

SCIENCE

STRALBERG



**A Landscape-Level Analysis of
Urbanization Influence and Spatial Structure in
Chaparral Breeding Birds of the
Santa Monica Mountains, CA**

**By
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Abstract

This study used point count censuses and GIS land cover data to assess the relationships between chaparral breeding bird abundance and urban encroachment at the landscape level. A set of chaparral-vegetated points across an urbanizing landscape in the Santa Monica Mountains of southern California was surveyed for birds in 1996-97 and mapped in a GIS. I first analyzed the effects of surrounding urbanization on eighteen individual species' abundances using Poisson regression models with four measures of surrounding urbanization. Then, due to the spatial distribution of point count locations over a 17,000 ha area, I also examined and modeled spatial dependence in four selected bird species using geostatistical methods.

Thirteen out of eighteen species examined exhibited significant ($p < 0.05$) responses to at least one measure of surrounding urbanization, with bootstrap resampling trials indicating relatively robust models. Eight "chaparral specialist" species and two woodland-associated species exhibited significant negative relationships with urbanization, while two urban-associated species and one "chaparral specialist" were positively associated. Most of these species were associated with surrounding urbanization proportion at large ($> 250\text{m}$) radius distances. Landscape pattern explained little additional variation in abundance, although responses to urban edge proximity in some species appeared to be greater in highly fragmented areas.

Exploratory geostatistical analyses, using semivariograms and Moran's I correlograms, revealed large- and small-scale spatial dependence in all four species examined. Large-scale trends were largely attributed to the urbanization gradient over which points were sampled. Remaining small-scale autocorrelation in urbanization model residuals was modeled with a spatial covariance structure, and results were compared with de-trended and non-spatial models. Conclusions about urbanization effects did not change for three of the four species examined. Semivariogram and correlogram analyses also provided further insight about the spatial structure and ranges of spatial autocorrelation in the species examined.

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Chapter 1:

Effects of Urban Encroachment on Chaparral Breeding Bird Species in the Santa Monica Mountains, CA

1.1. Introduction

In an ecological context, urbanization represents an extensive modification of the landscape in order to support increased human habitation (McDonnell and Pickett 1990). Ecological forcing functions created by the growth of cities and associated human activities, which can collectively be referred to as “urbanization,” have become increasingly common topics of ecological study, as “natural” systems become more difficult to find. Hydrology, nutrient cycles, microclimate and species composition are but a few of the ecological features that may be substantially altered by urbanization influences.

1.1.1. Urbanization in Southern California

The traditional model of urban expansion consists of an urban core surrounded by progressively less intrusive land-uses, such that agricultural lands often provide a transition zone from urban to natural areas (Hall 1966). In contrast, development in southern California has been uniquely different from this traditional model, with its decentralized settlement pattern rooted in an anti-urban bias and a “*faux-rural*” suburban ideal that was prevalent among early 20th century settlers and developers (Fulton 1997). Unlike other major U.S. cities, metropolitan Los Angeles was formed out of a series of centers that grew and merged together to form a “metrosea” of fragmented communities (Davis 1992). Los Angeles County alone has a current population of 9.6 million people (County of Los Angeles 1998).

Despite Los Angeles’ natural unsuitability as a major city—including the scarcity of natural water supplies, unstable geology, and the lack of a natural harbor—the “growth machine” set into motion around the turn of the century resulted in unprecedented land

development and population growth in the Los Angeles basin (Fulton 1997), replacing orange groves and asparagus fields with tract homes and freeways. As the flat, coastal plain approached saturation, developers turned to inland deserts and mountain areas, building on increasingly marginal lands. Thus much of post-World War II development has occurred on lands that are too steep, infertile or dry for agriculture (Scott 1995). In the region's mountains, this development pattern has resulted in an extensive urban-wildland interface, and landscapes dominated by two major land-use classes: native vegetation (mostly chaparral scrub and woodland) and residential development. Indeed, metropolitan Los Angeles has the longest "wild" edge (roughly 1100 kilometers long, by the crudest measure) of any major city in the U.S. (Davis 1998).

