that migrates to the southwestern United States to breed in dense riparian vegetation along river corridors. A decline in the number of the southwestern willow flycatcher resulted in the U.S. Fish and Wildlife Service (USFWS) listing the subspecies as Endangered in 1995 (USFWS 2002). Declines have been attributed primarily to a loss and alteration of riparian zones associated with anthropomorphic influence on floodplains, including grazing, that resulted in a reduction of water levels and degraded habitat (USFWS 2002).

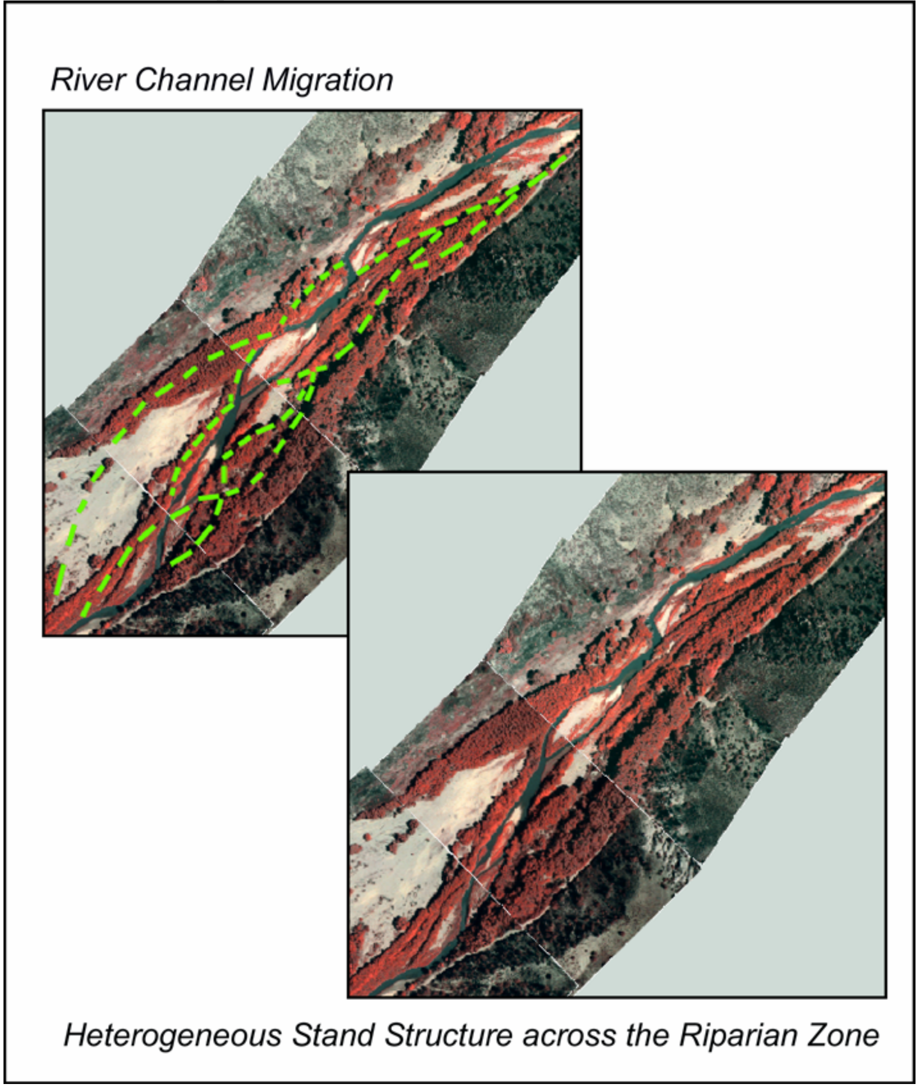
The southwestern willow flycatcher breeds from southern California eastward through Arizona, southern Utah, southern Colorado, New Mexico, and trans-Pecos Texas (Unitt 1987, USFWS 2002). Across the subspecies range, breeding habitat varies in species composition and canopy structure but nesting is almost exclusively near surface water or saturated soils in dense riparian vegetation (Sogge and Marshall 2000, USFWS 2002, Paradzick and Woodward 2003). The sites occupied by the flycatcher are distributed over a wide range of elevations but generally the flycatcher breeds at sites that are low to mid-elevation with approximately 80% of the sites below 1600 m (Sogge et al. 2002).

The larger populations of *E. t. extimus* occupy broad, lowland floodplains (Graf et al. 2002). In Arizona, with the exception of a high-elevation population in the White Mountains, (which might prove to not be a pure strain of *E. t. extimus* (Sedgwick 2001)), all of the populations with greater than 5 territories are distributed on broad, lowland floodplains (Paradzick and Woodward 2003). In New Mexico, the largest population is in the Cliff-Gila Valley, a broad, lowland floodplain (Stoleson and Finch 2003). An analysis of flycatcher distribution at one of the larger sites in Arizona, found that larger floodplains were more likely to support breeding flycatchers (Hatten and Paradzick 2003). The authors reason that the fluvial geomorphological processes and floodplain topography influence plant establishment (Hatten and Paradzick 2003). A significant amount of research has shown that topography and geomorphologic characteristics influencing channel migration and flooding can have a significant impact on the composition of riparian communities and the patterns of patch succession across the floodplain (Bradley and Smith 1986, Decamps et al. 1988, Nilsson et al. 1989, Szaro 1990, Gregory et al. 1991, Malanson 1993, Bendix 1994, Durkin et al. 1996, Dykaar and Wigington 2000; Muldavin et al. 2000, Nilsson and Berggren 2000).

Habitat selection by the flycatcher is expected to reflect its life history traits and should reflect the habitat structure of unmodified habitat the flycatcher evolved with historically. In 1910, while surveying the Colorado River from Needles to Yuma, ornithologist Joseph Grinnell recorded the dominant floodplain vegetation as cottonwood and willow and described the dynamics of the system, noting channel migration and the pattern of young to older forest in increasing distance from the channel. Grinnell also collected and observed "Traill's Flycatcher" on the survey (Grinnell 1914, in Periman and Kelly 2000). A riparian zone is, by nature, dynamic and structurally complex because channel migration, periodic flooding, and rapid growth rates of riparian vegetation create patterns in stands of various communities and ages across the floodplain (Nilsson and Berggren 2000) (Figure 1).

Flycatchers breed near lentic water (Appendix A). The presence of lentic water indicates a location on the periphery of an active channel, near to overflow channels and seeps. These stands should be structurally heterogeneous because there is potential to support a greater variety of seral stages within a short distance. Overflow channels, because of the location on the edges of the active floodplain (Figure 1), are often proximal to terraces, which support mature riparian forests with high canopies. Stands of intermediate ages should also be present because the edges of the active floodplain in a low-gradient valley don't experience devastating floods but every 3 – 25 years (Durkin et al. 1996). In addition, sapling growth and other primary stage growth are stimulated by the presence of water.

Figure 1: Older river paths marked by riparian stands of varying ages are visible in a high-resolution color-infrared air photo.



Habitat Structure and Avian Distributions

Patterns of species distributions and community structure are related to variation in vegetation structure (Cody 1985; Wiens 1989). Greater structural variation is believed to contribute to greater faunal species diversity, especially for birds (e.g., MacArthur and

MacArthur 1961; MacArthur, MacArthur, and Preer 1962; MacArthur, Recher, and Cody 1966; Pianka 1966; Recher 1969; Roth 1976; Cody 1978; Rice, Ohmart, and Anderson 1983; Fremark and Merriam 1986; Finch 1989; Urban and Smith 1989; Farley et al. 1994; Tews et al. 2004). Although there have been some studies that were at most, only limitedly successful in correlating structural complexity to bird species diversity (e.g., Austin 1970; Murdoch et al. 1972; Carothers, Johnson, and Atchison 1974; Wiens 1974; Willson 1974; Smith 1977), or have presented factors that may play a greater role (Petit, Petit, and Grub 1985; Rotenberry 1985), structural variation is shown to influence bird species composition (MacNally 1990).

The structural characteristics of vegetation have been shown to be highly predictive of individual species distributions (MacArthur et al. 1962; Whitmore 1975; Rickers, Queen, and Arthaud 1995). Rice, Ohmart, and Anderson (1983) found that when correlating species distributions with vegetation structure, criteria for single species tended to be independent of other species' selection criteria. Using remote sensing to map vegetation structure, Imhoff et al. (1997) found that structure was not well correlated with bird species diversity but species-specific distributions were well correlated to structural and floristic gradients in the landscape. They suggest that species-specific relationships should be considered when mapping bird species diversity. Similarly, Jeanneret et al. (2003) were unable to relate species diversity to vegetation or landscape features and argue that biodiversity needs to be addressed using multiple indicator species whose distributions are easier to model. Despite the difficulty relating structural heterogeneity to bird species diversity, habitat structure seems to be important when interpreting single species habitat relationships (Imhoff et al. 1997).

In particular, riparian structure is correlated with species distributions and species diversity. Riparian zones are dynamic by nature and are structurally diverse in a natural, healthy system. Riparian communities and canopy heights vary with distance from the active channel and the length of the interval between floods (Baker and Walford 1995; Durkin et al. 1996). Riparian systems support a disproportionately high number of species. It has been estimated that riparian ecosystems support more bird species than any other ecosystem in the western U.S. (Knopf and Sampson 1994). Finch (1989) found bird species diversity and structural complexity of the vegetation to be greater in lowland riparian areas when compared to riparian at higher elevations. Farley et al. (1994) completed bird surveys in three, different-aged stands of riparian on the Middle Rio Grande and found that stands with a mixture of different size-class of trees had greater avian diversity. Rice, Ohmart, and Anderson (1983) investigated selection criteria for riparian birds on the Lower Colorado River, Arizona, and determined that foliage height diversity was important for evaluating avian presence. Additionally, they found that foliage height diversity was often an important factor for habitat selection by a single species. The correlation between foliage height diversity and bird species diversity has been upheld in mesquite vegetation in the Verde Valley, Arizona (Stamp 1978).

Structural heterogeneity can be measured and interpreted as variation vertically within a stand or horizontally across a landscape and can be expressed on multiple scales. Horizontal heterogeneity is also expressed as 'patchiness' within a landscape (Roth 1976;

Wiens 1989). Horizontal variation in stand structure has been measured on scales as fine as the distance to the nearest shrub or tree (Roth 1976) and as great as across the entire North American continent (Davidowitz and Rosenzweig 1998). The scale of analysis must be large enough to capture variability but not great enough to generalize the variability in the structure of the vegetation. The scale of study should be specific to the plant community being studied (Malkinson, Kadmon, and Cohn 2003). Detecting spatial heterogeneity within a Southwestern riparian ecosystem that is linear and narrow by nature, means the scale of analysis must be finer than the width of the floodplain.

Analysis Scale

One of the great challenges in analyzing relationships between an organism and its environment is the frequently addressed (see Schneider 2001) problem of scale (Wiens 1989; Levin 1992). Ecosystem functioning is based on infinite interrelationships between ecosystem parts that interact on infinite levels and species distributions are therefore, influenced by multiple factors that are measured on many different scales. Identification of factors that are important to a species distribution requires careful consideration of the ecological relationships of the organism (Guissan and Zimmerman 2000; Austin 2002) and careful consideration of the scale of analysis (Levin 1992).

The scale of study will influence what predictors are selected for analysis, how they are quantified, and how the results are interpreted. Species-habitat modeling requires the identification of either: (1) the important resource characteristics that a species directly relies on for survival and productivity (biotic predictors (Martin 2001)/

direct predictors (Vaughn and Ormerod 2003)), or (2) processes that act on species distributions through a series of intermediate relationships (e.g., elevation, topography) (abiotic predictors (Martin 2001)/indirect predictors (Vaughn and Ormerod 2003)). The abiotic approach is appropriate for predicting species distributions as the data tend to be readily available on a broad scale, but lack strength for interpreting ecological relationships, something for which the biotic approach is preferred (Vaughn and Ormerod 2003). Biotic variables tend to involve more tedious, costly methods for acquiring data that generally covers a more limited extent but are able to provide a level of detail that is valuable for effectively identifying associations (Wright, Marcus, and Aspinall 2000).

The consideration of scale is particularly important for modeling structural heterogeneity because heterogeneity on one scale will be measured as homogeneity on another scale (Tews et al. 2002). Landcover data discards unnecessary detail by integrating lower-level patterns and grouping regions with similar characteristics. The level of classification (see Federal Geographic Data Committee 1997) will determine the level of aggregation and resolution of the landcover map, and the level of heterogeneity that can be derived from the map.

Spatial Autocorrelation

The reliance on statistics is increasingly a major part of wildlife-habitat and spatial analysis and the statistical approach needs to be strategic for appropriate interpretation of data. Peer-reviewed literature often neglects to address whether the assumptions of the statistical analysis are met (Lewis 2004), especially the assumption of independence in regression models (Lichstein, Simons, and Franzreb 2002). Generalized linear models assume the responses are independent observations and spatial correlation can be problematic because it violates the assumption of independence (Legendre 1993).

Site fidelity, clumped distributions, and small territories are characteristic of breeding flycatcher populations. Site fidelity, (individuals returning to the same territory in subsequent seasons), has been documented in color-banded flycatchers in Arizona (Luff et al. 2000) and Oregon (*E.t.adastus*) (Sedgwick 2004). This characteristic introduces the potential for temporal correlation. Distributions of this species are clustered within breeding sites (Hatten and Paradzick 2003), indicating conspecific attraction. Species clustering can result from discontinuity in the distribution of resources and preferred habitat, and/or from conspecific attraction (Tarof and Ratcliffe 2004). If conspecific attraction were to play a roll in the distribution of willow flycatchers, it would be a confounding factor in the analysis. Other authors have also noted conspecific attraction between closely related species such as the least flycatcher (*Empidonax minimus*) (Tarof and Ratcliffe 2004). Clear demonstration of conspecific attraction has not been established for the flycatcher but the role of site fidelity and social attraction has been noted by willow flycatcher scientists but the role is identified as a research need for the flycatcher (Kus and Sogge 2003).

METHODS

Study Site

The Gila River begins in the Mogollon Mountains in the Gila Wilderness of southwestern New Mexico (Figure 2). The river is free flowing in the state of New Mexico. As the river leaves the Mogollon Mountains, it enters the broad alluvial floodplain of the Cliff-Gila Valley. The upstream end of this wide valley begins at the Mogollon Creek inlet (33º 55’ N, 108º 35’ W) and runs south-southwest through the Cliff-Gila Valley for approximately 18 km. The floodplain is 1.2 – 2.0 km wide. Elevations range from 1350 to 1420 m.

The site is within the arid Southwest, but a true characterization of its climate is much more complex and features climatic variability. Climate data from the Cliff weather station for the years 1971-2000 (Figure 3) show June as having the hottest month with an average high of 33.4 C (92.1 F) and December as the coldest month with an average low of -5.9 C (21.8 F). Cliff receives an average annual precipitation of 40.5 cm (15.9 in). August receives the greatest amount of precipitation with an average of 7.3 cm (2.9 in). Precipitation events tend to be heavy thunderstorms and dramatic storms correlate with hurricanes in the Gulf from September to November. Peak stream flows from 1992-2002 were all within these months and ranged from 400 – 11,200 cfs in a river whose average monthly flow ranges from 59.5 cfs in June and 316 cfs in March (1971-2001). The driest months are April and May with 1.2 cm (0.46 in) average precipitation. The surrounding landscape reflects the aridity of the region with the hillsides around the valley dominated by honey mesquite (*Prosopsis glandulosa*), soaptree yucca (*Yucca sp.*), prickly-pear cactus (*Opuntia sp.),* and cholla cactus (*Opuntia spp.*).

Figure 2: Cliff-Gila Valley Study area in relation to the rivers and major mountain ranges of the region in southwest New Mexico.

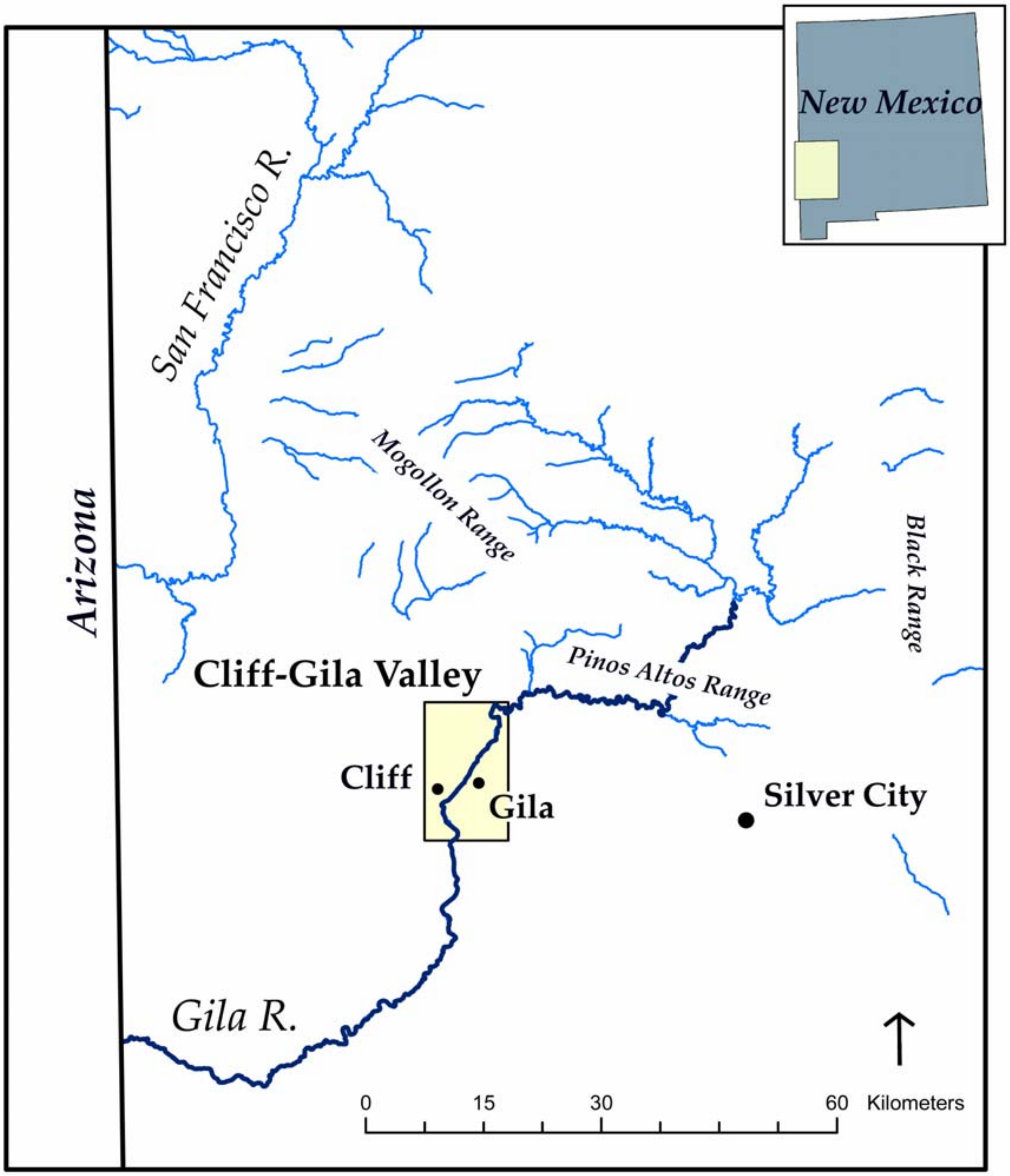
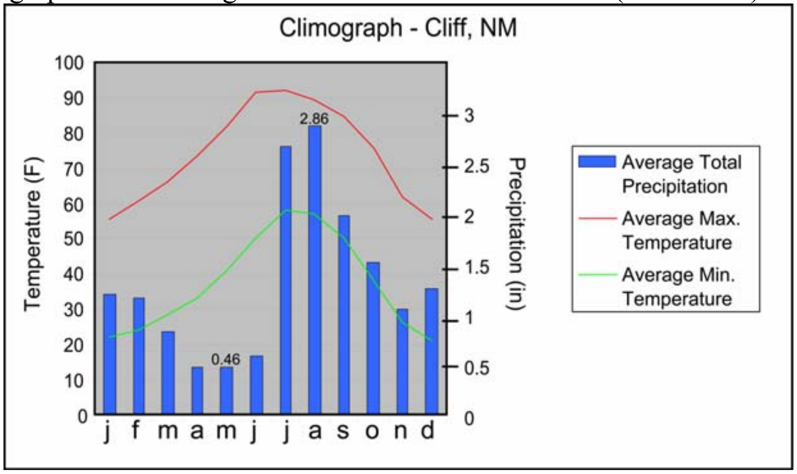


Figure 3: Climograph summarizing data from Cliff weather station (1971-2000).