This type of landscape mosaic is well-represented in the Santa Monica Mountains, a coastal mountain range containing a mosaic of interspersed suburban development and native chaparral vegetation, generally increasing in urbanization from west to east. Urbanization has occurred mostly along canyon bottoms, and often on ridgetops, resulting in "fingers" of development that penetrate the native chaparral habitat. In response to threats of large-scale developments and road construction, the United States Congress established the Santa Monica Mountains National Recreation Area in 1978 to conserve natural and cultural resources, as well as the "airshed" of the Los Angeles Basin (National Park Service 1999). Notwithstanding several major federal and state land acquisitions, most land in the Santa Monica Mountains is privately-owned. With some of the highest real estate values in the nation, these private lands remain subject to heavy development pressures.

Urban encroachment may have a diverse array of impacts on native wildlife and vegetation. From mountain lions (Edelman 1992, Smallwood 1994) to native ants (Human and Gordon 1997, Suarez et al. 1998), organisms of the chaparral and other Mediterranean-type ecosystems in southern California have been adversely affected by the direct and indirect effects of urban development, including habitat fragmentation, exotic species invasion, and other human disturbances.

Chaparral vegetation, although diverse in plant species, is quite uniform structurally, and contains relatively few bird species (Miller 1951, Small 1974). The birds that do occur and breed in chaparral tend to be somewhat specialized in their habits. Many species are ground-foragers with good running abilities, allowing them to navigate narrow alleyways under the dense scrub canopy (Small 1974). According to Miller (1951, p. 547), approximately 46 percent of bird species found in chaparral exhibit “primary or exclusive adherence to chaparral...a high proportion for a terrestrial formation.” Most of these species are year-round residents, characterized by small home ranges, low vagility (Soulé et al. 1988) and short natal dispersal distances (Baker et al. 1995). As a result, these birds may be particularly vulnerable to changes in the surrounding landscape, as they are continuously exposed to urbanization influences. Furthermore, the abundance of chaparral specialists may be closely tied to the ecological integrity of the chaparral vegetative community. Easily observed and monitored, some avian species may serve as chaparral indicators.

1.1.2. Avian Responses to Urbanization and Habitat Fragmentation

Studies along urbanization gradients have shown that total bird numbers generally increase with urbanization (largely attributable to a few abundant species), while species diversity decreases (Emlen 1974, Hohtola 1978, Beissinger and Osborne 1982, Jokimaki and Suhonen 1993). Factors associated with species’ declines in urban areas include changes in vegetation volume (Mills et al. 1989), foliage height diversity (Lancaster and Rees 1979), pedestrian and vehicular traffic (Emlen 1974), and increased domestic dog and cat predation (Soulé et al. 1988). In arid and semi-arid landscapes, some species may be drawn to water and cover provided by suburban landscaped gardens (Emlen 1974, Guthrie 1974, Vale and Vale 1976), but negative relationships have been demonstrated between species richness and housing density, as well as other measures of urbanization-related habitat change (Emlen 1974, Germaine et al. 1998).

In addition to direct habitat modification, urban development has resulted in the fragmentation of remaining natural areas. Referred to as “the single greatest threat to

biodiversity” (Noss 1991, p. 27), habitat fragmentation may result in the exclusion of species with large home ranges (Wilcove et al. 1986), as well as reductions in gene flow between isolated populations (Gilpin and Soulé 1986). The equilibrium theory of island biogeography (MacArthur and Wilson 1967), when extended to habitat fragments, predicts that smaller, more isolated patches will support fewer species, due in part to a higher probability of extinction when populations are small (Soulé et al. 1988, Kadmon and Pulliam 1993). Although the application of island biogeography theory to habitat fragmentation has been criticized as simplistic (Wiens 1994, Simberloff 1994), numerous forest fragmentation studies have demonstrated the so-called “area effect,” or tendency for larger habitat “islands” to support more species than similar smaller fragments (Blake and Karr 1984, Forman et al. 1976, Lynch and Whigham 1984, Whitcomb et al. 1981).

Furthermore, habitat fragmentation in urbanized landscapes may be different than fragmentation in (more widely studied) agricultural or timber production landscapes, in that transitions are more abrupt, and urban development is likely to constitute a less hospitable habitat for native species than forest clearings or agricultural fields.

Habitat fragmentation also expands the interface between natural habitats and urban development, thereby providing increased opportunities for urban elements to affect bird populations. Several studies of Neotropical migrant birds in Eastern U.S. forest woodlots have demonstrated significant negative relationships between avian diversity and surrounding urbanization density (Tilghman 1987, Dickman 1987, Friesen et al. 1995). Widely-recognized mechanisms include edge-related changes in vegetation composition (Saunders et al. 1991) and increased avian nest parasitism and predation rates (Robbins 1980, Brittingham and Temple 1983, Wilcove 1985, Langen et al. 1991, Engels and Sexton 1994). Non-native plant invasions (Mills et al. 1989), human disturbance (Dawson 1990) and various other features of urbanization (e.g., Johnsen and VanDruff 1986) have also been implicated in songbird declines.

Several recent studies have examined the effects of urbanization and habitat fragmentation on birds of southern California’s chaparral and coastal sage scrub habitats.

Soulé et al. (1988) applied the species-area relationship of island biogeography theory to chaparral canyon fragments in San Diego County, demonstrating that the number of “chaparral-requiring” resident bird species increased with fragment size and decreased with time since fragmentation. Bolger et al. (1997) revisited this area with a landscape approach to habitat fragmentation, showing that landscape composition and urbanization pattern were significant predictors of occurrence for many species examined, some of which were identified as edge/fragmentation-sensitive. In the less-fragmented eastern Santa Monica Mountains (examined in this study), Sauvajot (1997) found anthropogenic vegetation disturbances to be more important than urban development proximity in determining resident bird diversity and abundance.

1.1.3. Scale of Urbanization Influence on Birds

The effects of urbanization on breeding bird communities may be manifest at a variety of scales, with the importance of different ecological processes varying across scales (Addicott et al. 1987, Turner 1989) and potentially interacting between scales (Levin 1992). Just as different bird-habitat associations have been found at different spatial scales (Wiens and Rotenberry 1981, Riitters et al. 1997), the detectable effects of urbanization on bird populations are likely to be sensitive to the scale of sampling and analysis.

To date, a majority of studies examining the effects of urbanization on bird communities have focused on direct local impacts, examining bird population responses within urban areas, or immediately adjacent to urbanization activities (e.g., Scott 1993, Blair 1996, Clergeau et al. 1998, Germaine et al. 1998). For landscape-scale analyses, however, the extent of urbanization influence becomes an important consideration. The identification of the appropriate scale of influence or “ecological neighborhood” (Addicott et al. 1987) with respect to a particular process is an important part of predicting and understanding the relationships between urbanization and bird communities.

Previous studies have varied with respect to scale of urbanization influence examined, perhaps due to logistical constraints, and/or regional differences. Pearson (1993), in a study of Midwestern winter bird populations, did not detect landscape influences beyond 200m from a sampling location (maximum distance examined was 300m). Bolger et al. (1997), however, found significant associations between bird abundance and landscape composition at distances of up to 3000m. Given that a consistent pattern has yet to emerge, the examination of multiple potential scales of influence should help illuminate the ecological processes involved and how they may vary with scale.

1.1.4. Landscape Composition vs. Pattern

According to Opdam et al. (1995, p. S140), landscape pattern can be defined, for a particular species, as “the spatial configuration of patches of habitat and those landscape elements that influence dispersal.” In highly fragmented landscapes, these elements include patch configuration, size and insularity. Equilibrium models based on island biogeography and metapopulation theories predict species declines with increasing habitat loss and isolation (MacArthur and Wilson 1967, Levins 1969, Brown 1978, Opdam 1991, Hanski 1994).