Two rural towns share the valley; Gila is on the east and Cliff is on the west side. Most of the Cliff-Gila Valley is used for grazing and hay farming. Except for a quarter section of Forest Service property, the valley is private property up to the Gila National Forest boundary just below Mogollon Creek. There are only four main roads, two run parallel along the toe of the uplands, and State Highway 210 and State Highway 189 cross the floodplain. The only other roads on the floodplain are dirt roads that access pastures. There are only two permanent structures within the 100-year floodplain, and only one of these is occupied. Human modifications to the floodplain include levees, dykes, earthen irrigation ditches, landscaping, grazing and agriculture. Water is removed from the system for irrigation and the river is seasonally dewatered below the main ditch diversions for approximately 2.5 km.

Anthropogenic changes to floodplain morphology are evident but the river is free to migrate across the active channel. The Gila River is an anastomosing river (multiple channels) with a well-developed floodplain in a low-gradient valley (Rosgen 1994).

Throughout the mid-1900s the river was channelized and straightened. Currently channel patterns are characteristic of a compound channel described by Graf et al. (2002). This term applies to a river exhibiting hybrid morphology of two natural archetypes, which indicate anthropogenic changes to the floodplain have partially channelized a naturally braided system (Graf et al. 2002). Beaver activity is common and occasionally the beavers are successful in temporarily damming a main channel. In one location, a channel was dammed, the river changed course, and the entire channel has been a long series of ponds since 2001.

The floodplain of the valley supports low-elevation riparian woodland that is breeding habitat for a diverse and populous community of breeding birds. The riparian zone has been shown to support some of the highest non-colonial breeding bird densities north of Mexico (Stoleson and Finch 1997). Fremont cottonwood (*Populus fremontii*) forms the canopy of a large majority of the patches adjacent to the river. The community type of the young to middle-aged patches below the floodplain terraces and levees fits the community type Fremont Cottonwood-Gooding Willow/Seepwillow (*Populus fremontii-Salix gooddingii/Baccharis salicifolia*), described by Muldavin et al. (2000). Bluestem willow (*Salix irrorata*) is also common in these younger stands. Nursery bars are populated with seepwillow. The prevalence of cottonwood in the canopy and Gooding's willow as the subcanopy associate within the patches on the higher terraces indicates the mature patches would be of the same community type as on the active floodplain but anthropogenic changes have influenced the composition of the riparian community. Instead, the subcanopy is dominated by both boxelder and Gooding's willow, and in many stands, the boxelder is the most common tree, forming a closed gallery forest below the cottonwood canopy. Other tree species are present either that are remnants of other community types, or that have dispersed from cultivation and include: Arizona walnut (*Juglans majoris),* velvet ash (*Fraxinus velutina),* Arizona sycamore (*Platanus wrightii*), and Siberian elm (*Ulmus pumila*). Arizona alder (*Alnus sp.*) is occasionally present where there is standing water. Mature Salt cedars (*Tamarix spp.*) are uncommon and scattered throughout the valley, however a disconcerting number of saplings have been appearing in younger stands within the last few years (pers. obs.).

Landcover Mapping

A landcover map discards unnecessary detail by integrating lower-level patterns and grouping regions with similar characteristics. The goal of the mapping was to delineate riparian stands with homogeneous canopy structure. Stands were defined as relatively homogeneous in age and vegetation community, and patches were defined as contiguous woody riparian vegetation with distinct boundaries with non-woody landcover. I characterized stand structures using the height of the canopy and the presence or absence of additional foliage layers under the canopy (Appendix A). The resulting map was then analyzed for stand proportions, stand diversity and the quantity of riparian vegetation and related to flycatcher distributions.

Landcover Classifications

Canopy heights were categorized as being high, medium, or low. Stands with high canopy structure could also have a subcanopy and/or an understory. Medium-height canopy might have an understory but would not have reached the level of maturity where one shorter tree species could form a separate subcanopy below the canopy. Similarly, low canopy heights would indicate a young stand of saplings and/or shrubby willow and therefore, would not have more than one distinct layer. Seven stand types were distinguished and mapped (Table 1).

Table 1: Riparian landcover stand classifications

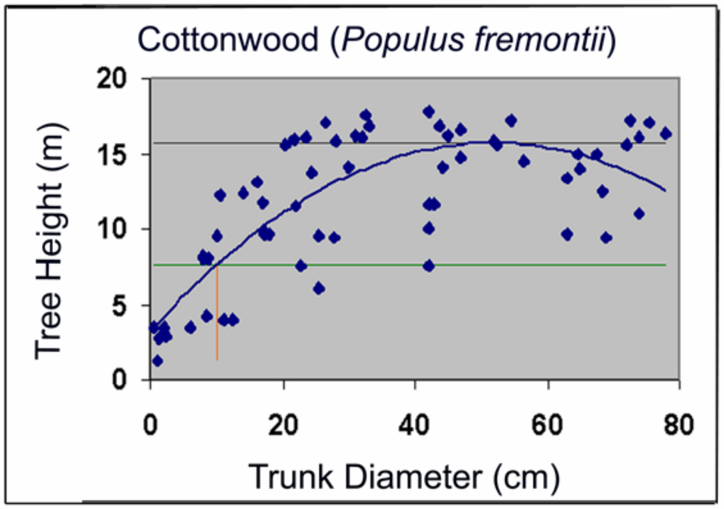
Abbreviation	*Grid Code*	*Description*
LO	1	Low Habitat, Canopy < 8 m
MD	2	Medium Height Canopy (7.6 - 15.8 m), No Understory
ML	3	Medium Height Canopy (7.6 - 15.8 m), Understory Present
HS	4	High Canopy (> 15.8 m), No Subcanopy, No Understory
HL	5	High Canopy (> 15.8 m), No Subcanopy, Understory Present
HM	6	High Canopy (> 15.8 m), Subcanopy Present, No Understory
AL	7	High Canopy (> 15.8 m), Subcanopy Present, Understory Present

Canopy heights were chosen to reflect the age of the stand. Height classifications indirectly measure the tree trunk diameters in the stand and the openness below the canopy, both of which are important in characterizing the structure of the vegetation. Canopy heights were categorized as high, medium or low. I used a combination of three methods to define the limits of each height category: (1) I projected all of the canopy height data (n=466) over Digital Ortho-quadrangless (DOQ) in ArcMap and reviewed the heights within patches that I felt were representative of old, middle-aged, or young patches; (2) I interpreted scatterplots of height-diameter data.

I found that evaluating the height-diameter relationship for cottonwood was the best method for determining the limits for the height categories. Projecting point data with canopy height attributes onto a digital orthoquad gave an indication of approximate height values that might be used to represent older and younger stands. However, this technique had limitations because of the need to precisely define limits. As an improved method, I interpreted a polynomial trend line through a scattergraph of cottonwood tree heights on the y-axis and the corresponding trunk diameter on the x-axis (Figure 4). The point at which the polynomial trend line begins to descend is the point where continued tree growth is mainly in girth. It follows from this that the floor of a forest at this stage should become more open as tree canopies grow in girth in correlation with trunk diameter growth. I used cottonwood because it is the canopy species of a large majority of the patches. I excluded tree data with heights greater than 20-meters in the scatterplot because there were a number of outliers with very large trunk diameters and relatively short heights. I assumed that those trees were in a stage of decline and that main trunks had broken off. The point at which the first derivative of the polynomial trend line is zero is the point where the relative maximum height-to-girth growth is attained. I graphically assessed where the first derivative was zero and set the lower limit of a high stand at this value (15.8-meters). For the lower limit, I simply calculated the height of a

10-cm cottonwood from the polynomial trend line (7.6-meters). I adopted 10-cm as the criterion for defining a juvenile cottonwood (Busch and Smith 1995).

Figure 4: Height-diameter polynomial trendline through a scatterplot of cottonwood tree measurements used to refine category break points for classifying stands by height.



Vegetation Sampling

Mapping riparian is a difficult task because riparian systems are dynamic in nature, and limited in extent. Map production requires an understanding of the vegetation patterns as they are related to landscape features and disturbance (Muller 1997). To better understand these patterns, I sampled vegetation along six transects running perpendicular to the river channel. Transects were laid out in 100-meter intervals and circular plots (0.02 ha) were established along the transects every 50-meters. Plot size was chosen to coincide with the plot size of existing RMRS vegetation data. I selected an area of the study site where all stages of vegetation were represented including naturally regenerating vegetation on the floodplain and mature stands on terraces with varying degrees of human modification and access to water. All of the transects were laid out in relation to one point, randomly selected in ArcMap 8.2. Each point was entered into a GPS unit but once in the field, I moved some of the points to the nearest location where the entire plot was within one homogenous cover type. I selected one additional plot because its characteristics were not represented by other sample points. I skipped points in areas where I had vegetation data from RMRS. I completed 23 samples. In addition to these points, I completed vegetation sampling at 15 locations in the valley, randomly selected in ArcMap within areas where existing vegetation data was sparse and/or where I was less familiar with the stand characteristics.

I sampled vegetation at each plot using a rapid assessment method (modified from James and Shugart 1970; B. Norris, pers. comm.). The plot was quartered along the cardinal directions and the diameter-at-breast-height (DBH) (cm) of the largest tree, and its species were recorded for each quadrant. Canopy coverage was estimated and recorded as a rating (1=1-10%, 2=11-25%, 3=26-50%, 4=51-75%) for total cover, total canopy cover, total subcanopy cover, and total understory cover. The species contributing to each layer were recorded and given a rating according to the proportion of foliage it contributed to that layer. Canopy height at the center of the plot was measured using a clinometer. I recorded the substrate type and the plot position relative to any levees.

Map Production

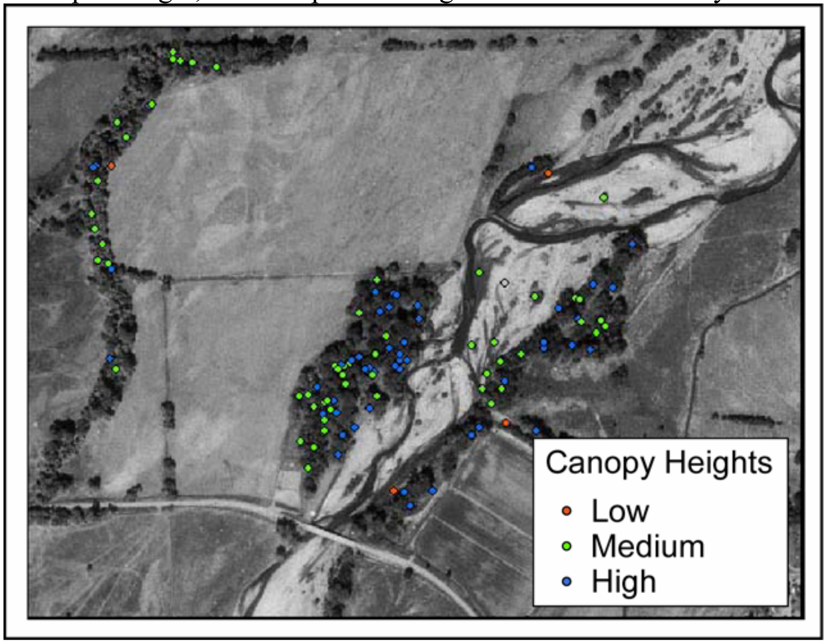
I incorporated a variety of tools to produce a landcover map delineating homogeneous patch types. I had a great number of resources that were extremely useful.

I do not believe it would have been possible to create the map on the level of detail that did with using only air photo interpretation. The tools I used to map the riparian vegetation included:

- 3.75-minute Digital Orthophoto Quadrangles (DOQ), 1-meter resolution (1996) for the entire study site.
- Scanned color air photos (1999) that I georeferenced in ArcMap (Gila National Forest)
- Orthophoto composites flown March, 2001 (2-meter resolution) (U.S. Bureau of Reclamation, Upper Gila River Fluvial Geomorphology Study) (Gila National Forest).
- Geo-referenced vegetation data at willow flycatcher nest sites and null sites (Gila Flycatcher Project 1997-2002, Rocky Mountain Research Station).
- Vegetation sampling – Rapid Assessment Method
- Personal Observations (full-time field work May – August or later 1997-1999, 2001-2003)

Vegetation data were displayed in ArcMap for reference while delineating riparian stand types for a landcover map. Rapid assessment plot measurements were added as attributes to spatially referenced points and projected over a DOQ in ArcMap. I did the same for RMRS vegetation data taken at nest trees (n=334) and null points (n=90) (>33 m from a flycatcher nest) (Stoleson and Finch 1997; Stoleson and Finch 1998; Stoleson and Finch 1999a). I added selected variables as attributes to spatially referenced point data including: stem counts for all species of tree stems (≥10cm DBH) within an 8-meter radius and for all species of sapling stems (<10cm DBH) within a 4-meter radius, and canopy heights averaged from 9 points within the plot. I made copies of the point projections so I was able to display each parameter of interest simultaneously. Each point was displayed with a color indicating a categorized value for the parameter of interest (Figure 5). The stem count data and the canopy coverage ratings were valuable for determining areas of the stand with an understory and subcanopy. Canopy height data was of course, valuable in determining the height category for a stand.

Figure 5: Sample area from ArcMap project with geo-referenced canopy-height data projected over Digital Ortho-quadrangle; colors represent height classes used in analysis.



Rather than delineating each of seven stand types, I mapped the extent of each canopy layer (understory (low height), subcanopy (medium-height), and high canopy) and then combined the resulting layers. Patterns emerged from studying the vegetation measurements in relation to the spatial position on the floodplain and this simplified the task. Understory foliage cover rated high (>26%) for every plot that was on the active floodplain. Additionally I reviewed stem count data throughout the site and found that greater numbers of saplings (>12) were highly correlated with nearness to water or saturated soils. To facilitate mapping the understory layers and low-level vegetation, I delineated the active floodplain and sources of water on the higher terraces such as channels draining irrigated pastures and other small ponds. These areas of potential riparian regeneration were clipped with a riparian layer so that understory vegetation extents were limited to areas that supported vegetation.

The extent of stands with a medium-height canopy or the presence of a subcanopy within a high stand was determined with a combination of orthophoto interpretation, canopy height data and familiarity with the area. The orthophotos were excellent for visualizing the structure of the canopy. The level of detail that one can discern on these photographs is high enough to see individual tree crowns well. High canopies in the valley are formed from the crowns of large cottonwoods, which were easily differentiated from the densely packed, tall, straight trees of the middle-aged patches. I relied heavily on my familiarity with the patches in the valley for identifying areas with a high canopy but with no subcanopy. The character of these patches is distinct, with tall cottonwoods that tend to be in decline. The air is warmer and drier and the stand is very open and is not densely shaded.

The next step was to combine the layers into one raster landcover map. Before combining the layers, polygons marked the location of each individual canopy layer, and there were as many as three layers of polygons in any given location. The polygons present determined the stand type (e.g., medium-height layer present and high-height layers present would mean the stand had a high canopy and a subcanopy but no understory). The task was to combine these layers into one map delineating the seven stand types I had defined. First, I rasterized each layer and then used a map calculator in

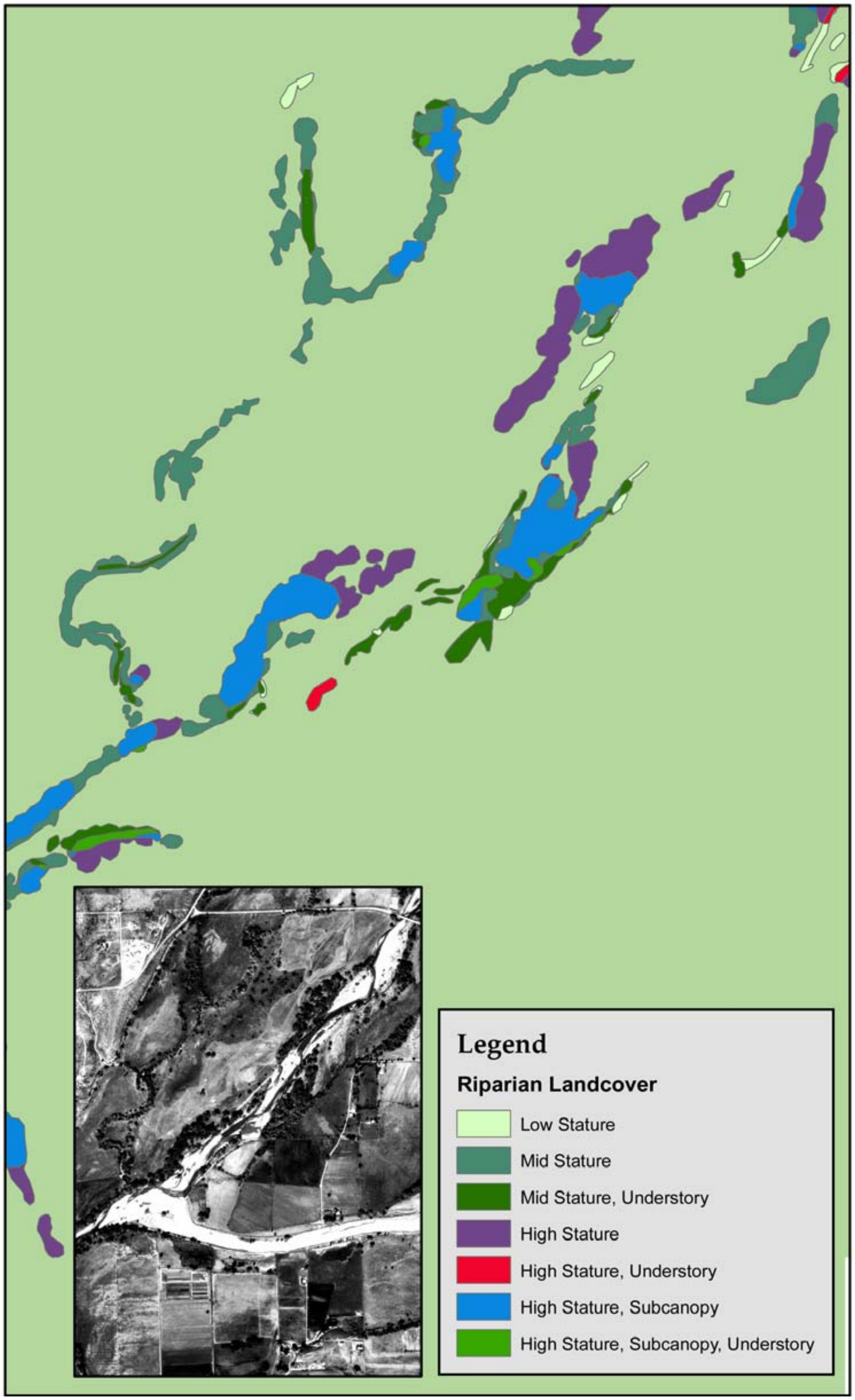
ArcMap to sum cell values. The cell values corresponding to the canopy layers were assigned so they would combine to unique values. The resulting map had grid codes with eight values, seven of which corresponded with a stand type, and a value of zero that corresponded to non-riparian (Figure 6).

Structural diversity was quantified with the Simpson's Diversity Index (SDI). SDI integrates relative abundance and number of each feature in a specified plot (Neumann 2001). The stand proportions were used to calculate SDI:

$$SDI = \sum_{i}^{N} \left(1 - \pi_i\right) \cdot \pi_i$$

where π_i is the relative proportion of the *i*th cover type (Simpson 1948). I calculated the index for canopy-layer diversity, which assessed the diversity of the seven different stand types.

Figure 6: Selected section of riparian landcover map produced for analysis



Scale

Important to spatially-explicit habitat modeling is the resolution and extent of the analysis, two concepts commonly referred to with the use of the term 'scale'. The grain, or minimum mapping unit, had to be small enough so that the character of the stands was not lost. Riparian zones are narrow and linear and heterogeneity within these limited areas could only be expressed using a small grain. I selected 5-meters for the grain, which was approximately half the distance of the smallest stand width.

Analysis extent must be biologically relevant to the organism or ecological process being modeled (Levin 1992). The flycatcher has a very small territory size, and in the Gila Valley it is not uncommon to have territories with radii smaller than 30-meters (Stoleson and Finch 1999b). I was attempting to capture characteristics of the stand that varied by floodplain features so stand characteristics were evaluated beyond the size of a flycatcher territory. Determining the most biologically relevant scale has been the subject of a good deal of research (e.g., Wiens 1989; Levin 1992; Schuft et al. 1999; Thompson and McGarigal 2002) but selection of the one, best extent depends on interpreting factors that might not be perceivable to a human. Thompson and McGarigal (2002) showed that the best scale to describe a habitat-use relationship for Bald eagles was not always consistent for each habitat feature within the same study site. Analysis of a digitized map in a GIS provides greater opportunity to repeat analyses on varying scales. Some authors have been successful in varying scale for analysis of riparian (Schuft et al. 1999) and avian-habitat relationships (Thompson and McGarigal 2002; Hatten and Paradzick 2003).

Rather than selecting a single scale of analysis, I varied the extent in four phases. I used a circular "window" for the analysis. I selected a 200-meter radius as the maximum extent because most of the stands are within 200-meters of the river. I decreased the extent by 50-meters for each analysis (Figure 7). For every scale, I used neighborhood functions to sum the amount of each stand type within the moving window (Figure 8). As the analysis window passes, the composition on the map is quantified within the extent and the value is assigned to the center cell. Stand quantities were assessed individually and output as a raster dataset for each stand type and for high, medium and low canopy heights. Stand quantities were converted to proportions using the map calculator to divide the value of each pixel by the total area of the search neighborhood.

Figure 7: Extents used in analysis are projected over digitized color-infrared air photos (6 inch resolution) (2001) in the Gila River Bird Area; points are nest locations.

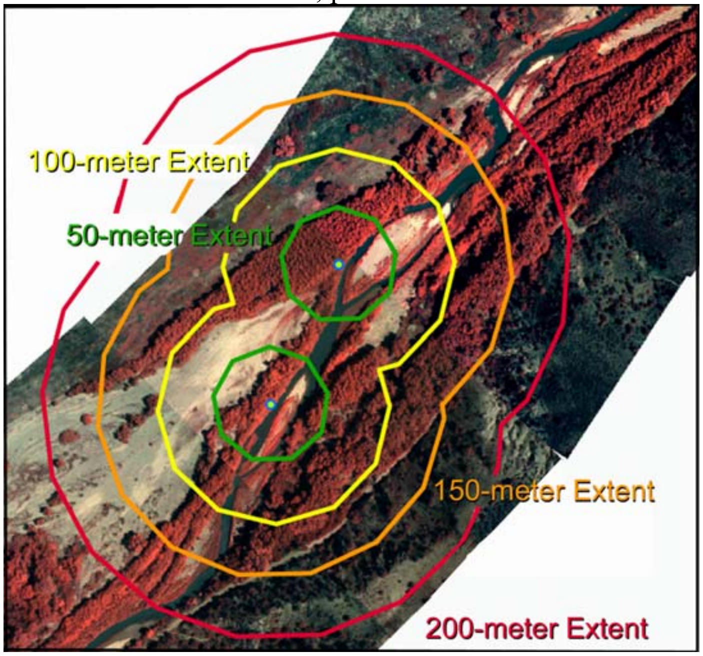
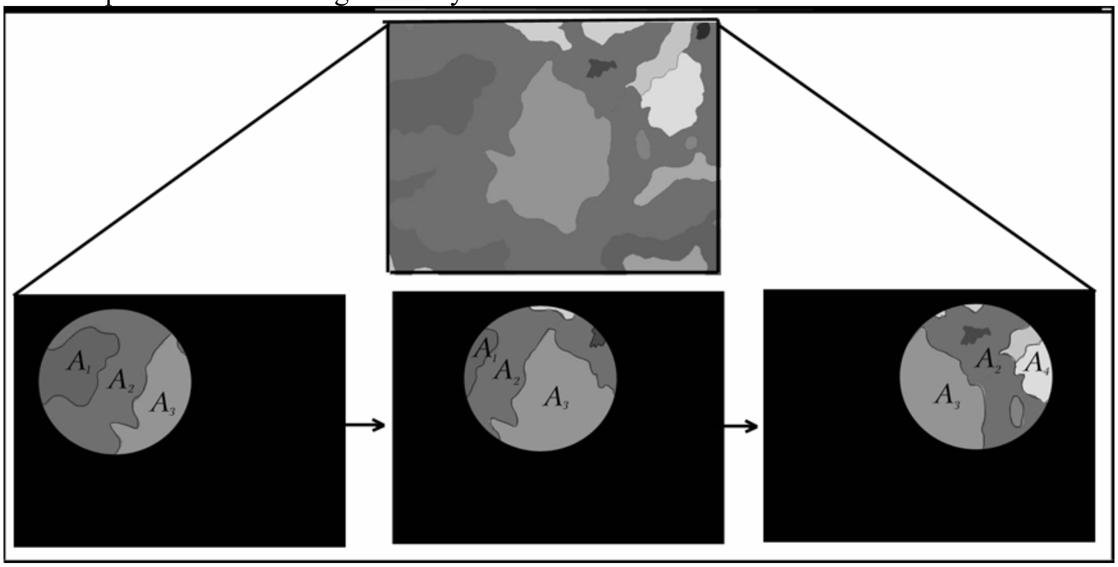


Figure 8: Conceptual figure of a moving analysis window, of a given analysis extent, passing over riparian landcover map, the area of each stand class is calculated and the value is assigned to the center pixel of the resulting raster layer.



Data Selection

Data used to develop the model were extracted from presence/absence point locations. For the presence locations, I acquired UTM-coordinates with a GPS unit at sites where nests had been located and monitored by the USDA Rocky Mountain Research Station between 1997 and 2003 (n = 793). I selected a subset of this data for analysis (see Temporal and Spatial Autocorrelation section below). Absence data are less reliable than presence data because detection failures are possible. However, Brotons et al. (2004) found that despite the inability to assume complete absence in presence/absence models, they performed with higher accuracy than models built with presence-only data. Additionally, presence information in this dataset is relatively dependable. Over eight years of monitoring this population, there have been four to seven biological professionals hired each year to collect breeding data. Each person, with his or her own interpretation of what constitutes flycatcher habitat, had the opportunity to explore the area and discover more flycatcher territories. The information base was broadened each year with every new territory that was discovered.

Absence data were points randomly chosen within a layer of "unsuitable" riparian vegetation. Unsuitable vegetation was delineated by excluding flycatcher habitat from a riparian map layer. Flycatcher habitat was demarcated with a 30-meter buffer around the nest features. I visually assessed various sized buffer layers and determined that the 30-meter buffer most precisely excluded unsuitable vegetation. Larger buffers incorporated too much vegetation that I felt to be unsuitable for breeding flycatchers. I defined unsuitable vegetation as mature cottonwood bosques or short stature, shrubby, less mesic vegetation. The resultant unsuitable vegetation layer was made by converting the 30-meter buffer layer to grid format and "erasing" the area from a riparian grid by combining and reclassifying the layers, resulting in a layer of unsuitable riparian vegetation. Random points were selected within the unsuitable vegetation using a VB Macro, "Random Point Generator". The null points were reviewed for accuracy and four were removed because they were located in vegetation where singing flycatchers had been observed but a nest was never located. These were replaced by randomly selecting four more points.

Variables for statistical analysis were obtained from the grids at locations where breeding flycatchers were both present and absent using Avenue Script GridPig v.2.6 (Hare 2003). Variables included proportions for each stand type, stand diversity, and proportion of riparian stands for each of the four scales. Additionally, the area (hectares (ha)) and perimeter (1x100 m) of each contiguous patch of riparian were calculated and rasterized. Patch area was defined as the amount of contiguous riparian vegetation and was measured in hectares. These were captured as additional variables to be used in statistical analysis. From the area and perimeter, I calculated patch perimeter-area ratio (PAR). A patch that is small and highly convoluted will have a high PAR, which is characteristic of some of the younger patches on the floodplain and the lowest values of PAR indicate a larger patch with a proportionally large amount of core area. PAR tends to decrease with patches of greater size, even when shape is held constant (MacGarigal et al. 2002).

Data Analysis

The objective of the analysis was the formation of an inductive model rather than a predictive model. The inductive modeling approach is used here in an attempt to advance understanding of the general factors influencing the distribution of the southwestern willow flycatcher, which might be applicable across the flycatcher's range. The goals were to (1) determine the relative value of each of the independent variables, (2) to interpret patterns that are expressed in the data, and (3) build a multiple variable model that selects the central variables that influence flycatcher presence.

The focus of the analysis was to define the gross structural characteristics of occupied riparian vegetation. Logistic regression was used to model flycatcher presence/absence where presence/absence was the modeled response and stand characteristics within progressively increasing distances, patch area, patch perimeter, and patch perimeter-area ratio were the explanatory variables. Emphasis was placed on understanding the importance of stand heterogeneity and the amount of riparian vegetation to flycatcher distribution. R v.1.7 (Ihaka and Gentleman 1996), was used for most statistical analyses, and GS+ v.5.3.1 demo was used for spatial statistics. Some code used in R was acquired from Thompson (2004).

Model-Building

To explore relationships between presence and each variable, estimated response functions were examined for the shape. Single-variable response functions were evaluated using locally-weighted running line smoothers, or lowess smoothes (Hastie and Tibshirani 1990). Ideally, the fitted response will have a monotonic sigmoidal shape (Neter et al. 1996).

Trend estimates for the stand height variables suggested non-linear responses. Variable transformations were unable to provide a more appropriate response for logistic regression. I explored the option of using Generalized Additive Modeling (GAM) techniques, which are used to implement non-parametric smoothers in regression models (Guisan and Zimmerman 2000). However, because the modeling objectives were to infer general habitat preferences that might be applicable beyond the study site, I decided to categorize the stand height variables (low, medium, and high) to use as dummy variables in linear logit models. I found the results to be simple, yet effective in selecting levels of stand height variables that influenced the probability of flycatcher presence. Significant parameter estimates indicated that the estimated probability of flycatcher presence for a given level was significantly different from the estimate for the other levels. Odds ratios were calculated by exponentiating the difference between the two parameter estimates (Agresti 2002) and are an estimate of the odds of flycatcher presence at one level compared to the odds of presence at the other level (Agresti 2002). To categorize stand height variables, (1) square root transformations were applied where they helped to normalize the distribution of negatively skewed low-stature stand cover variables, and (2) all stand cover variables were categorized into low, medium and high groups. Low values fell between zero and the mean, medium values were between the mean and one standard deviation, and high were values above one standard deviation.

I used logistic regression with each continuous and each dummy variable as a single predictor to further describe its relationship with the probability of flycatcher presence. Logistic regression assumes model errors are distributed binomially and a logistic link function, the logit (log-odds), is used to transform the linear predictor onto the binary response. Regression coefficients were estimated using maximum likelihood, and the odds-ratio and profile-likelihood 95% confidence limits were employed to evaluate the strength and direction of each relationship (Agresti 2002). Akaike's Information Criteria (AIC), which measures lack of model fit (Burhnam and Anderson 1998), was used to assess the relative strength of the models.

Forward stepwise variable selection was used for model building. There were a large number of variables produced by varying the extents so stand height categories that did not have significantly different levels of fit were excluded from the stepping procedures. The likelihood-ratio test statistic was used to evaluate variable entry. A step was evaluated as justified when the amount of deviance explained in the more complex model was high relative to the loss in degrees of freedom. The likelihood-ratio test statistic (LRT) is the difference in deviance between the two models and has an approximate null chi-squared distribution (Agresti 2002). P-values were used to assess the significance of the more complex model.

Model Evaluation

The final model was checked for overdispersion which arises when model variance, which is a function of the mean in logistic regression, is larger than the mean fit (Agresti 2002). Overdispersion is a violation of the assumption of generalized linear models that the variance is a known function of the mean. I calculated the overdispersion parameter ($\hat{\phi}$) for the final model, which is greater than 1.0 when overdispersion is present. To account for overdispersion, the standard errors of the parameter estimates were multiplied by the square root of the overdispersion parameter (Agresti 2002) the new confidence intervals were evaluated for any inclusion of zero.

The final model was further evaluated with a variety of tests aimed at checking systematic lack of fit. Goodness-of-fit was tested, (1) with the Hosmer-Lemeshow statistic, and (2) by conducting influence diagnostics. The Hosmer-Lemeshow statistic is calculated from partitioning the predictors and comparing observed and fitted values (Agresti 2002). Influence diagnostics were conducted using *Dffits,* which tests for leverage of single observations. *Dffits* is the change in the parameter estimate when an observation is deleted divided by its standard error (Neter et al 1996). After evaluating the validity of each influential observation's spatial location and variable value, the model was reevaluated without the observations, and parameter estimates were compared to the original parameter estimates. Any significant changes in the coefficients, especially where model interpretation changes would indicate spurious fit and that the model might need to be reconsidered if reasons for lack of fit cannot be determined.

Scale

To evaluate scale-dependent relationships between flycatcher presence and the quantity and diversity of the canopy layers, each analysis extent was used independently in tests for association and output from each extent was compared to the others. Systematically varying the extent output 4-7 calculated variables for each canopy height, riparian quantification, and diversity calculation. First, the differences in means and the spread of the data were evaluated. Where the data were distributed normally, boxplots of presence data and absence data were graphed and evaluated for the nature of the differences. The distribution of the stand-height data were negatively skewed so the mean and the nonparametric bootstrapped confidence intervals for the presence and absence data were graphed in place of boxplots (DiCiccio and Efron 1996).

Two statistics were used to evaluate the strength of the relationship between flycatcher presence and each scale of analysis: (1) Residual deviance after single-variable logistic regressions were fit, (2) the F-statistic from analysis of deviance of the same models. Residual deviance was selected rather than model AIC because it was helpful to compare all values with null deviance, which is maximum deviance. Additionally, it wasn't necessary to consider the number of parameters in the model since the models being compared had identical degrees of freedom.

Temporal and Spatial Autocorrelation

The potential for temporal and spatial correlations in the data set were high because site fidelity, clumped distributions, and small territories are characteristic of breeding flycatcher populations. Generalized linear models assume the responses are independent observations and spatial correlation can be problematic because it violates the assumption of independence (Legendre 1993).

To correct for possible temporal correlation, I selected only one year of the dataset for analysis. Data from 2002 was appealing because it held information regarding renests. The flycatchers will often renest after a nest fails and renest attempts were identified in the data in 2002. This information allowed for the removal of subsequent nest attempts in the same territory. Renests are a potential source for spatially correlated data because of their certain proximity. Removing renests did not remove all potential for spatial correlation however.

I evaluated spatial correlation structure by examining Moran's I correlograms (Odland 1988) and semivariograms using the Pearson's standardized residuals from the final model. GS+ v.5.3.1 demo version was used for these tasks and, because it is the demonstration version, only 144 observations were allowed in the analysis. I randomly selected two sets of 144 observations and used the second set to validate the outcome of the first. The smallest lag distance that produced at least 20 to 50 pairs per bin was used in order to identify the expected small-scale correlation. The main purpose for evaluating the correlation structure was to identify the effective distance, or range where correlation exists between pairs of observations. The range was determined from the variogram model that best fit the data. The range was important for incorporating spatial correlation into the final model.

Spatial correlation was fitted to the existing model additively using a modified version of the "autologistic" method developed by Augustin, Mugglestone, and Buckland (1996). The autologistic method adds a term to the selected logistic regression model that incorporates spatial correlation and the environmental covariates. The term is an average of the predictions of all closely spaced points, weighted by the distance between them. The methods developed by Augustin, Mugglestone, and Buckland are designed for presence/absence sampling on a regular grid but I modified this by defining a maximum distance, or neighborhood of influence, rather than defining the number of neighboring squares to be considered. Lichstein, Simons, and Franzreb (2002) used a similar method for ordinary least squares regression where they used a spatial neighborhood defined by the maximum distance of autocorrelation. The algorithm used by Lichstein, Simons, and Franzreb, incorporated residuals from OLS regression and was therefore not appropriate for logistic regression. Selection of the size of the neighborhood depends on the range that the points are thought to be correlated and was determined from variogram modeling in the step above. This was incorporated into the autocovariate equation (Augustin, Mugglestone, and Buckland 1996):

$$autocov = \frac{\sum_{j=1}^{ki} w_{ij} y_j}{\sum_{j=1}^{ki} w_{ij}}$$

where *w* is defined as the inverse of the spatial distance (meters) between points *i* and *j*, y_j is the fitted probability at *j*, and k is the number of points within the given search neighborhood. The autocovariate was calculated for each observation and an autologistic model was fit that contained a term for the added predictor. Model improvement was assessed with the likelihood-ratio test, where the expected loss of deviance must be great enough to offset the loss of degrees of freedom, and the significance of the new parameter estimate.

RESULTS

Single-Variable Logistic Regression

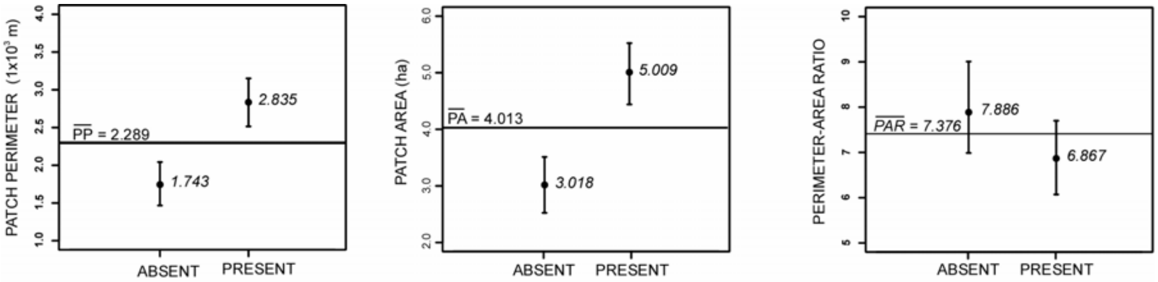
The results of single variable modeling provided support for the hypothesis that canopy heterogeneity is positively correlated with flycatcher presence but the strength of the relationship was dependent on the scale of measurement. The effect of an increasing amount of riparian within the vicinity was positively correlated with flycatcher presence when lower search radius were used but when a larger search radius was implemented, the relationships were not as clear. Patch area and patch perimeter proved to be more significant than the quantity of riparian when describing flycatcher patterns and were both positively correlated with the presence of the birds. Generally, high levels of low stature habitat were also positively correlated with flycatcher presence.

Patch Size and Shape

In general, larger patches were more likely to support flycatchers. Mean patch area for presence data was 5.01 ha (nonparametric bootstrapped 95% CI: 4.52 to 5.54) compared with 3.02 ha (nonparametric bootstrapped 95% CI: 2.54 to 3.51) for the absence data (Figure 9). Mean perimeter for presence data was 2.84×10^3 m (nonparametric bootstrapped 95% CI: 2.53×10^3 to 3.16×10^3) and 1.74×10^3 m (nonparametric bootstrapped 95% CI:1.45×10^3 to 2.03×10^3) for the absence data (Figure 9). Perimeter-area ratios were slightly lower for the presence data (mean = 6.91, nonparametric bootstrapped 95% CI: 6.15 to 7.77) than for the absence data (mean =

7.95, nonparametric bootstrapped 95% CI: 6.98 to 9.02). Patches with greater quantities of core area have lower PAR, indicating higher core area might be associated with flycatcher presence (Figure 9).