The effects of landscape pattern are less well-studied in landscapes with interconnected suitable habitat still remaining. Andrén (1994) concluded, through a review of fragmentation studies, that in landscapes with more than 30 percent of suitable habitat remaining, the effects of habitat fragmentation are primarily due to habitat *loss*, rather than fragmentation pattern (i.e., patch size and isolation). In other words, if the proportion of remaining “habitat” in a landscape is above this critical proportion, then the landscape is well-connected and species will be able to disperse; otherwise, dispersal distances become important in determining species abundance and persistence (Gardner et al. 1991, Metzger and Décamps 1997). Other studies have identified different critical habitat thresholds (e.g. With and Crist 1995, Keitt et al. 1997).

Thus, depending on the proportion of suitable habitat remaining in a landscape, fragmentation pattern *per se* may be of varying importance to bird distribution and abundance.

1.1.5. Urban Edge Proximity and Direct Human Influence

Habitat fragmentation may provide increased opportunities for wildlife to come into contact with human activity and other urban elements (e.g., domestic animal predators, invasive species, chemical pollution), via the lengthening of the urban-wildland interface. Previous studies have indicated that in fragmented landscapes, certain chaparral bird species exhibit edge-sensitivity—with respect to urban development, as well as other habitat edges (Bolger et al. 1997, Sisk et al. 1997). In contrast, Sauvajot (1997), in a similar, yet less fragmented area, found no effects of urban edge proximity on bird abundance, but did find a significant reduction in both species richness and abundance of resident species in areas of human disturbance (i.e., cleared and eroded surfaces, such as roadcuts and landslips).

Habitat edges of all kinds are known to attract certain bird species, while repelling others, often due to high predation risk. Miller et al. (1998) found evidence that trails may serve as habitat edges for some species, attracting more habitat generalists, and deterring specialist species. Increased rates of nest predation were also found near trails. In addition, recreational trails may serve as “conduits” for urban/human influences into natural areas.

1.1.6. Research Objectives

Wiens (1994) describes habitat fragmentation as a dynamic process in which habitat continuity is disrupted, producing a variety of patterns, ranging from “small breaks in an otherwise homogeneous habitat” to “widely scattered units of remnant habitat in a transformed matrix.” The eastern portion of the Santa Monica Mountains represents just such a fragmentation continuum (Figure 1.1). The variation in landscape composition—from primarily chaparral to primarily urban development—allows for an examination of

landscape-level urbanization effects on chaparral ecosystems. Although the effects of urban edge proximity on resident birds in the Eastern Santa Monica Mountains have been examined previously (Sauvajot and Beuchner 1991, Sauvajot 1997), no previous landscape-level analyses have been undertaken.

In this study, I investigate the effects of urban encroachment and habitat fragmentation on breeding chaparral birds (year-round and summer residents) in the eastern Santa Monica Mountains. While most studies of habitat fragmentation have focused on the last phase of the fragmentation process (isolated habitat patches), my study also considers urbanization in its beginning and intermediate stages, where much of the remaining habitat is still interconnected.

My research questions were:

1. Is chaparral bird abundance affected by the proportion of urbanization in the surrounding landscape? If so, which species decline, and which species increase with increasing urbanization? What characterizes urbanization-sensitive species?
2. At what spatial scale (between 250m and 4000m) does urbanization proportion affect bird abundance? What is the maximum spatial extent of urbanization influence?
3. What is the importance of landscape pattern, when urbanization proportion is constant?
4. What are the effects of urban edge proximity and hiking trail density on bird abundance?

1.2. Methods

1.2.1. Study Area

This study was conducted in the eastern end of the Santa Monica Mountains, which belong to the Transverse Ranges of coastal Southern California. Located in middle of

metropolitan Los Angeles (Figure 1.2), the study area is bounded by Topanga Canyon to the west, the eastern boundary of Griffith Park to the east, Mulholland Drive to the north, and western Los Angeles and Sunset Blvd. to the south. Two interstate freeways, the 405 and 101, intersect the study area.

“True” or “hard” chaparral is the dominant vegetation cover in the study area. This Mediterranean-climate vegetation community is characterized by tough, waxy evergreen shrubs that are adapted to drought and frequent fire (Schoenherr 1992). Other vegetation types in the area include coastal sage scrub, oak woodland, walnut woodland, and sycamore/oak riparian corridors (Figure 1.3).