Figure 9: The differences between mean patch measurements for presence and absence data. Means and bootstrapped nonparametric confidence limits are given for patch area, patch perimeter, and patch perimeter-area ratio.

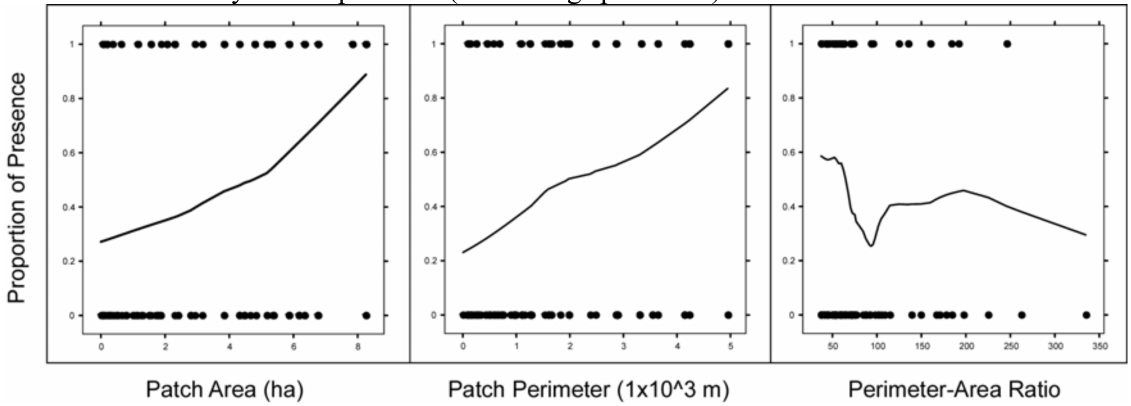


Tests of single-variable logistic regression showed patch area and perimeter to be positively correlated with flycatcher presence. These two predictors outperformed all of the other predictors in single-variable tests (Table 2). Patch area performed slightly better than patch perimeter. Response functions showed strong increasing trends and were appropriate for logistic regression (Figure 10). Parameter estimates from logistic regression were positive and significant. AIC values were 230.27 and 232.97 for area and perimeter respectively, which were lower than all other variables tested. Interpretation of the odds-ratios calculated from the parameter estimates showed that at the mean patch area (4.01 ha), the estimated probability of flycatcher presence increased by about 0.075 with a 1-ha increase in area, and at the mean perimeter (2.29×10^3 m), estimated probability of flycatcher presence increased by approximately 0.12 with 1000-meter increase in perimeter.

Table 2: Results of logistic regression with continuous variables as single-variable predictors modeling the probability of flycatcher presence. Parameter coefficients, coefficient standard errors, P-values of the Z-statistic, and AIC values from each regression are provided.

	Intercept	Estimate	SE	Pr(>|z|)	AIC
Canopy Heterogeneity					
50-meter extent	-2.03644	0.18787	0.04789	< 0.001	238.62
100-meter extent	-1.82602	0.23698	0.06119	< 0.001	239.09
150-meter extent	-1.56244	0.25538	0.07795	0.001	244.63
200-meter extent	-0.86962	0.17018	0.08727	0.051	252.38
Riparian					
50-meter extent	-1.78909	0.15288	0.04156	< 0.001	241.11
100-meter extent	-1.73397	0.21639	0.05733	< 0.001	240.04
150-meter extent	-1.52025	0.24229	0.07476	0.001	244.90
200-meter extent	-0.84549	0.16237	0.08461	0.055	252.51
300-meter extent	-0.32203	0.07895	0.11032	0.474	255.79
400-meter extent	-0.5512	0.1599	0.1478	0.279	255.12
500-meter extent	-0.5613	0.1883	0.1819	0.300	255.22
Patch Area (ha)	-1.2054	0.2995	0.0060	< 0.001	230.27
Patch Perimeter m x 10^3	-1.1120	0.4887	0.1071	< 0.001	232.95
Perimeter-Area Ratio	0.3830	-0.0523	0.0354	0.139	253.91

Figure 10: Scatterplot smoothes of the data representing the relationship between patch characteristics and flycatcher presence (smoothing span = 2/3).



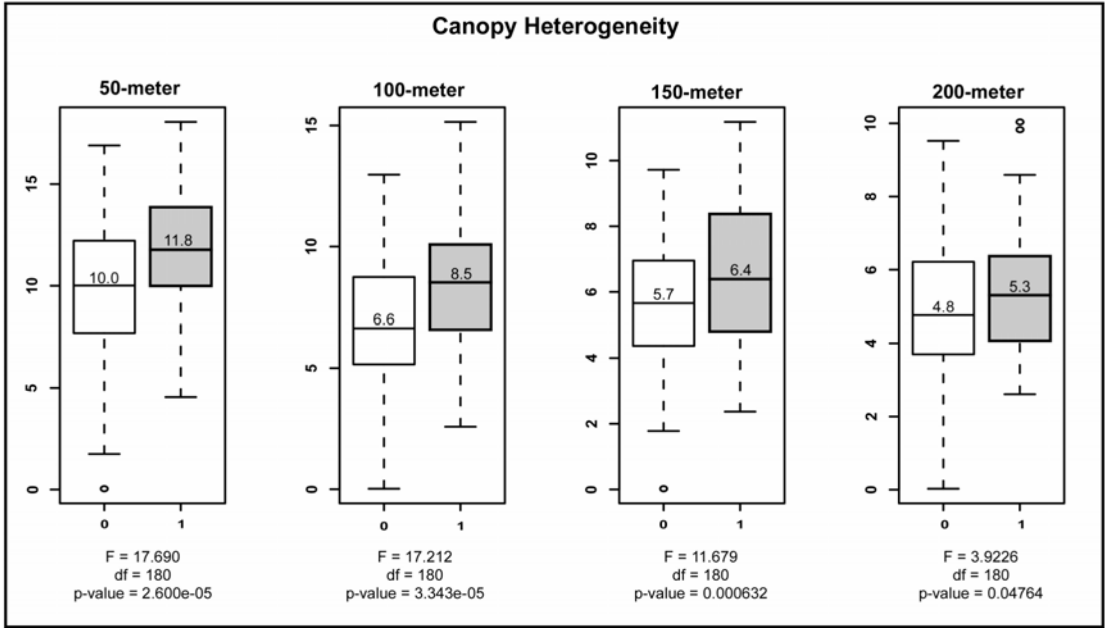
PAR was not significantly correlated with flycatcher presence. The parameter estimate was negative, the smoothed scatterplot presence trended downward with increasing PAR (Figure 10), and the mean value for the presence data was lower than the mean value for the absence data (Figure 9). However, the coefficient from logistic regression was not significant (P=0.139) and there was a large dip in the lower section of the smooth (Figure 10). The F-statistic from ANOVA output was also not significant (P=0.124).

Stand Heterogeneity

Stand heterogeneity at all scales exhibited a positive relationship with flycatcher presence. Stand heterogeneity variables at all scales were reasonably normally distributed and boxplots showed the median value of presence data to be greater than the median of absence data for all extents (Figure 11). The F-statistics from ANOVA output were significant at all scales (<0.05), providing support for the alternative hypothesis that the difference in means between presence and absence is not equal to zero. A positive trend was evident in plots where lowess smoothes were fit to scatterplots of the data (Figure 12).

Single-variable logistic regression models were fit to the data using stand heterogeneity at each extent as a predictor and flycatcher presence as the response. Parameter estimates for all scales that were below 200-meters were positive and significant (P <0.05) (Table 2). The parameter estimate for the 200-meter extent was positive but the P-value was only moderately significant (0.0512). At the mean value of canopy heterogeneity for the 50-meter extent variable, there is an increase in the proportion of flycatcher presence of 0.047 for an unit increase in the diversity index. The diversity index in the data ranged from 0.04 to 18.06 and a unit increase is approximately 5-6% of the heterogeneity at the site.

Figure 11: Boxplots compare canopy heterogeneity data by presence (1)/absence (0).



In addition to presence/absence, flycatcher densities tended to be higher where there were a greater number of stand types within the vicinity. In ArcMap, the numbers of stand types within incrementally increasing search radii were calculated and flycatcher density was averaged across the resulting values. The number of stand types within a given search radius was plotted against the mean flycatcher density (Figure 13), which showed that the greatest flycatcher densities for each search radius tended to be highest where there were a greater number of stand types. Maximum flycatcher density was achieved where five stand types were found within a 25-meter radius. As the search radius increased, maximum flycatcher densities were found at incrementally greater numbers of stand types. Maximum flycatcher density, within a 100-meter search radius, was found where there were seven stand types. For all search radii, flycatcher densities dropped off quickly when there were eight stand types within the vicinity. This might be influenced by the low amount of coverage that is adjacent to eight stand types.

Figure 12: Scatterplot smoothes of the data representing the relationship between stand heterogeneity at each scale of analysis and flycatcher presence (span=2/3 (blue), span=1 (gray), span=1/3 (green), span determines the degree of smoothing).

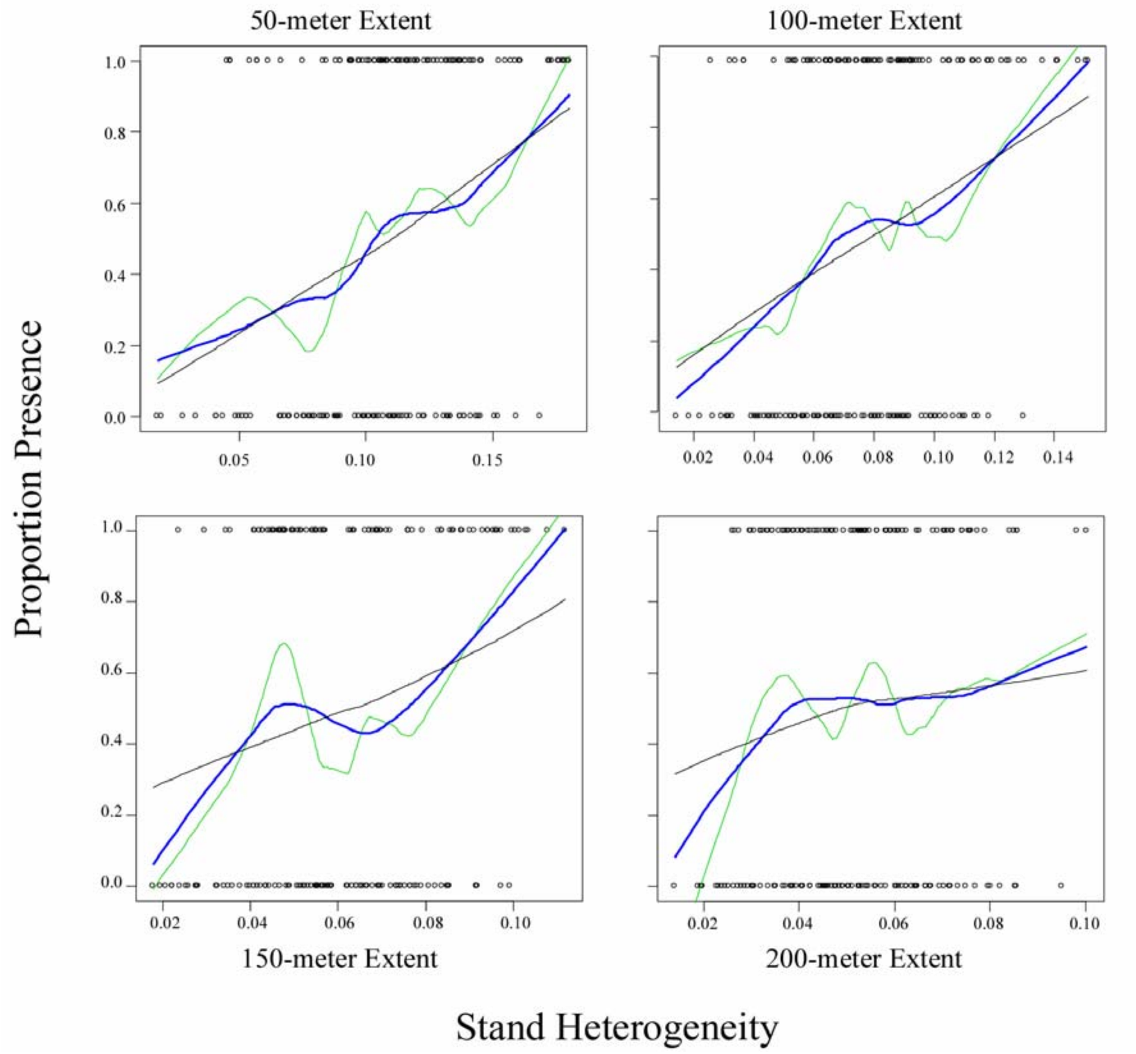
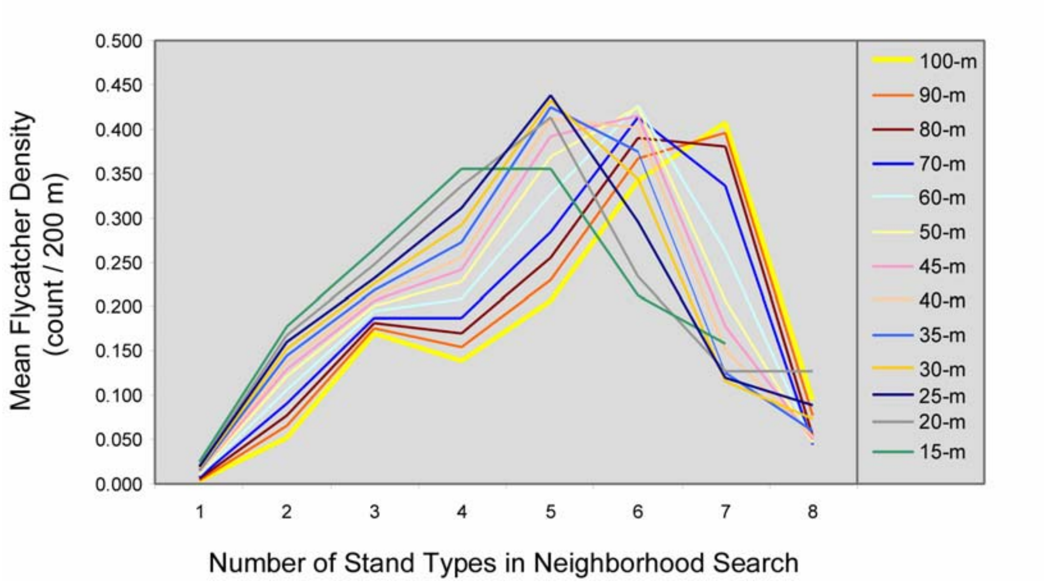


Figure 13: In a GIS, the number of stand types are counted within a given search radius and flycatcher density is averaged for the values on the resulting map layer. Mean flycatcher density tends to be greatest where there are five to seven stand types within the vicinity but densities drop off quickly with eight stand types.



Riparian Extent

Flycatchers nested in stands with a greater quantity of riparian vegetation when measured within extents less than 300-meters. Scatterplot smoothes showed the response to be increasing with increasing quantity for all scales but a relatively smooth trend was only evident for variables measured at the lower extents (Figure 14). The median quantity of riparian vegetation for presence data was greater than the median quantity for the absence data for the 50- to 200-meter extents (Figure 15). The F-statistics from analysis of deviance were significantly higher for these extents, except the 200-meter (P-value = 0.053). The median values for the 300 to 500-meter extents were either slightly lower for the presence data (300-meters) or almost equal. The spread of the data for these higher extents however, was more defined and the minimum value was always higher than the minimum for the absence data (Figure 15). The pattern suggests the flycatchers might be selecting for medium to medium-high quantities of riparian at the higher extents.

Figure 14: Scatterplot smoothes of the data representing the relationship between the quantity of riparian vegetation at each scale of analysis and flycatcher presence (span=2/3 (blue), span=1 (gray), span=1/3 (green), span determines the degree of smoothing).

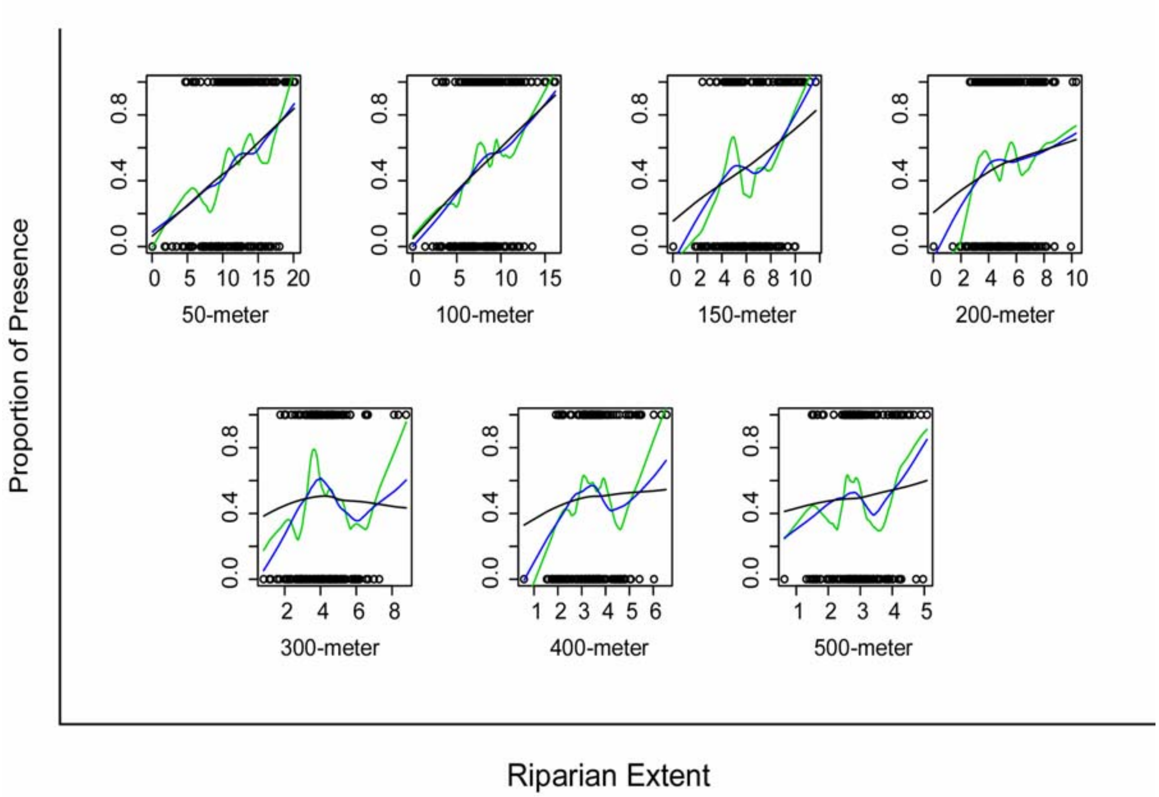
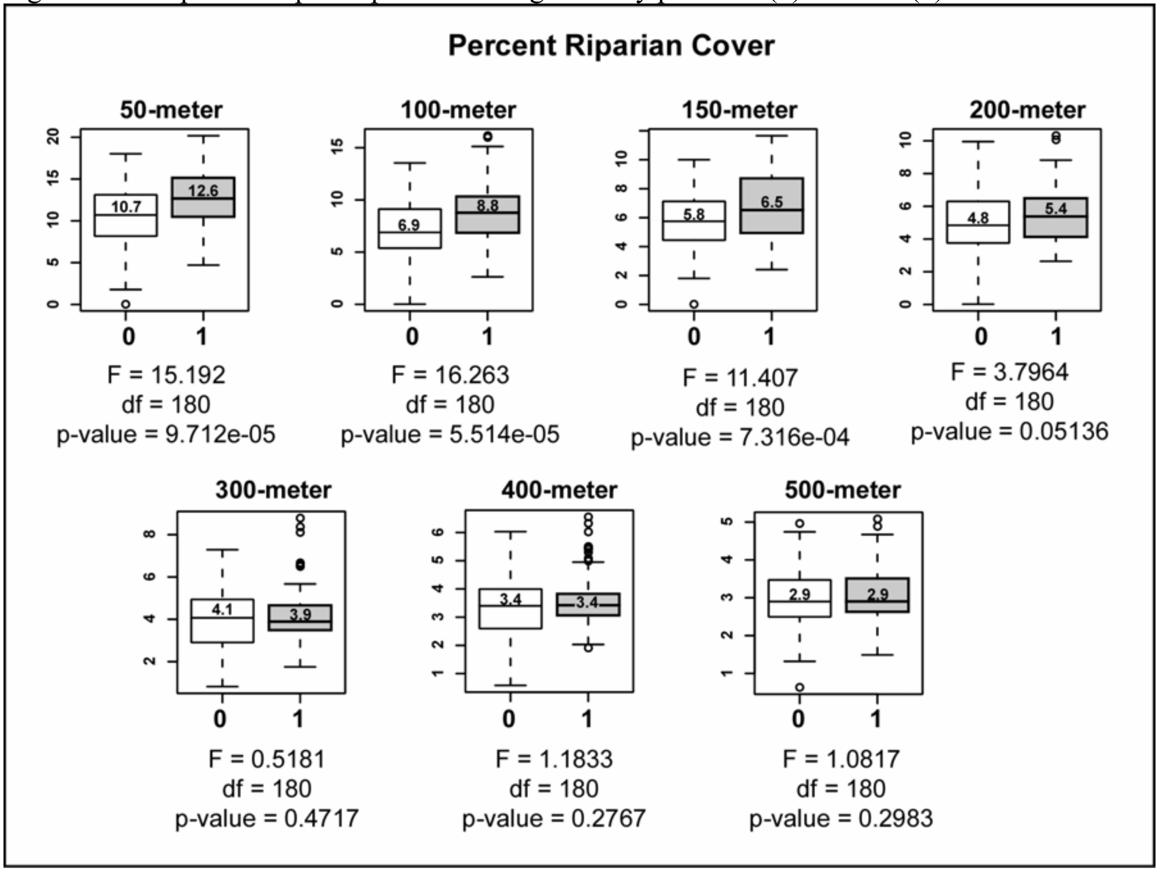


Figure 15: Boxplots compare riparian coverage data by presence (1)/absence (0).



Single-variable logistic regression models were fit to the data using the quantity of riparian within each extent as a predictor and flycatcher presence as the response. Parameter estimates for all scales that were below 200-meters were positive and significant ($P < 0.05$) (Table 2), except for the parameter estimate for the 200-meter extent, which was positive but only moderately significant (0.055). The odds-ratios were 1.17 (95% CI: 1.07 to 1.26) for the 50-meter extent, 1.24 (95% CI: 1.11 to 1.40) for the 100-meter extent, and 1.27 (95% CI: 1.11 to 1.48) for the 150-meter extent. To convey the effect on the probability of flycatcher presence, the mean riparian quantity at 100-

meter extent (8.036%) was substituted into the single-variable model and the incremental rate of change in probability was equal to 0.054 with a 1% increase in riparian coverage over the area.

Low Stature Stands

The quantity of low stature stand cover within the given extent tended to be higher where flycatcher nest sites were located when compared to null sites (Figure 16) but the response did not vary in a linear fashion from low to mid-level, to high. Lowess smoothes of the binomial response exhibited an increasing trend line at all scales of measurement, but only for the high values of the predictor (Figure 17). Where there were only low quantities of low stand cover, the presence response trend was flat or decreasing. This suggests that the flycatchers are neither selecting for nor against low levels of low stature stand cover but at medium to high levels, greater quantities increase the probability of presence.

The qualitative description presented from a review of the smoothed data was confirmed with parameter estimates from the logit models (Table 3). The logit for the low levels, at all scales, was close to zero, indicating the predicted probability of presence was no higher or no lower than predicted at the other levels. The logits indicated that flycatcher presence was significantly lower where there was a moderate-level of low stature habitat within a 100-meter and 150-meter search radius. Odds ratios comparing levels estimated that the odds of flycatcher presence where there is a low amount of low stature habitat are 1.84 and 2.25 higher compared with a moderate amount for the 100-meter and 150-meter extents respectively (Table 3), (approximately 2 to 1 odds). The value of the logits also indicated that flycatcher presence was significantly higher where there was a high level of low stature habitat within a 100-meter and 150-meter search radius. Odds ratios estimated that the odds of flycatcher presence where there is a high quantity of low stature habitat are 6.25 and 7.14 times greater than where there is only a moderate quantity of low stature habitat for the 100-meter and 150-meter extents respectively.

Figure 16: The differences between mean coverage of low stature stands for presence (1) and absence (0) data. Means and bootstrapped nonparametric 95% confidence limits are given for each extent of analysis.

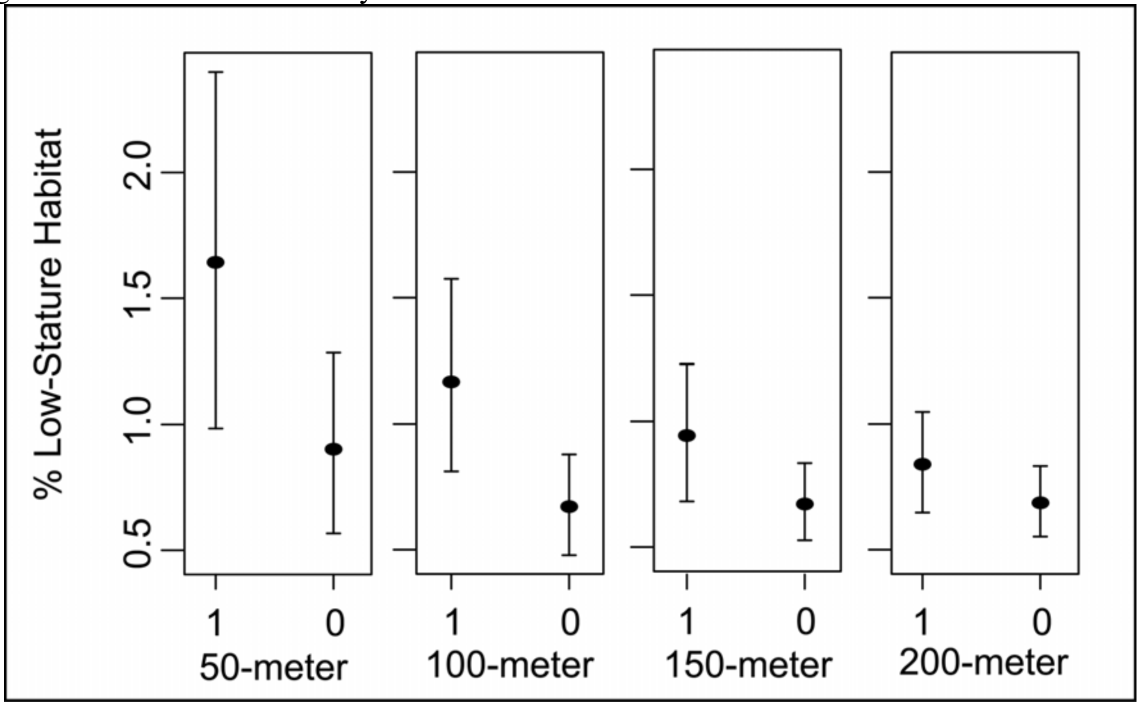
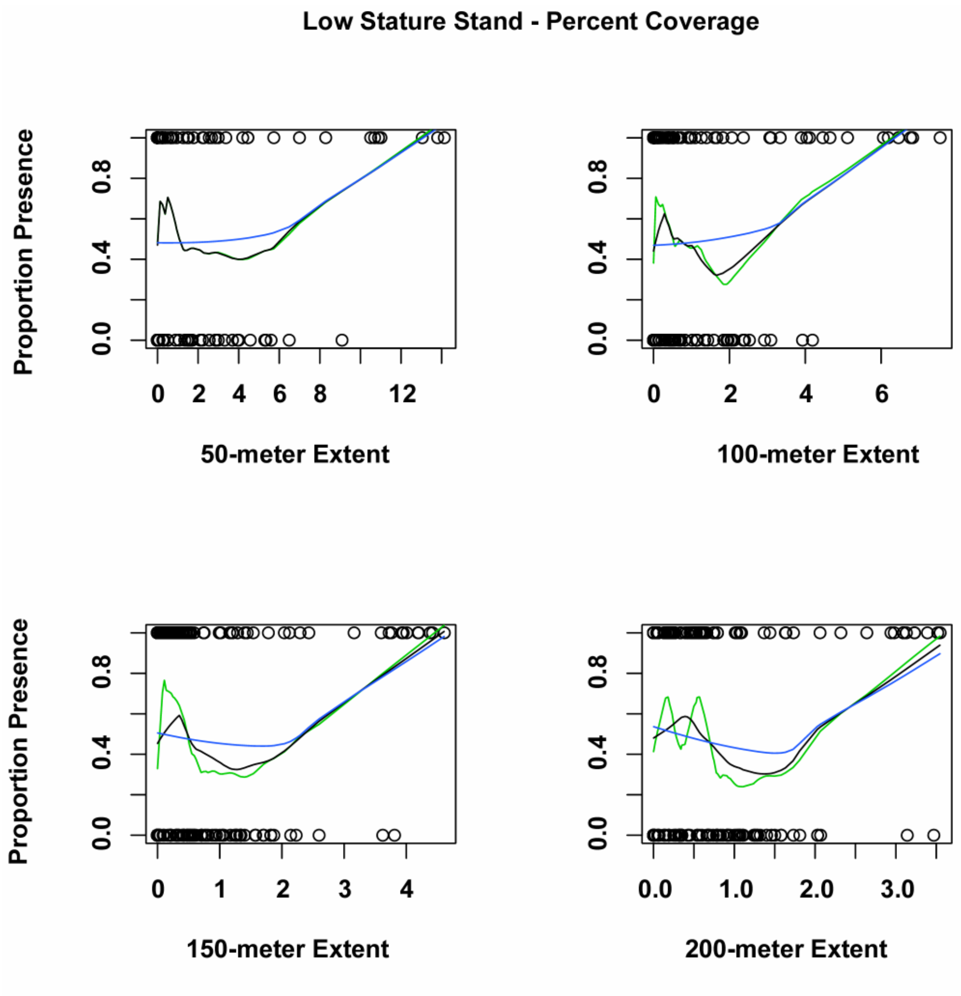


Figure 17: Scatterplot smoothes of the data representing the relationship between low stature stand cover at each scale of analysis and flycatcher presence, (span=2/3 (blue), span=1 (black), span=1/3 (green), span determines the degree of smoothing).



Medium-Stature Stands

The level of cover in the medium-height stand category within the analysis window was nonlinearly related to flycatcher presence. In general, for all extents, scatterplot smoothes showed an increasing probability of flycatcher presence up to a low- to moderate-level of medium height stand cover followed by a declining relationship at the higher levels of medium height stand cover (Figure 18). The trend began to decline at a level of approximately 4% for the 50-meter extent and 2% for the 100-meter extent. These values correspond to approximately 315 m^2 and 630 m^2 of area respectively. Plotted means and non-parametric bootstrapped confidence intervals for the presence/absence data did not reveal a difference in means but the presence data did appear to have slightly less variation (Figure 19).

Figure 18: Scatterplot smoothes of the data representing the relationship between medium stature stand cover at each scale of analysis and flycatcher presence (span=2/3 (blue), span=1 (black), span=1/3 (green), span determines the degree of smoothing).

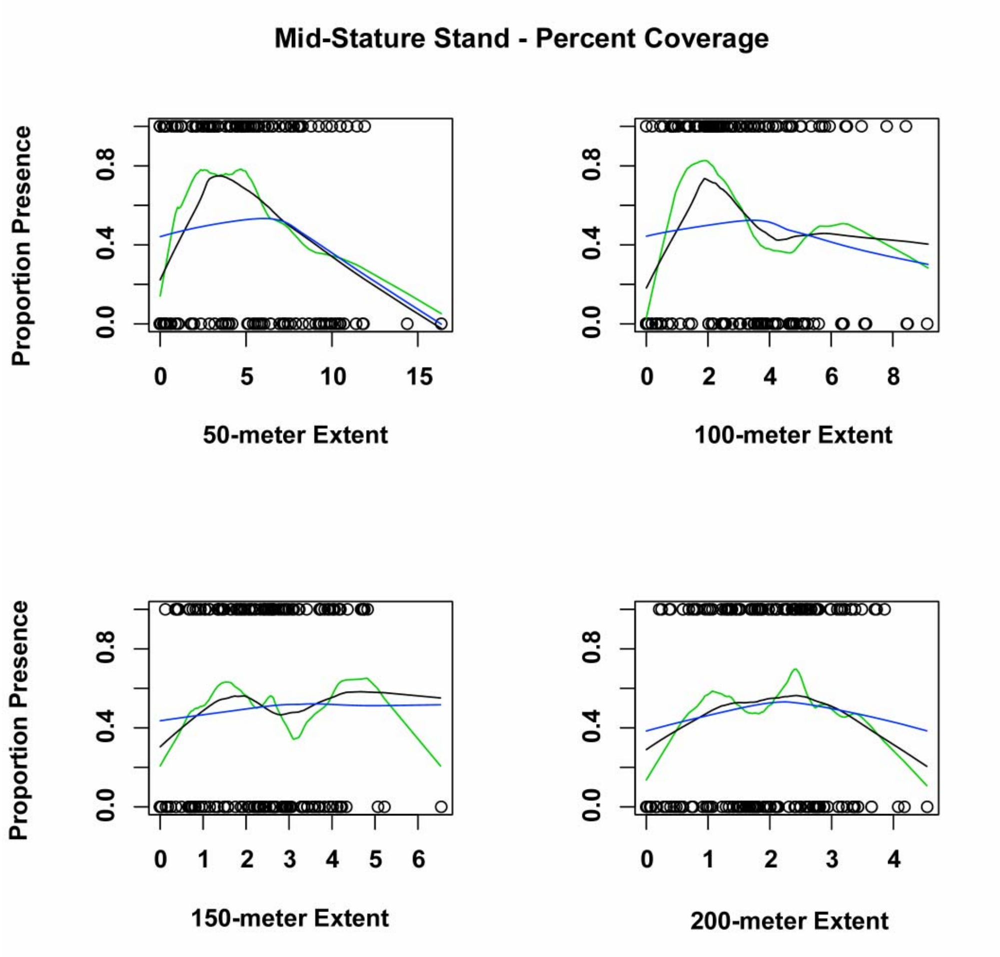
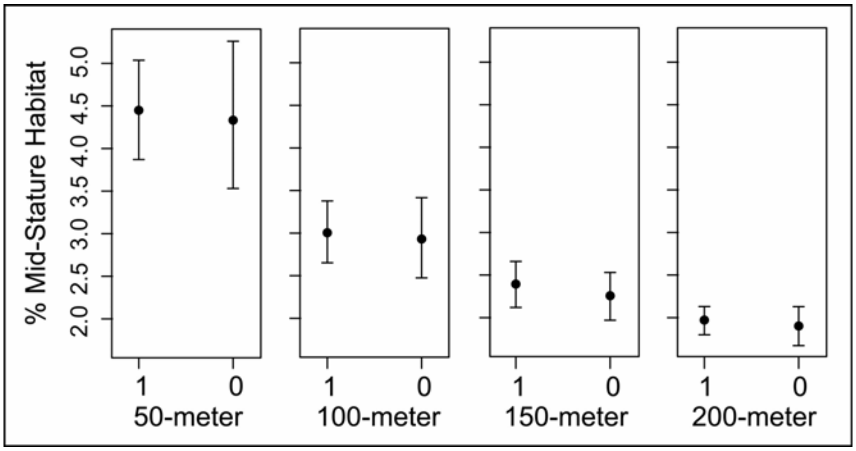


Figure 19: The differences between mean coverage of medium stature stands for presence (1) and absence (0) data. Means and bootstrapped nonparametric 95% confidence limits are given for each extent of analysis.



Parameter estimates from the logit models using the levels of medium stature stands indicated a tenuous relationship between flycatcher presence and the quantity of medium stature stands. Significant parameter estimates confirmed the smoothed responses and indicated that the predicted probability of flycatcher presence was a lowest where there was a high level of medium stature habitat and was low where there was a low level of medium stature habitat (Table 3). The medium-stature stand levels did not significantly vary from one another in their ability to predict flycatcher presence, with the exception that at the 50-meter extent, mid-level, and high-levels significantly varied from the other levels. The odds ratio, calculated by exponentiating the difference between the mid-level and high-level parameter estimates obtained by the fit of a logit model with the 50-meter extent dummy variables, was 3.7. This indicates that the odds of presence where there is a moderate level of mid-height habitat are 3.7 times greater than the odds of presence at a high-level of medium height habitat.

Table 3: Logits modeled with dummy variables for stand height categories, profile-likelihood 95% confidence intervals, P-value of the Z-statistic for each coefficient, and odds ratios comparing the estimated probability of flycatcher presence at two levels (low to medium, and medium to high) and corresponding 95% confidence intervals.

		Logit	95% CI Logit		P-value (>|z|)	Odds Ratio	95% CI Odds Ratio	
Low Cover w/in 50-meter Radius								
	Low	0.0000	-1.9237	1.9333	0.078	1.60	2.01	1.27
	Medium	-0.4700	-2.6197	1.6961	0.215	0.34	0.10	1.10
	High	0.6190	-0.2735	1.5979	0.187			
Low Cover w/in 100-meter Radius								
	Low	-0.0304	-2.1309	2.0877	0.005	1.84	2.21	1.50
	Medium	-0.6419	-2.9258	1.6854	0.027	0.16	0.04	0.55
	High	1.1631	0.2261	2.2810	0.023			
Low Cover w/in 150-meter Radius								
	Low	0.0317	-2.0710	2.1527	0.002	2.25	2.62	1.89
	Medium	-0.7802	-3.0359	1.5140	0.037	0.14	0.04	0.46
	High	1.1631	0.2261	2.2810	0.023			
Low Cover w/in 200-meter Radius								
	Low	0.1699	-1.6988	2.0533	0.001	3.23	3.81	2.75
	Medium	-1.0033	-3.0358	1.0410	0.179	0.16	0.05	0.48
	High	0.8267	-0.0244	1.7830	0.068			
Mid Cover w/in 50-meter Radius								
	Low	-0.1777	-1.8960	1.5206	0.006	0.51	0.52	0.50
	Medium	0.4964	-1.2328	2.2098	0.178	3.65	1.50	9.49
	High	-0.7985	-1.6358	-0.0409	0.047			
Mid Cover w/in 100-meter Radius								
	Low	0.1777	-1.5886	1.9474	0.544	1.46	1.46	1.46
	Medium	-0.2007	-1.9672	1.5666	0.849	0.75	0.29	1.91
	High	0.0870	-0.7377	0.9215	0.835			
Mid Cover w/in 150-meter Radius								
	Low	0.0260	-1.5552	1.6137	0.356	1.17	1.18	1.17
	Medium	-0.1335	-1.7189	1.4571	0.576	0.67	0.28	1.56
	High	0.2683	-0.4501	1.0101	0.467			
Mid Cover w/in 200-meter Radius								
	Low	-0.1777	-1.8344	1.4723	0.280	0.64	0.64	0.64
	Medium	0.2647	-1.3957	1.9218	0.919	1.63	0.67	4.00
	High	-0.2231	-1.0023	0.5343	0.565			
High Cover w/in 50-meter Radius								
	Low	-0.3830	-1.9306	1.1667	0.975	0.52	0.52	0.52
	Medium	0.2647	-1.2741	1.8121	0.138	1.01	0.44	2.33
	High	0.2513	-0.4440	0.9672	0.481			
High Cover w/in 100-meter Radius								
	Low	-0.4829	-2.2224	1.2633	0.861	0.45	0.44	0.45
	Medium	0.3238	-1.4028	2.0625	0.060	0.92	0.36	2.28
	High	0.4055	-0.3839	1.2382	0.321			
High Cover w/in 150-meter Radius								
	Low	-0.2288	-1.9042	1.4587	0.220	0.77	0.78	0.77
	Medium	0.0267	-1.6518	1.7199	0.073	0.57	0.23	1.38
	High	0.5878	-0.1663	1.3997	0.136			
High Cover w/in 200-meter Radius								
	Low	-0.2232	-1.8002	1.3626	0.360	0.76	0.77	0.74
	Medium	0.0571	-1.5342	1.6608	0.113	0.67	0.28	1.57
	High	0.4595	-0.2513	1.2102	0.213			

Overall, medium-height stand quantity did not perform very well as a single predictor. Nonparametric responses were tested for correlation between the quantity of medium-stature stands for each extent and flycatcher presence using penalized regression splines and generalized cross validation but even these optimized fits were unable to explain a significant proportion of deviance in the data.