The western section of the study area (approximately 10,000 ha) is largely unfragmented, with urbanization occurring primarily at the edges and as enclaves within the dominant chaparral and coastal sage scrubland. The middle section (approximately 5,000 ha) is highly fragmented by residential development, although most remaining chaparral patches are interconnected. In both areas, most urbanization took place more than 25 years ago, although new developments are still occurring, particularly in the westernmost section. The eastern section, Griffith Park, is a large (approximately 2,000 ha) habitat island surrounded on all sides by urbanization (maximum distance from urbanization ~1,200m), and located a mere ten kilometers from downtown Los Angeles. Adjacent land use consists primarily of single-family residential development, but a range of residential, commercial and industrial land uses also surround the study area (Figure 1.1).

1.2.2. Field Data Collection

All bird abundance data were collected along trails and fire roads in Northern Mixed Chaparral vegetation (modified Holland 1986 classification) at least 100m from urban development. Census locations (points) were selected from a geographic information system (GIS) trail map of the study area created by the National Park Service, based on Harrison (1994) and supplemented with GPS-recorded trails. A stratified random sample was used to obtain representation in each section of the study area. All points were

dominated by a combination of Laurel Sumac (*Rhus laurina*), *Ceanothus* spp. (*C. megacarpus* and/or *C. spinosus*), and Chamise (*Adenostoma fasciculatum*). Each point represents a 100m radius area of chaparral vegetation, not overlapping with any other area sampled. I sampled 78 points in both 1996 and 1997, and an additional 29 locations were added in 1997 to increase coverage of areas with high levels of urbanization. The locations of all census points were recorded with a global positioning system (GPS) and mapped in an Arc/Info Geographic Information System (GIS) (Figure 1.3).

I used 100m fixed-radius point counts (Ralph et al. 1993) to estimate bird abundance at each census location. Each point count lasted for ten minutes, and was conducted between 5:30 and 9:30 a.m. PST. I counted all terrestrial birds seen or heard, except those that flew over without landing. For simplicity, I omitted swallows, swifts and raptors, which were difficult to count accurately. In both 1996 and 1997, two counts were conducted at each point between mid-May and late July—one early and one late in the season. In 1996, counts were conducted from June 8 through July 28. In 1997, I conducted counts between May 19 and July 11.

1.2.3. GIS Methods

I used GIS land-use data (1:24000, from 1990 aerial photos, courtesy of Southern California Association of Governments and National Park Service) to obtain landscape measures. Using Arc/Info GIS version 7.1.1, I calculated, for each census location, four different measures of urbanization influence in the surrounding landscape:

Urbanization Extent. For each census location, I first calculated the area within a 250m radius circle consisting of urban land uses (including golf courses, urban parks and other human-constructed green spaces). I then calculated the area of additional urbanized land contributed by consecutively larger circles, each radius twice as large as the previous (500m-1000m-2000m-4000m). For the 250m circle, and each additional buffer ring, I divided the urbanized land area by total area to obtain an urbanization proportion (see Figure 1.4).

Fragmentation Index. For these same buffer distances, I also calculated a fragmentation index, using the total length of urban/wildland edge within that radius of the point, standardized by the total area. This represents the degree to which the surrounding landscape is penetrated by urbanization, or the “convolutedness” of the urban-wildland interface.

Distance to Nearest Urban Edge. To examine species’ edge-sensitivity and response to urbanization proximity, I calculated the distance (m) from the center of each census location to the nearest urban development. Due to sampling constraints, each point was located at least 100m from the urban/chaparral edge.

Trail Density. To examine the effect of human activity (i.e., hikers, cyclists, horses, dogs) and/or micro-scale edge effects, I calculated the density of trails within a 250m radius of each point (meters of trail per square kilometer). Only a 250m radius was used because the patchy coverage of the existing trail maps did not allow me to examine larger areas.