High-stature Stands

The quantity of high stature stand cover within the given extent tended to be higher where flycatcher nest sites were located when compared to null sites (Figure 20) but the relationships were not very strong. The mean for the presence data was greater than the absence data for all extents but the non-parametric bootstrapped standard errors revealed a fair amount of overlap (Figure 21). At the 100- and 150-meter extents, moderately significant logit values (Table 3) indicated that moderate levels of high stature habitat had a lower estimated probability of flycatcher presence than at high quantities, and a higher estimated probability of presence than at low quantities.

Figure 20: Scatterplot smoothes of the data representing the relationship between high stature stand cover at each scale of analysis and flycatcher presence (span=2/3 (blue), span=1 (black), span=1/3 (green), span determines the degree of smoothing).

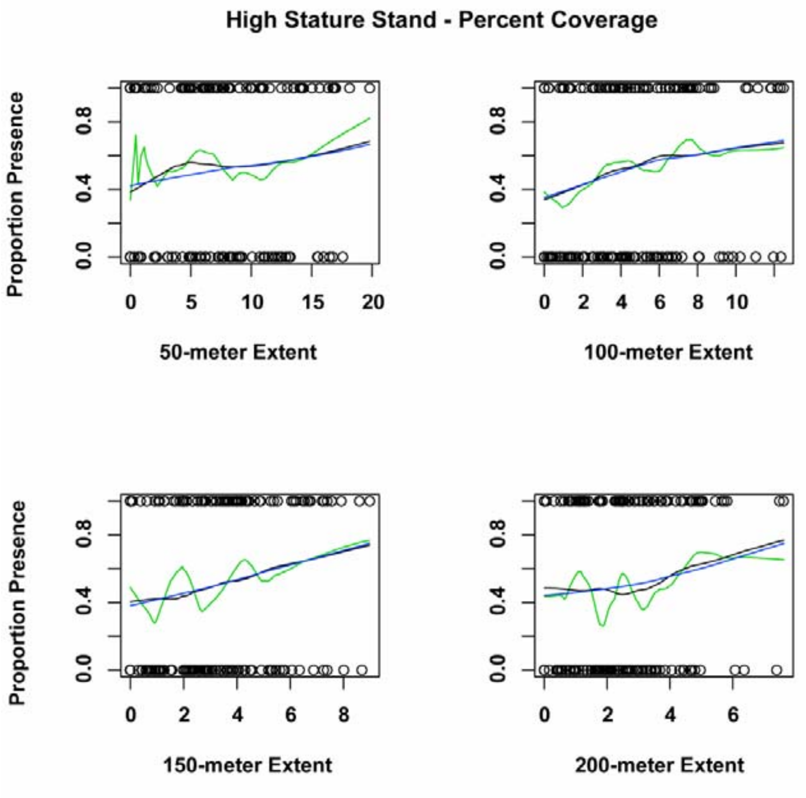
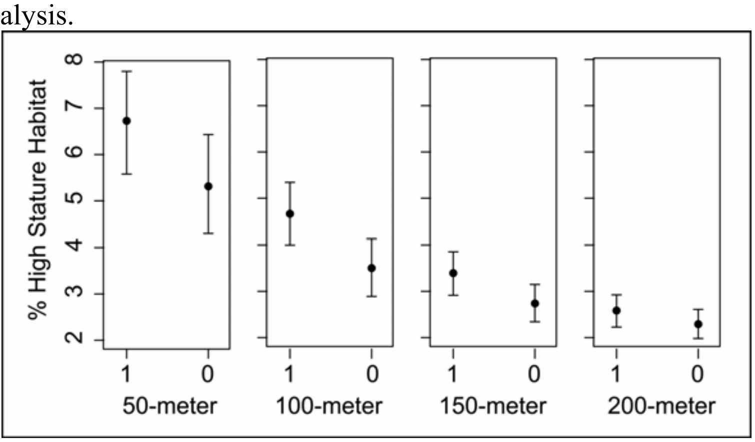


Figure 21: The differences between mean coverage of high stature stands for presence (1) and absence (0) data. Means and bootstrapped nonparametric 95% confidence limits are given for each extent of analysis.



Scale

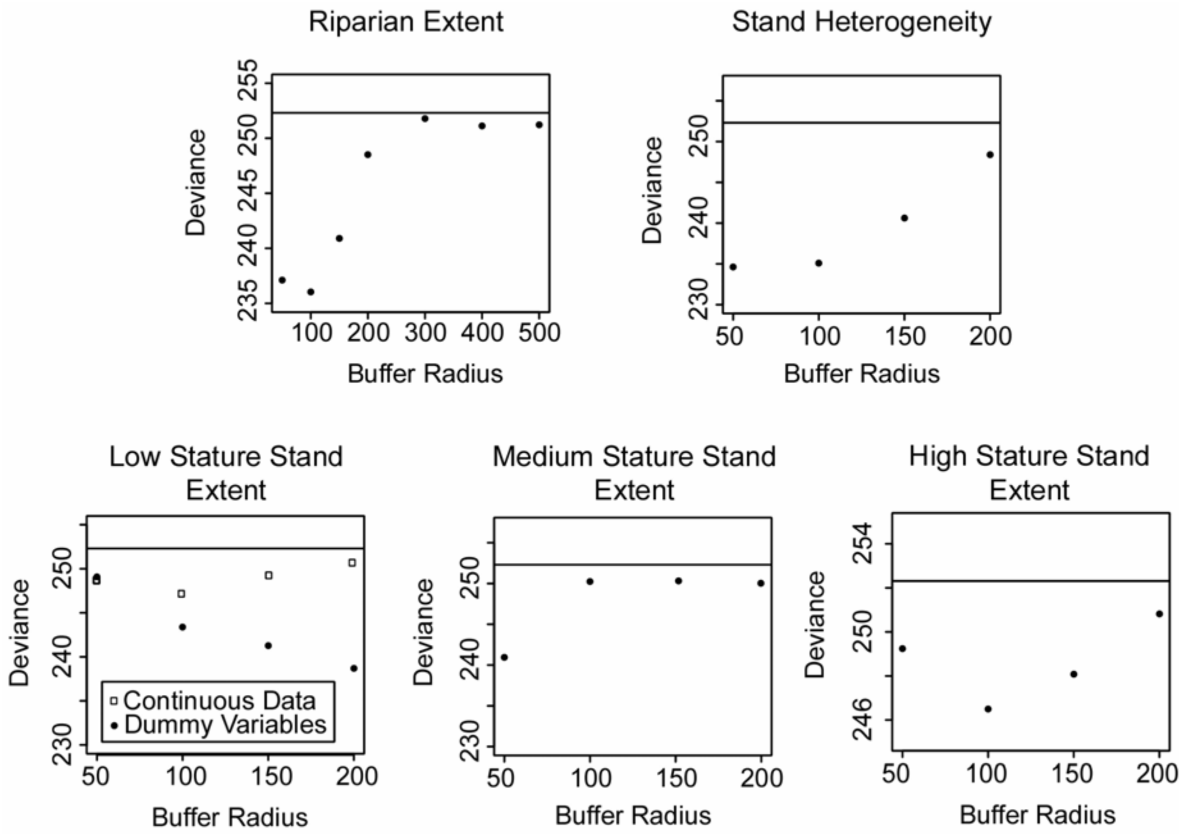
Stand Heterogeneity

With respect to extent, flycatchers nested in stands with greater canopy heterogeneity at all scales but the strength and shape of the relationship was dependent on scale with the lower extents exhibiting the strongest, and most clear, positive trend. For all parametric statistics, including likelihood ratio statistic and Pearson's chi-squared from contingency tables of categorized variables, the two lesser extents were very similar in the degree of association with flycatcher presence with the 50-meter extent performing only slightly better (Table 4). The association between presence and stand heterogeneity quickly decreased when the extent increased to 150-meters and again to 200-meters. The 200-meter extent predictor explained significantly more deviance than the null model (LRT=3.922, df=1, P=0.048) but residual deviance at this scale approached null model deviance. Residual deviance was plotted across scales and appeared to approach null model deviance in an asymptotic pattern as scale increased (Figure 22).

Overall, the 50-meter extent performed slightly better when considering statistics output but the 100-meter extent response function was a more idealistic fit. The lowess smooth with the 100-meter extent predictor revealed a more even response than the 50-meter extent (Figure 12). This was confirmed by optimizing the fit using penalized regression splines and generalized cross validation (GCV), which fit a straight line for the 100-meter extent using only 1 degree of freedom. The optimized fit with the 50-meter extent predictor was a function using 6.2 degrees of freedom. For the 50-meter extent, the smoothed fit was able to explain 11.9% of the deviance compared with explaining

7.0% of the deviance when forcing a straight line to fit the data. Output for all tests were similar for the 50- and 100-meter extents and it is possible that the true "best extent" is in-between the two measurements.

Figure 22: Residual model deviance from single variable logistic regressions for the quantity of riparian habitat, stand heterogeneity, and from logit models with dummy variables for the quantity of high, medium, and low stature habitat, plotted against the extent of analysis. Null model deviance is graphed as a straight line across each plot.



Riparian Extent

Statistics for single-variable logistic regression pointed to the 100-meter search radius as the most effective extent to correlate flycatcher presence with the quantity of riparian vegetation. The AIC values, F-statistics, likelihood ratio statistics and Pearson's chi-squared values from contingency tables of categorized variables all revealed a similar pattern in the output across the scales. The two lesser extents performed similarly but the 100-meter extent slightly outperformed the 50-meter extent (Table 4). As seen in the pattern of residual deviance plotted across scales, correlation between flycatcher presence and greater quantities of riparian vegetation decreased quickly as the extent was broadened and beyond a 200-meter extent, there was very little correlation (Figure 22).

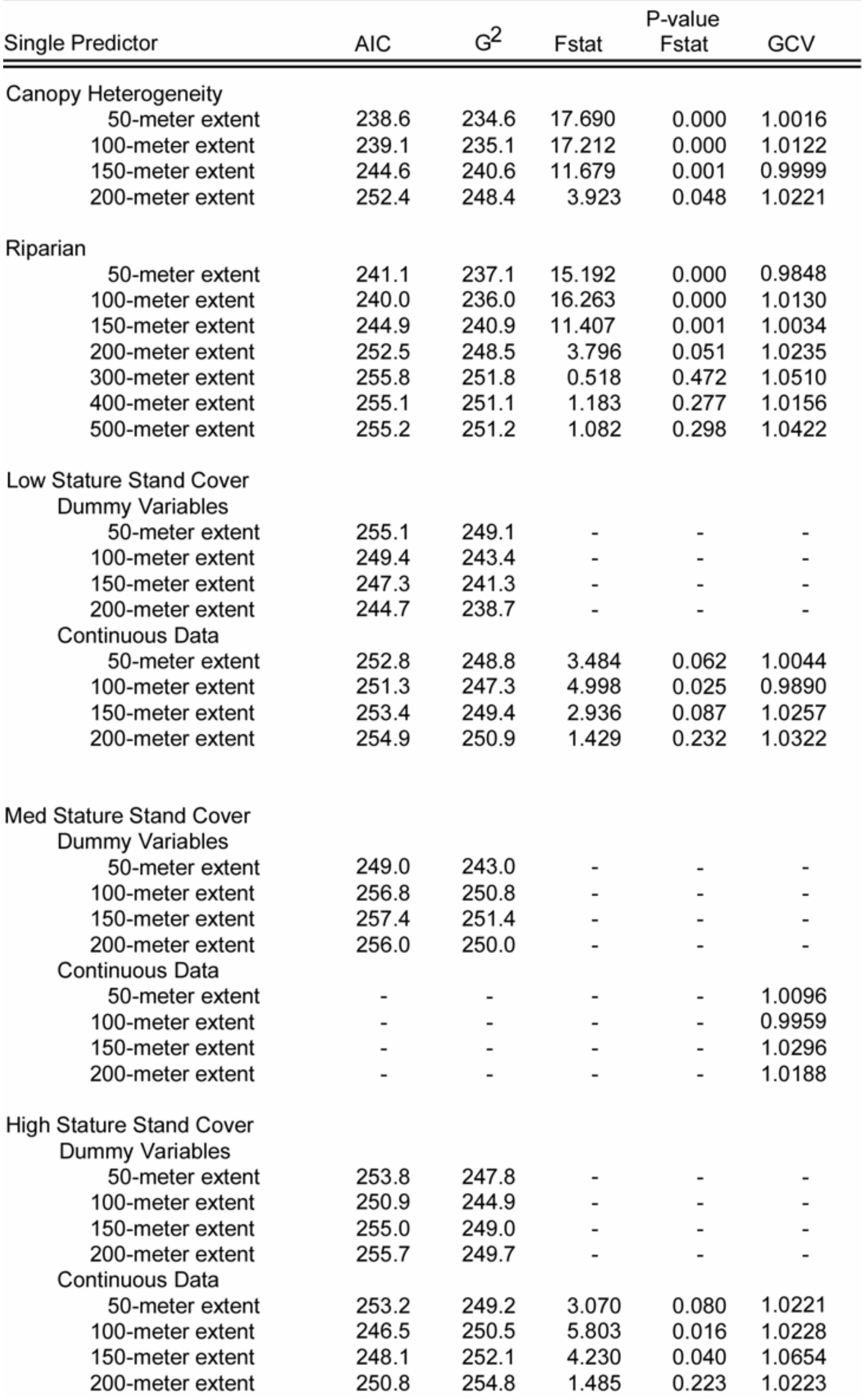
Low Stature Stands

For the quantity of low stature habitat, the interpretation of scale dependency was different for logistic and optimized fits. The 200-meter extent dummy variable predictors explained the greatest amount of deviance in the data when evaluating logistic regression (Table 4). However, when optimizing the fit with penalized regression splines in GAMs, the 150-meter extent explained the greatest amount of deviance (7.53% compared to 6.18% (200-meter), 5.90% (100-meter), and 3.05% (50-meter)), but the model using the 100-meter radius predictor had the best GCV score because the 150-meter and 200-meter scale models were penalized for using smoothing functions with higher degrees of freedom. Reported residual deviance (G^2) from fitting the logit models was lowest at the 200-meter extent (238.69, 179df) and residual deviance increased as the extent shrunk ($G^2_{150} = 241.27$, $G^2_{100} = 243.38$, $G^2_{50} = 249.08$, $G^2_{null} = 252.31$) (Figure 22, Table 4). Residual deviances from logit regressions were likely influenced by the break points for categories. For this reason, I reviewed output from logistic regression using the continuous data (percent coverage) and found that residual deviances were higher than when running models with the dummy predictors, and although residual deviance was lowest when running the model with the 100-meter extent predictor (Figure 22), I selected the 200-meter scale as the best extent, using absolute lowest residual deviance as the criteria.

Medium Stature Stands

A comparison of deviance from logit models were used to evaluate the most effective scale for describing the relationship between flycatcher presence and the quantity of medium-stature stand cover. Deviance was lowest for the 50-meter extent variable ($G^2_{50} = 242.98$, $G^2_{100} = 250.84$, $G^2_{150} = 251.42$, $G^2_{200} = 250.03$, $G_{\text{null}} = 252.31$, on 179 df) (Figure 22). Additionally, the 50-meter extent was the only scale at which any logit values were significantly different from one another (Table 4). Although the 50-meter extent variable performed slightly better than the other extents, overall, the variable did not perform very well as a single predictor.

Table 4: Statistics used in scale selection including: (1) Akaike's Information Criteria (AIC), Residual Deviance (G2), F-statistic from analysis of deviance (Fstat) and P-value, and Generalized Cross Validation scores (GCV) from GAMs using penalized regression splines.



Single Predictor	AIC	G^2	Fstat	P-value Fstat	GCV
Canopy Heterogeneity					
50-meter extent	238.6	234.6	17.690	0.000	1.0016
100-meter extent	239.1	235.1	17.212	0.000	1.0122
150-meter extent	244.6	240.6	11.679	0.001	0.9999
200-meter extent	252.4	248.4	3.923	0.048	1.0221
Riparian					
50-meter extent	241.1	237.1	15.192	0.000	0.9848
100-meter extent	240.0	236.0	16.263	0.000	1.0130
150-meter extent	244.9	240.9	11.407	0.001	1.0034
200-meter extent	252.5	248.5	3.796	0.051	1.0235
300-meter extent	255.8	251.8	0.518	0.472	1.0510
400-meter extent	255.1	251.1	1.183	0.277	1.0156
500-meter extent	255.2	251.2	1.082	0.298	1.0422
Low Stature Stand Cover					
Dummy Variables					
50-meter extent	255.1	249.1	-	-	-
100-meter extent	249.4	243.4	-	-	-
150-meter extent	247.3	241.3	-	-	-
200-meter extent	244.7	238.7	-	-	-
Continuous Data					
50-meter extent	252.8	248.8	3.484	0.062	1.0044
100-meter extent	251.3	247.3	4.998	0.025	0.9890
150-meter extent	253.4	249.4	2.936	0.087	1.0257
200-meter extent	254.9	250.9	1.429	0.232	1.0322
Med Stature Stand Cover					
Dummy Variables					
50-meter extent	249.0	243.0	-	-	-
100-meter extent	256.8	250.8	-	-	-
150-meter extent	257.4	251.4	-	-	-
200-meter extent	256.0	250.0	-	-	-
Continuous Data					
50-meter extent	-	-	-	-	1.0096
100-meter extent	-	-	-	-	0.9959
150-meter extent	-	-	-	-	1.0296
200-meter extent	-	-	-	-	1.0188
High Stature Stand Cover					
Dummy Variables					
50-meter extent	253.8	247.8	-	-	-
100-meter extent	250.9	244.9	-	-	-
150-meter extent	255.0	249.0	-	-	-
200-meter extent	255.7	249.7	-	-	-
Continuous Data					
50-meter extent	253.2	249.2	3.070	0.080	1.0221
100-meter extent	246.5	250.5	5.803	0.016	1.0228
150-meter extent	248.1	252.1	4.230	0.040	1.0654
200-meter extent	250.8	254.8	1.485	0.223	1.0223

High Stature Stands

High stature stand cover was more correlated with flycatcher presence at the 100-meter extent but in general, high stature stand cover did not perform well as a predictor. Residual deviance from the logit models indicated that the amount of high-stature stand cover within a 100-meter extent was the scale most correlated with flycatcher presence ($G^2_{50} = 247.82$, $G^2_{100} = 244.90$, $G^2_{150} = 248.95$, $G^2_{200} = 249.65$, $G_{null} = 252.31$, on 179 df) (Figure 22). Selection of the 100-meter extent as the best extent was confirmed when running logistic regression with continuous data (percent cover) as predictors (Table 4). The parameter estimates for the logistic regression models however, were not significant for any level or any scale. GCV scores output from running the continuous data in GAMs were not conclusive because they did not vary by more than 0.0005 for the 50-meter, 100-meter, and 200-meter scales.