1.2.4. Statistical Methods

I analyzed individual species abundance, rather than species richness or other diversity measures, since, in general, the same set of species was found throughout the study area. I restricted my analyses to species that were easy to count and for which twenty or more individuals were counted during at least one field season (1996 or 1997). All abundance measures represent number of singing males, except when the total number of singing males counted in either year was less than twenty. In these cases, I analyzed total individuals (visual and auditory detections), rather than the number of singing males, for both years. To best represent the capacity of the habitat in each year, I used the maximum of two counts as a measure of species abundance.

Although counts of animal abundance can often be approximated by a normal or lognormal distribution, the Negative Binomial (White and Bennetts 1996) or Poisson distribution is usually more appropriate (Dawson 1981). The Poisson is a discrete

function, often positively skewed, with variance equal to the mean. To investigate the scale at which each species was affected by urbanization (if at all), I fit a set of nested generalized linear models for each bird species. Using the generalized linear models procedure in SAS version 7, I specified a Poisson distribution with a dispersion parameter estimated by the deviance, and a log link function (SAS 1997). Generalized Estimating Equations (GEE) (Liang and Zeger 1986) were used to model the repeated measures (1996 and 1997) correlation structure in the data.

Using measures of urbanization proportion within each buffer radius (i.e., <250m, 250-500m, 500-1000m, 1000-2000m, 2000-4000m), I assessed the added contribution of each urbanization variable to the model, and thus the maximum scale at which surrounding urbanization explained significant additional variation in bird abundance. Score tests (Tarone 1988) were used to detect significant improvements in model fit with each consecutive radius distance. I then added a measure of large-scale habitat fragmentation (length of the urban/wildland edge, standardized by area) within the maximum response radius, as determined above, to detect additional responses to landscape pattern (above and beyond urbanization extent). The overall influence of urbanization and fragmentation combined was evaluated using score tests (Tarone 1988) for the significance of these parameters at the maximum response radius for each species.

Finally, using this maximum response radius, I constructed GEE Poisson regression models for each species' abundance (again using a repeated measures covariance structure). I initially included the following independent variables and interaction terms:

YEAR	Year (1996 or 1997)
URBX	Urbanization proportion within maximum response radius <i>X</i>
FRAGX	Level of fragmentation (total length of urban edge) within maximum response radius <i>X</i>
EDGEDIST	Natural log of the distance from a point to the nearest urban edge
TRAIL	Trail density (m/km ²) within a 250m radius

URBX*URBEDGE Interaction between urbanization proportion (within radius X) and distance to nearest urban edge

The inclusion of the interaction term was to test the hypothesis that edge sensitivity varies according to the level of urbanization in the surrounding landscape. The urbanization and fragmentation variables were included only if they were found significant in the previous scale analysis.

I examined the significance of each parameter estimate in the model, and eliminated non-significant variables to construct the “best” possible model for each species. I then performed a pseudovalidation of each final model, using a “bootstrap” resampling approach (Efron and Tibshirani 1986) to obtain confidence intervals for model parameters and detect potential sampling biases (Crowley 1992). For each species, fifty random samples of points, each equal in size to the original sample ($n = 107$), were taken with replacement, and used to fit the final models. Mean parameter estimates and confidence intervals were calculated according to Little and Schenker (1995), and parameter estimates were judged robust when confidence intervals did not overlap zero. When models with several urbanization terms were not robust, scaled-down models including just the most significant urbanization variable were also fit with a bootstrap sample.

1.3. Results

1.3.1. Species Encountered

Of the 38 species detected in this study (Appendix 1.1), 18 species were easy to count and relatively common in the study area, according to my criteria (Appendix 1.2). By far, the most commonly encountered species was the Wrentit, followed by the Spotted Towhee, California Towhee, Western Scrub-Jay and Bewick’s Wren. These species were virtually omnipresent throughout the study area, with over ninety percent site occupancy in each year of the study (Appendix 1.2).