Multivariate Modeling

The final logistic model retained canopy heterogeneity at a 50-meter extent, patch area, patch perimeter, and two dummy variables coding for (1) moderate levels of low stature habitat at 200-meter radius (M.L20), and (2) moderate levels of medium-stature habitat from the 50-meter analysis extent (M.M05). The equation for the final model was:

$$\mathrm{Ln}\left(\frac{\pi}{1-\pi}\right)_{\mathrm{m.m05}} = -5.71 + 0.336 * \mathrm{CD05} + 0.024 * \mathrm{PAR} + 0.429 * \mathrm{PA}$$

$$\mathrm{Ln}\left(\frac{\pi}{1-\pi}\right)_{\mathrm{base}} = -7.24 + 0.336 * \mathrm{CD05} + 0.024 * \mathrm{PAR} + 0.429 * \mathrm{PA}$$

$$\mathrm{Ln}\left(\frac{\pi}{1-\pi}\right)_{\mathrm{m.L20}} = -9.58 + 0.336 * \mathrm{CD05} + 0.024 * \mathrm{PAR} + 0.429 * \mathrm{PA}$$

where π is the proportion of presence and $(1 - \pi)$ is the proportion of absence, CD05 is canopy heterogeneity within a 50-meter extent, PAR is the perimeter-area ratio, and PA is patch area (ha). Parameter estimates and profile-likelihood 95% confidence intervals, significance of the Z-statistic, deviance, null deviance, and the AIC are reported in Table 5.

Fitting the dummy variables was equivalent to fitting logistic regression separately for the data where the dummy codes are equal to one (Agresti 2002). Where the dummy variable coding for the presence of a moderate level of low stature habitat within a 200-meter search radius is equal to one, the intercept term is a greater negative value and flycatcher presence will vary similarly to the base model but the estimated probability will be lower. The base model is the logistic regression where the dummy variables are zero (i.e., low and high levels of medium stature habitat within 50-meter extent, and low and high levels of low stature habitat within a 200-meter extent). The intercept term where M.M05 = 1, has the greatest value and the function will have the same shape as the base model but the estimated probability will be greater.

The parameter estimate for the canopy heterogeneity variable was positive and the effect of the variable in the model is similar to the single-variable effects reported in the above section. The odds ratio for the parameter estimate was 1.40, which indicates that the odds of presence increase by 40% given a one value increase in the Simpson's Diversity Index used to calculate the variable when all other variables are held at constant values. The probability function is the log of the probability of presence over the probability of absent. The odds ratio gives the percent change of this function with a 1 step increase in the predictor.

The parameter estimate for patch area was positive and the value was slightly higher than the output for single-variable logistic regression. The odds ratio was 1.54. The odds ratio indicates that with an area increase of 1 hectare, the odds of flycatcher presence will increase by 54%.

Perimeter-area ratio was positively correlated with flycatcher presence when it was considered with the other influences. The estimate for PAR was relatively small due to the large range in values of the variable. The value of PAR will vary with area when shape is held constant, and the lowest PAR values are reported for larger patches with a high proportion of core area. A negative relationship between presence and PAR is a logical relationship. As a single variable, the parameter estimate was negative but was not significant and the mean value was lower for the presence data compared with the mean value for the absence data. During backward stepping procedures, dropping PAR always resulted in a significant gain in deviance. On the contrary, analysis of deviance of the final model reported the lowest value of explained deviance when PAR was added to the model, except for one of the sequences considered. From the exercise of adding terms to the model in different orders and evaluating the deviance explained for each variable, it seemed as though PAR performed better when it was added after canopy

Table 4: Model output for the three multi-variate models considered in the analysis: (1) Autocorrelated model from logistic regression (LogReg), (2) Autologistic model (ACV), and (3) the Autologistic model without the predictor Patch Area. Estimated model coefficients, corresponding profile likelihood 95% Confidence Intervals, and P-values of the Z-statistic are given for each term in the model. Model selection statistics are provided in the table below.

	Model Coefficients			Profile Likelihood 95% Lower - Upper Confidence Intervals						P(|Z|)		
Term*	LogReg	ACV	ACV-PA	LogReg	LogReg	ACV	ACV	ACV-PA	ACV-PA	LogReg	ACV	ACV-PA
(Intercept)	-7.248	-6.846	-6.113	-10.163	-4.667	-10.051	-4.030	-9.049	-3.529	<0.001	<0.001	<0.001
CD05	0.336	0.211	0.201	0.181	0.508	0.040	0.399	0.032	0.386	<0.001	0.020	0.025
PAR	0.024	0.019	0.015	0.122	0.366	0.060	0.327	0.031	0.275	<0.001	0.004	0.013
PA	0.429	0.163	-	0.256	0.619	-0.071	0.399	-	-	<0.001	0.170	-
M.L20	-2.329	-1.381	-1.106	-3.444	-1.338	-2.665	-0.196	-2.291	0.001	<0.001	0.027	0.056
M.M05	1.540	1.121	0.967	0.754	2.396	0.200	2.105	0.081	1.905	<0.001	0.020	0.036
ACV	-	5.309	6.004	-	-	3.387	7.573	4.225	8.098	-	<0.001	<0.001

Statistic*	LogReg	ACV	ACV - PA
AIC	187.78	153.83	153.7
deviance	175.78	139.83	141.7
df	176	175	176
HOS.GOF(P)	6.5 (0.59)	7.3 (0.50)	16.0 (0.04)
C-hat	0.93	1.05	1.06

* HOS.GOF = Hosmer Lemeshow Goodness of Fit statistic, P-value tests for significant differences between observed data and predicted probability; C-hat=Overdispesion Parameter; CD05=Canopy Heterogeneity w/in 50-meter radius;
PAR=Patch Perimeter-Area Ratio; PA = Patch Area; M.L20=dummy variable where moderate quantity of low stature habitat within 200-meter radius = 1, low and high quantity = 0; M.M05=dummy variable where moderate quantity of medium stature habitat within 50-meter radius = 1, low and high quantity = 0.

heterogeneity, which indicated that it might explain deviance that canopy heterogeneity misses.

Model Evaluation

Goodness-of-fit tests indicated the final model was a decent fit. Hosmer-Lemeshow statistic calculated from grouping observed and fitted values according to the estimated probability of success into 10 groups equaled 6.52 (df=8). The corresponding P-value (0.59) indicates the observed values do not significantly differ from the expected values. The overdispersion parameter ($\hat{\phi}$) did not indicate any overdispersion in the final model ($\hat{\phi}$ = 0.93). Dffits and the diagonal elements of the hat matrix found four points that were significantly influential. A comparison of parameter estimates from a regressing the data without the four influential points and the final model found that the changes in the values of the parameter estimates were negligible: (1) they did not change the interpretation of the final model results, and (2) the new coefficient values were within one standard error of the original coefficient values.

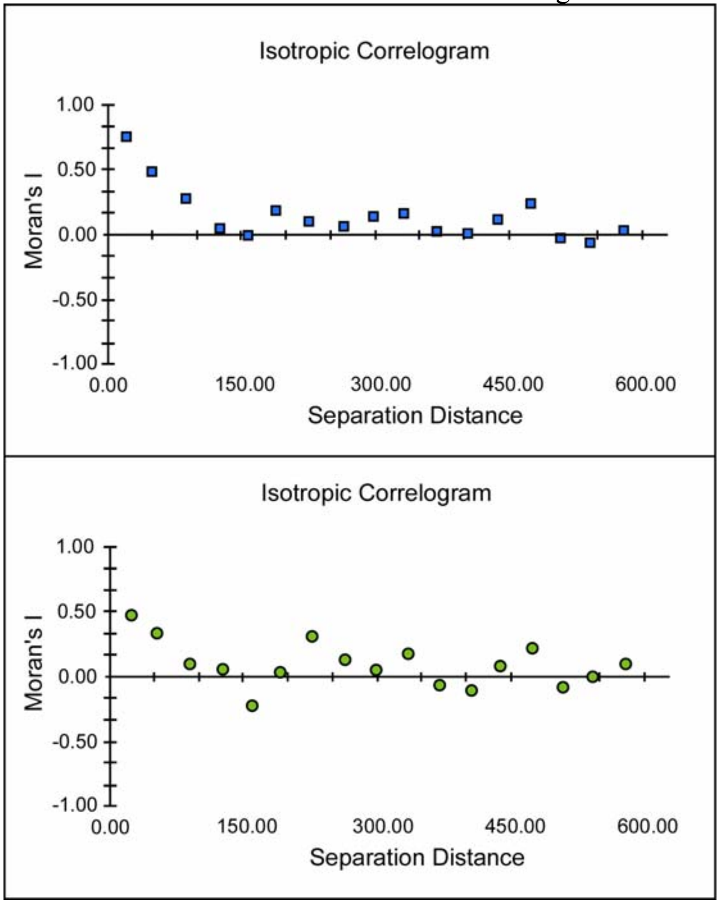
Autologistic Model

Moran's I, calculated from the Pearson's standardized residuals from the final model and plotted against distance, showed a clear pattern of spatial correlation (Figure 23). Moran's I, which is on a scale from 0 to 1, was 0.76 in the first bin and the values declined precipitously until reaching negligible values in the 4th lag bin and beyond (with the exception of an unexplained spike to 0.25 in the 14th bin). The active lag distance of

35 meters contained a minimum of 26 pairs per lag bin, and although this is on the low end of the suggested minimum, the semivariogram and correlogram (Figure 23) were smooth and did not exhibit irregular variation (Burrough and McDonnell 1998). A Gaussian model was used to determine the range. It fit the data well and is appropriate where there is a smooth pattern of correlation (Burrough and McDonnell 1998), which would be expected where predictors also vary smoothly. The effective range for this model was 116 m, which was used as the maximum distance for calculation of the autologistic term.

Addition of the autocovariate term to the final model significantly improved the model fit and reduced the degree of autocorrelation present in the system (Figure 23). The autologistic model included the same parameters as the final multivariate logistic regression model with the added autocovariate term. A likelihood-ratio test between models rejected the model without the autocovariate term (LRT = 35.6, df=1, $P<0.001$). Correspondingly, the AIC dropped from 187.78 to 153.83. Moran's I were calculated from the Pearson's standardized residuals from the autologistic model and plotted in correlograms to verify any reduction in autocorrelation (Figure 23). Moran's I in the first bin was 0.47, which indicates there is still a degree of spatial correlation but it was reduced from the multivariate logistic regression model.

Figure 23: Moran's I correlogram of standardized Pearson's residuals from final multivariate logistic regression model (top panel) and autologistic model (lower panel). The pattern in the top panel shows a rapid decline in correlation between points as the distance between them increases, and is a good indication of spatial autocorrelation between near points. The lower panel shows a reduction in spatial autocorrelation with the addition of the autologistic term.



Model Evaluation

The autologistic model with all terms in the final multivariate model included was selected as the final model but only after assessing the fit of more simple models. After adding the autocovariate term, the patch area coefficient was no longer significantly different from zero (P=0.16) (Table 5). It was dropped from the final autologistic model and a likelihood-ratio test between models rejected the more complex model in favor of the model without the patch area term (LRT = 1.9, df=1, P=0.17). The AIC changed only by 0.13 after dropping patch area. However, the goodness-of-fit tests performed on this model and on the autologistic model indicated the autologistic model was a better fit to the data. The Hosmer Lemeshow goodness-of-fit statistic provided evidence that predicted flycatcher presence was not significantly different from observed presence when incorporating the autologistic model (HOS.GOF=7.3, P=0.50). In contrast, flycatcher presence predicted with the model without the patch area term was significantly different from observed presence (HOS.GOF=16.0, P=0.04). There is a small degree of overdispersion present in both the autologistic model with patch area ($\hat{\phi}=1.05$) and the model without patch area ($\hat{\phi}=1.06$). The standard errors were corrected to account for overdispersion but the confidence intervals did not widen significantly. As a predictor, patch area performed well in all aspects of the analysis. Goodness-of-fit statistics suggest that its inclusion improved model performance so, despite the insignificance of the parameter estimate, it was retained in the final model.

DISCUSSION

Territory Characteristics

The results of this analysis suggest that the estimated probability of flycatcher presence is greater where there is a greater amount of structural heterogeneity within 50 meters, in patches with greater area and with more core area, and where there is more riparian within 100 meters. The results support the stated hypotheses: (1) flycatchers will be present in areas that have more riparian cover, and (2) that structural complexity of the vegetation as measured horizontally across the floodplain will significantly predict flycatcher presence. The hypotheses were based on predicting stand structure of a riparian zone on a broad lowland floodplain in the arid Southwest where open, lentic water is present, given the general preference for these locations.

Habitat selection by the flycatcher should reflect the structure of unmodified habitat that the flycatcher evolved with historically and would be expected to reflect its life history traits. Riparian habitat in the Southwest is highly degraded by human changes to floodplains (Graf 2001) but pristine Southwestern riparian habitat would likely have been much more extensive and structurally heterogeneous. In 1910, while surveying the Colorado River from Needles to Yuma, ornithologist Joseph Grinnell recorded the dominate floodplain vegetation as cottonwood and willow and described the dynamics of the system, noting channel migration and the pattern of young to older forest in increasing distance from the channel. Grinnell also collected and observed "Traill Flycatcher" on the survey (Grinnell 1914, as cited in Periman and Kelly 2000).

The results of this study were based on the hypothesized structure of a riparian zone on a broad lowland floodplain in the arid Southwest where open, lentic water is present. Other researchers have contributed to understanding the flycatcher's habitat needs in terms of canopy structure. Hatten and Paradzick (2003) found that vegetation density within a 4.5 ha of flycatcher habitat exhibited high variability in vegetation density. Much work has supported the notion that flycatchers prefer structurally varied habitat although most are based on quantifying tree structure immediately adjacent to the nest rather than across the habitat patch. Stoleson and Finch (2003) found that in the Cliff-Gila Valley, flycatcher presence was positively correlated with foliage density in the subcanopy, percent canopy cover, and number of boxelder stems. Allison et al. (2003) found that female flycatchers breeding on two sites in central Arizona preferentially built nests close to breaks in the canopy and in areas of the habitat with high foliage density at the nest height and below. Sedgwick and Knopf (1992) found differences in habitat structure between nest sites and song perch sites, nest sites having a more homogenous willow thicket structure and song perch sites having higher gap distances and variability in willow patch size. Bombay, Morrison and Hall (2003) found that willow flycatcher (*Empidonax traillii adastus*) nest sites were negatively associated with foliage density in the first meter off the ground although nests were placed in areas of high shrub density.

Life history traits evolve as strategies to maximize survival and breeding productivity and habitat selection is an inherent part of the process. Habitat selection is a factor in the reduction of risk of death or reproductive loss from starvation, predation, brood parasitism, and exposure to extreme temperatures. The riparian habitat inhabited by breeding southwestern willow flycatcher must offer the minimum of these amenities in order for survival including, food, protection from nest predators, brood parasites and extreme climatic conditions. Specific foraging and nesting requirements may be different (Martin 1988) and selection of habitat will reflect the needs of both. Canopy gaps offer forage opportunity and provide for territorial defense. Heterogeneous canopy structure affords variation in foliage density and balances the opposing requirements. Areas of low foliage density facilitate movement throughout the territory and areas of dense foliage are effective for nest concealment and maintain cooler microclimate conditions.

Survival requires sufficient food source and a means of getting the food. The southwestern willow flycatcher is an aerial forager that mainly hawks flying invertebrates from the air or hover-gleans them from vegetation (Sedgwick 2000). Foraging techniques are likely to play a role in habitat preference. When foraging, the flycatchers generally sit unmoving adjacent to a foliage opening or edge and make short darting flights out to capture flying insects. Flycatcher habitat is likely to have openings in the foliage or be near to an edge, including gaps in the subcanopy or understory (Harris, Sanders, and Flett 1987; Sedgwick and Knopf 1992; Allison et al. 2003; Bombay, Morrison and Hall 2003) and the canopy breaks may in part be providing foraging sites for the willow flycatcher (Allison et al. 2003).

Nest depredation is believed to be the cause for most nest failures (Ricklefs 1969) and nest site selection has likely evolved mainly in response to reducing risk of nest depredation (Martin 1993). Numerous studies of various avian species show that nest-site selection and/or nest success is correlated with vegetation density (Murphy 1983; Huhta et al. 1998; Braden 1999; Sodhi et al. 1999; Powell and Steidl 2002; Bombay et al. 2003), especially for nesting guilds more susceptible to predation (Martin 1988). Selection of concealed nest sites and aggressive nest defense are both methods by which rates of nest loss can be reduced (Murphy 1983). In the dense habitat occupied by the willow flycatcher, an open area in which to forage and to defend it's nest from predators and brood parasites might be beneficial. *Tyrannidae* (the family to which the willow flycatcher belongs) are notable for their aggressiveness in nest defense (Bent, 1942; Murphy 1983; Stoleson, Whitfield, and Sogge 2000). Antidotal evidence of this flycatcher's temperament are included in the Life History Series by Arthur Clevland Bent and include a letter from Irene G. Wheelock in 1904, "Although so busy, this Flycatcher is never so occupied as to miss a chance of driving another bird, great or small, away from the special clump of alders which the pugnacious mite has preempted for his own." Similarly, in 1895, Major Bendire wrote, "…they are pugnacious, quarrelsome little creatures, making up in courage and determination what they lack in size" (Bent 1942, p.202). Eastern Kingbirds, another bird of the family, prefer more open habitats compared with another species nesting in the same substrate, presumably because it is easier to detect predators and defend their nests (Murphy et al. 1997). Strategic placement of a nest in a hidden location within a territory with open areas in the periphery may aid flycatchers (*Tyrannidae*) in aggressive nest defense (Murphy 1983). Cain, Morrison and Bombay (2003) found that higher distance to nearest tree seemed to limit predator activity and improve chances of nest success. Nest sites will be associated with breeding productivity and should provide concealment and song perch sites will be more open, providing visibility, defense and foraging opportunities (Sedgwick and Knopf 1992).

Environmental conditions within dense riparian habitat starkly contrasts the surrounding conditions, especially in the Southwest where the sunlight is intense and the air is hot and dry. Sogge and Marshall (2000) point-out the flycatcher is a relatively late nester and its short breeding season coincides with the hottest time in the year. They propose that dense vegetation provides protection against the extreme heat.

Dense foliage near water provides protection from extreme weather by altering microclimate conditions within the habitat. The importance of microclimate conditions is especially imperative with nesting, in both hot and cold climates. Birds face the challenge of keeping eggs and altricial nestlings (naked, entirely dependent and unable to regulate their own body heat) above or below lethal temperatures (Gill 1990). Habitat characteristics that ameliorate the microclimate conditions of a nest will improve chances of success and influence the daily energy requirements of the adult (Gill 1990). In a study on the least flycatcher (*Empidonax minimus*) in Canada, Darveau and Galtheir (1993) found that broods raised in a declining habitat with relatively low foliage cover were fed more food than nestlings in a healthy patch, suggesting that the nestlings had greater nutritional needs as a result of thermal stress. Characteristics of acorn woodpecker (*Melanerpes formicivorus*) nests associated with favorable microclimate conditions are correlated with higher reproductive success (Hooge, Stanback, and Koenig

1999). Murphy (1985) showed that eastern kingbird (*Tyrannus tyrannus*) nestlings loose mass on days with high air temperatures.

Scale and Modeling Riparian Habitat

The results of this analysis indicate that habitat characteristics within a close proximity are more correlated to flycatcher presence than those within a greater extent. This finding is consistent with results from another multi-scaled study of flycatcher habitat (Hatten and Paradzick 2003). The nature of riparian habitat limits the potential for defining habitat associations on a greater scale when selecting biotic predictors in a bottom-up approach as in this investigation.

Comparisons of varying analysis extents suggest that the willow flycatcher selects habitat based on characteristics in relatively close proximity to its territory. This seems to be true for canopy structural heterogeneity, for the quantity of all riparian, and the quantity of low, medium, and high stands within the given extent. Structural heterogeneity is more strongly correlated to flycatcher presence when it is considered within a 50-meter extent and flycatcher selection of greater quantities of riparian habitat is most pronounced at 100-meters. The quantity of riparian habitat classified by canopy height is also most correlated with flycatcher presence at the 100-meter scale. The degree of sensitivity between all riparian characteristics and flycatcher presence decreased quickly beyond a 100-meter extent.

These results are in close agreement with anther study. Results from a multi-scaled analysis of flycatcher habitat in Arizona (Hatten and Paradzick 2003) show that the greatest amount of variability from a multivariate logistic regression model is explained with the smallest extent (4.5 ha / 119.7 m radius) of a series of extents tested (4.5 – 72 ha). The smallest extent is very close in value to the 100-meter radius that was most correlated with flycatcher presence to the quantity of riparian habitat in the Cliff-Gila Valley. Two of the predictors in the best multivariate model from the Arizona study are also quite similar in nature to the significant predictors from this study: (1) the amount of dense vegetation within the search radius, and (2) the standard deviation in Normalized Differentiation Vegetation Index (NDVI). NDVI is calculated with satellite imagery and is a measure of the density and biomass of vegetation. The standard deviation in NDVI is analogous to canopy heterogeneity because it measures variability in vegetation density. The smallest extent used in the Arizona study was higher than the smallest extent from this investigation (50-meters) and had they calculated these variables for lower extents, they might have found the standard deviation NDVI to be most associated with presence on a slightly lower extent.

Other multi-scaled studies of birds also show that preferences related to habitat selection are most correlated with presence at lower extents. Bald eagle habitat selection is more pronounced at the smallest extent (50-500 m search radius) when presence of perch trees and foraging habitat are considered (Thompson and MacGarigal 2002). Landscape factors are less important than local factors in determining bird abundance in the southern Appalachian Mountains (Lichstein, Simons and Franzreb 2002).

When comparing the deviance explained from regressing the response on the predictors of varying extents, an asymptotic approach to null deviance is evident near to the 200-meter radius. This indicates there is a threshold near to the 200-meter radius such that when considering a greater amount of land area the response to changing levels of the predictor will no longer exist. This effect is likely due to the nature of the riparian ecosystems in the Southwest. Unlike the eastern U.S. where vast deciduous forests have been fragmented, the riparian forests of the West are narrow and fragmented by nature (Knopf and Sampson 1994). To better visualize and compare the extent sizes, I calculated buffers around the nest points in ArcMap. The 200-meter search radius includes a good proportion of non-riparian habitat whereas the lower extents typically do not extend far beyond the riparian zone. This is also true for a section of river 18 km downstream from the Cliff-Gila Valley that was not mapped in this study but supports nesting flycatchers (Figure 7).

Modeling riparian vegetation provides a particular conundrum to the modeler because of the high spatial resolution that is required in capturing the characteristics of a narrow, linear ecosystem (Muller 1997; Congalton et al. 2002). Traditional landscape metrics used in landscape ecology “lack clear structural-functional relationships and are inadequate for characterizing the linear nature of riparian-stream networks” (Schuft et al. 1999,1157).

Mapping riparian habitat is also problematic because of its dynamic nature. The vegetation communities in the riparian zones form dynamic and complex landscapes that are a result of periodic flood disturbances and rapid growth through various successional stages (Ohmart and Anderson 1986; Stromberg, Patten, and Richter 1991; Carling and Petts 1992; Farley et al. 1994; Johnson 1994; Baker and Wolford 1995; Cordes, Hughes, and Getty 1997; Dykaar and Wigington 2000; Lytle and Meritt 2004). Models built from mapped riparian layers in a GIS are subject to either generalization or detail inaccuracy. These problems might advocate modeling a more temporally stable process to make associations with a species' distribution.

The key to clarifying habitat preferences when a habitat is highly heterogeneous over a short distance might be the considerations of large-scale processes that influence vegetation expression. The abiotic approach has been successful in clarifying influences on bird species abundance in Yellowstone (Hansen and Rotella 1999). Floodplain elements and features are maintained by complex functional interactions with elements and features on many scales (Graf 2001). Vegetation is an element of the floodplain that has perceivable patterns of expression that vary from the headwaters to an ocean delta; patterns that are most correlated with substrate characteristics (Nilsson et al. 1989). Avian species have predictable distributions based on habitat characteristics and are shown to be associated with either the presence of specific vegetation species (Wiens and Rotenberry 1981; Rotenberry 1985), or habitat structure (MacArthur et al. 1962; MacArthur 1964; Pianka 1966; Roth 1976; Rice, Ohmart, and Anderson 1983; Fremark and Merriam 1986; Urban and Smith 1989; Farley et al. 1994). Variation in riparian community structure, physical structure, and extent are influenced on a broad-scale by elevation (Baker 1989, Bendix 1994), drainage basin morphology (Baker 1989; Bendix 1994), sediment size (Nilsson et al. 1989; Baker and Walford 1995; Goodson et al. 2002), stream gradient (Hupp 1982; Bendix 1994); flood regimes (Johnson 1994; Hughes 1990;

Stromberg 2001; Levine and Stromberg 2001), disturbance (Bendix 1994; Goodson et al. 2002) and patch age (Baker and Walford 1995).

Abiotic processes have been approached as influencing flycatcher distributions. Graf et al. (2002) researched the characteristics of the fluvial systems, river basins and watersheds where the flycatcher breeds in the context of conservation of the riparian habitat on which the flycatcher depends. This report was mostly descriptive but the approach is unique in its attempt to describe important characteristics of willow flycatcher habitat solely by the processes affecting riparian expression. Floodplain characteristics were included as a part of the analysis of flycatcher habitat in the investigation by Hatten and Paradzick (2003).

The abiotic/indirect approach of modeling riparian habitat with large-scale processes in order to predict the distribution of a riparian obligate bird species might be an effective approach but interpretation of the results would likely have limited value compared to the results of this study. I overcame the difficulties of mapping a dynamic ecosystem that requires high spatial resolution to capture heterogeneity because of my intimate knowledge of the habitat and the implementation of a great number of tediously obtained vegetation samples. The predictors tested in this modeling approach were biotic variables derived from a landcover map that were hypothesized to directly influence the flycatcher's distribution. The biotic approach taken in this study tends to involve more tedious, costly methods for acquiring data that generally covers a more limited extent but are able to provide a level of detail that is valuable for effectively identifying associations (Wright, Marcus, and Aspinall 2000; Aspinall 2002; Vaughan and Ormerod 2003).

Spatial Autocorrelation and Conspecific Attraction

In the analysis I sought to address the issue of spatial correlation in an attempt to account for the potential of violating the assumption of independence (Legendre 1993) and found the autocovariate term explained more variation than any of the other variables. The autocovariate term accounts for clustering and its superior performance indicates that conspecific attraction might be a factor in the flycatcher's distribution.

There have not been any empirical reports on conspecific attraction in the willow flycatcher but clumped distributions have been described (Hatten and Paradzick 2003). Conspecific attraction among bird species is rarely put to empirical tests because of the practicality (but see Muller et al. 1997; Tarof and Ratcliffe 2004) so the lack of studies on conspecific attraction among willow flycatchers is not surprising. It is frequently reported that evidently suitable flycatcher habitat remains unoccupied (Sogge et al. 2003; Kus, Beck, and Wells 2003; Paradzick and Woodward 2003; Farmer, Rothstein, and Homgren 2003; Kulba and McGillivray 2003; Lynn et al. 2003; Brodhead and Finch 2003a), which might be a result of flycatcher's settling in sites with higher conspecific density.

Conspecific attraction indicates that a species benefits by settling near others of its species (Muller et al. 1997) or that resource allocation is spatially heterogeneous (Brown, Mehlman, and Stevens 1995). Conspecific attraction counters the idea that reproductive success will decline in areas of high conspecific density because of intraspecific competition - an assumption of density-dependent models (Morris 1995). Suggestions for the benefits of conspecific attraction are limited to two main ideas: (1) naïve animals will associate good habitat with other conspecifics and learn by settling near them (Muller et al. 1997), and (2) high densities allow for opportunistic extrapair copulations (Morton et al. 1990; for review of causes of extrapair copulations see: Neudorf 2004). The alternative explanation says that resource heterogeneity explains clumped distributions, which is the basis for spatial modeling.

Resource heterogeneity is a strong candidate for explaining clustering in the flycatcher but the results of this analysis indicate that is not the sole explanation. McCabe (1991) discusses willow flycatcher (*E. traillii*) distributions at a site in Wisconsin, and explains the close proximity of the flycatchers to one another as evidence for ample resources within the habitat. The study design of this investigation was based on modeling spatial heterogeneity of habitat resources. Correlation between presence and the variables measured was evident, but the autologistic term outperformed the other predictors. This is an indication that clustering is driven by something other than the habitat's heterogeneity. The possibility exists that the autologistic term outperformed the measured predictors because the study design excluded a more meaningful environmental predictor. This is reasonable, but because comparable predictors performed well in models describing flycatcher habitat preferences in Arizona (Hatten and Paradzick 2003), it seems likely that the predictors do have influence on flycatcher distributions.

Heterogeneity of food resources is a plausible factor driving clumping in the distribution of the willow flycatcher. Although there is a paucity of research on this topic and heterogeneity in food resources and nest predation rates are shown to be unrelated to clumped distributions of the least flycatcher (*Empidonax minimus*), there is some evidence of a relationship between the flycatcher's distribution and prey distribution. Delay, Stoleson, and Farnsworth (2002) sampled insects in three patches of similar size but distinct by the amount of water at the site and the density of flycatchers, including a site where flycatchers were absent from apparently suitable habitat, and found that flycatcher densities were inversely proportional to Hymenoptera (bees and wasps). Hymenoptera were found by this and another study to be a main component of fecal samples (Delay, Stoleson, and Farnsworth 2002; Durst 2004). Although this provides some evidence that diet may influence flycatcher distributions, the diet studies I reviewed show that the flycatcher's diet varies by location, by habitat, and differs from arthropod community samples in the habitat (Drost et al. 2001; Delay, Stoleson, and Farnsworth 2002; Durst 2004). Given the varying patterns and given that the flycatcher consumes a high diversity of insect taxa (Drost et al. 2001; Delay, Stoleson, and Farnsworth 2002; Durst 2004), more research is needed before conclusions can be drawn.

Naïve birds nesting near conspecifics is a factor hypothesized to be driving clumped distributions but there isn't currently enough information to determine if this could be a driving factor. Muller et al. (1997) found this to be a factor for house wrens. If a majority of the adults in a population were naïve birds, this might play a role but age structure for the willow flycatcher is relatively unknown. Kenwood and Paxton (2001) evaluated age structure for an Arizona population of the flycatcher and report that a majority of captures are second year birds but there is a caveat: until a bird is caught in a subsequent season it can not be aged more specifically than "after hatch year". All first time captures that were not juveniles were classified as second year birds. If the age structure was indeed weighted heavily on young birds, it might possibly be a contributing factor but more research would be needed.

Given the suggestion that conspecific attraction plays a roll in willow flycatcher distributions, there is some indication that the pursuit of extrapair copulations might be a motivating factor. The same idea is developed to explain clumped distributions of the least flycatcher (Tarof and Ratcliffe 2004), for colonial bird species (Collias and Collias 1969; Wagner 1993), and for birds in general (Neudorf 2004). In 1987, polygyny was considered rare among North American bird species (Briskie and Sealy 1987). Increasingly, DNA fingerprinting has shown that extrapair copulations are widespread practice among bird species even when they are considered monogamous (Ratti et al. 2001). Polyterritoriality, the maintenance of two or more territories to take advantage of polygynous mating, is common for a European passerine, the pied flycatcher, and there are records of this behavior in a number of other species including the Acadian flycatcher (*Empidonax virescens*) (Ford 1996).

The willow flycatcher is considered to be a typically monogamous species (Sedgwick 2000) but reports from genetic studies in Arizona show that approximately half of the females are associated with polygynous males (Davidson and Allison 2003) and an average proportion of 0.21 (+/- 0.7 SE) of males were polygynous (Pearson 2002). Polygynous behavior in the willow flycatcher is first reported in 1986 (Prescott) and two observations from different geographic locations were reported in 1989 (Sedgewick and Knopf). Reports of polygyny are frequently made for the tyrant flycatchers including the least flycatcher (*E. minimus*) (Briskie and Sealy 1987; Tarof and Ratcliffe 2004), Acadian flycatcher (*E. virescens*) (Ford 1996), western wood-pewee (*Contopus sordidulus*) (Eckhardt 1976), indicating polygyny might be common for this family of birds to which the flycatcher belongs.

The results of the autologistic model in this analysis indicate that conspecific attraction might play a role in habitat selection. The pursuit of extrapair copulations might be a reasonable explanation as extrapair copulations have been highly documented. However, heterogeneity of food resources cannot be discounted as a driving factor for clumped distributions, especially given that food resources have an obvious association with survival, and that prey resource distributions are relatively unstudied. More work might show food to be highly influential in the flycatcher's distribution and extrapair copulations to be secondary, and a result of high-density breeding.

CONCLUSIONS

In this analysis, variability and quantity of stand types in a southwestern riparian zone were found to be associated with the distribution of the southwestern willow flycatcher, an endangered bird, breeding exclusively in these habitats. The conceptual model supported by this analysis is based on identifying characteristics of riparian zones where lentic water occurs because they are hypothesized to be fundamental characteristics of the flycatcher's habitat. Here, I discuss how the results of this analysis might be applied to planning for habitat management and restoration aimed at recovering this endangered species.

As stated in the method's objectives, I attempted to produce an inductive rather than predictive model to elucidate generalities of flycatcher habitat that might be applicable beyond the study site. It has been argued that modeling with empirical presence/absence data incorporates biological interactions and stochasticity, which is an effective method for modeling a realized niche rather than the fundamental niche, and therefore, it is often difficult to extrapolate beyond the geographic boundaries of the analysis (Guisan, Edwards, and Hastie 2002). I believe that because the approach taken in this analysis was based on hypotheses founded on fundamental qualities inherent of all habitat occupied by southwestern willow flycatchers (i.e., water and high canopy density), the results are applicable beyond the scope of the Cliff-Gila Valley.

The results of this analysis provide support for the proposed hypothesis, and suggest that the estimated probability of flycatcher presence is greater where there is a greater amount of structural heterogeneity, in patches with greater area, and where riparian vegetation is more extensive. The results also indicate: (1) that a greater quantity of low-stature habitat is positively associated with flycatcher presence, especially when considering habitat within an increasing distance from the territory; (2) that the flycatchers were associated with a moderate quantity of medium stature habitat but selected against high or low quantities of medium-stature habitat; and (3) although the associations between flycatcher presence and high-stature habitat were not strong, the results did give some indication that increasing quantities of high-stature habitat influenced flycatcher presence. This knowledge can be applied to planning for habitat management and restoration for recovery of this endangered species in two ways: (1) clearing should be minimized, and (2) planning should consider floodplain hydrology, both human modified and natural, and promote the presence of stagnant water.

Mature riparian stands that are not suitable for flycatcher occupation are nevertheless important to the character of the riparian zone. The results show that newer growth might be more suitable to flycatchers where mature stands remain within the area, as the presence of mature stands effectively expand the reach of the riparian zone. This suggestion is supported by the results that show there is a positive trend of association between flycatchers and high stature habitat. Microclimate effects from increasing shade and reducing evaporation are provided as reasonable explanations for the influence of habitat beyond the territory of the flycatcher. In light of this, removal of vast amounts of vegetation for tamarisk control (see Fleishman et al. 2001; see Walker, in press) are likely to be detrimental to possible flycatcher settlement, not only because the flycatchers use tamarisk for nesting substrate (Sogge et al. 2003), but also because more extensive habitat beyond the territory of the flycatcher is associated with its presence.

Habitat management and restoration should plan for sources of stagnant water because of the clear relationship with the flycatcher, and because of its influence on canopy heterogeneity. The close relationship between flycatchers and lentic water and saturated soils is well established (Sedgewick 2000) and habitat suitability will depend on the presence of water. Where slow-moving water is present, riparian growth and health is promoted.

In a natural fluvial setting, slow-moving water is more likely to be present on the periphery of the active river channel, where open water is retained in oxbows, seeps, and overflow river channels. It logically follows that stand heterogeneity will be greater because young habitat regeneration is on the periphery, proximate to mature stands on the higher terraces that are protected from flooding at longer intervals. Natural fluvial processes promote natural habitat regeneration therefore, when possible, river channels on broad lowland floodplains should be allowed to migrate across the active channel, which will promote ponding in oxbows, seeps, and overflow river channels. Restoration efforts in the Cliff-Gila Valley and the nearby Gila River Bird Area, have shown that not only is it possible to augment these natural processes in habitat restoration (Boucher et al. 2003), but that the regenerated habitat can support breeding flycatchers (Boucher et al. 2003; Brodhead and Finch 2003b).

Natural river morphology is not exclusive to flycatcher occupation however, as human-induced modifications to the landscape are often responsible for the development of hydrological conditions that are associated with the flycatcher (i.e., saturated soils, or near to open water). Kus, Beck, and Wells (2003, 18) noted that close to half of the sites in California that support flycatchers are “dependant upon supplemental flows produced by agriculture and urban runoff, effluent outflow, or river regulation (e.g., canals, dams, reservoirs) for maintenance of existing habitat conditions.” Many of the largest of the flycatcher populations inhabit reservoir deltas that have been colonized by some of the most extensive riparian woodlands in the Southwest (Marshall and Stoleson 2000). The study site in this analysis supports one of the largest populations of the willow flycatcher where overland and subsurface flows from irrigation have created swampy and saturated soil conditions at many of the flycatcher breeding sites (Boucher et al. 2003, personal observation). The restored site in the Cliff-Gila Valley (mentioned above), takes advantage of irrigation return to feed a long labyrinth of ponds interspersed with narrow strips of riparian habitat growing on gravel rises.

Lastly, the results of this research show that conspecific attraction might influence the distribution of the willow flycatcher. Although the results are not conclusive, clumped distributions are shown to be a factor in flycatcher distribution. If conspecific attraction influences flycatcher distributions, potentially suitable habitat might not be occupied. This phenomenon has been noted by researchers studying the willow flycatcher (Sogge et al. 2003; Kus, Beck, and Wells 2003; Paradzick and Woodward 2003; Farmer, Rothstein, and Homgren 2003; Kulba and McGillivray 2003; Lynn et al. 2003; Brodhead and Finch 2003a). The potential that costly habitat restoration and management efforts might fail to attract flycatchers despite habitat suitability might be a source of concern. However, records show that flycatcher settlement changes from year to year (Sogge et al. 2002; Durst et al. 2005), and where new habitat fails to attract flycatchers immediately, future settlement might occur. Additionally, promoting and establishing healthy riparian will positively influence ecosystem health (Knopf et al. 1988; Finch 1999) and might positively influence other riparian obligate avian species of concern such as the western yellow-billed cuckoo (*Coccyzus americanus occidentalis*) and Bell's vireo (*Vireo bellii*).

Emphasizing an imminent threat of loosing a rich and diverse biological community, Noss (2000) identified Southwestern riparian ecosystems as one of the most highly endangered ecosystems of the United States. The importance of riparian systems to bird species richness and diversity is staggering. Riparian habitat supports more bird species than any other type of habitat in the western USA (Knopf and Sampson 1994). This study confirmed the importance of riparian stand heterogeneity, such as is found where natural river migration is allowed, and the importance a greater quantity of riparian vegetation within the riparian zone to the southwestern willow flycatcher. The animal subject of this study is an endangered bird whose distributions are correlated with the characteristics of an endangered habitat that exist where this habitat is healthy. These results underscore the need for preserving riparian systems.

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APPENDIX A

HABITAT PHOTOGRAPHS

Photograph from the study site, an example of an extensive low-stature stand.

Photograph taken from within a low-stature stand.

Photograph taken from within a high-stature stand with a subcanopy and understory.

Photograph taken from within a high-stature stand with subcanopy but no understory.

Photograph of a medium-stature stand with no understory (see next photo).

Photograph from within a medium-stature stand (see previous photo) with no understory.

Photograph taken from within a medium-stature stand with understory - understory vegetation is growing in an overflow channel and supports a pair of breeding flycatchers.

Stand classifications are chosen to reflect the age of the stand and the character from within the stand.

Profile of two adjacent stands with different stand structure.

Heterogeneous stand structure along the Gila River.

Photograph of flycatcher habitat showing the characteristic lentic water (slow-moving) and dense riparian foliage.

Photograph of flycatcher habitat adjacent to a filled overflow river channel (lower-left corner).