Of species encountered, only the Wrentit is a true chaparral specialist. In coastal areas, however, several other species have a primary affinity for chaparral, including the Ash-throated Flycatcher, Bewick's Wren, California Quail, California Thrasher, California Towhee, Orange-crowned Warbler, Phainopepla, Rufous-crowned Sparrow, and Spotted Towhee (Miller 1951, Garrett and Dunn 1981). The remaining species may be considered habitat generalists with respect to chaparral, in that their primary habitat affinities are for other vegetation communities. The Mourning Dove, Northern Mockingbird and Western Scrub-Jay can be classified as suburban-associated species (Marzluff et al. 1994, Blair 1996); the Black-headed Grosbeak and Northern Flicker are primarily riparian woodland-associated; and the Blue-gray Gnatcatcher, Nuttall's Woodpecker, and Oak Titmouse may be considered oak woodland species (Miller 1951).

1.3.2. Responses to Surrounding Urbanization Proportion at Various Scales

The abundances of eleven (out of eighteen) species were significantly associated with surrounding urbanization proportion ($p < 0.05$) at one or more scales (Table 1.1).

Negatively associated with urbanization were the Ash-throated Flycatcher, Bewick's Wren, Blue-gray Gnatcatcher, Black-headed Grosbeak, California Towhee, Phainopepla, Rufous-crowned Sparrow, Spotted Towhee and Wrentit. The Northern Mockingbird and Western Scrub-Jay exhibited significant positive associations ($p < 0.05$) with urbanization. The Bewick's Wren and Western Scrub-Jay were only weakly associated with urbanization proportion ($p > 0.01$).

Different species exhibited different scales of urbanization influence (Table 1.1). All of the above-listed species, except the Phainopepla, Spotted Towhee and Western Scrub-Jay were significantly associated ($p < 0.05$) with urbanization proportion at the smallest scale tested, a 250m buffer radius. The Rufous-Crowned Sparrow was affected *only* at this scale. The remaining species exhibited significant responses to urbanization at larger scales, with maximum urbanization response radii of 500m for the Wrentit; 1000m for the Ash-throated Flycatcher, Bewick's Wren, Black-headed Grosbeak, California Towhee and Phainopepla; 2000m for the Northern Mockingbird and Spotted Towhee; and 4000m

for the Blue-gray Gnatcatcher and Western Scrub-Jay. Species exhibiting no significant relationship ($p > 0.10$) with urbanization proportion at any scale included the California Quail, California Thrasher, Mourning Dove, Northern Flicker, Nuttall's Woodpecker, Orange-Crowned Warbler and Oak Titmouse.

1.3.3. Responses to Large-Scale Landscape Pattern

Only the Spotted Towhee exhibited an additional significant response ($p < 0.01$) to fragmentation of the surrounding landscape, as measured by length of the urban-wildland edge within 2000m (Table 1.1). After accounting for the negative effect of urbanization proportion, fragmentation had a positive effect on Spotted Towhee abundance.

1.3.4. Responses to Urban Edge Proximity and Trail Density

Several species exhibited significant responses to urban edge proximity. The Northern Mockingbird and Orange-Crowned Warbler were negatively associated with distance to nearest urban edge (Table 1.2), while the California Thrasher was positively associated. In addition, for several species (Bewick's Wren, Blue-gray Gnatcatcher, Phainopepla, Northern Mockingbird and Wrentit), there was a significant interaction ($p < 0.05$) between urban edge distance and surrounding urbanization proportion, indicating a landscape-dependent response to urban edges. This effect was negative for the Phainopepla, and positive for all other species. For the mockingbird and Phainopepla, urban edge distance overwhelmed the effect of urbanization proportion.

Trail density was only marginally negatively significant for three species (the California Thrasher, Rufous-crowned Sparrow and Wrentit) in the presence of the other urbanization measures (Table 1.2).

1.3.5. Annual Variations in Abundance

Most of the species examined had higher recorded abundances in 1997 than in 1996, although the Phainopepla was more abundant in 1996 (Table 1.2). Species whose

abundance did not change significantly from one year to the next include the Blue-gray Gnatcatcher, California Towhee, Northern Flicker and Oak Titmouse.

1.3.6. Model Robustness

Bootstrap resampling trials for the full final models generally supported results obtained with the original empirical models (Table 1.3). The more complicated models were less robust, however, and interaction terms, in particular, tended to have large variances. Urbanization proportion, at least in the scaled-down models, was a fairly consistent predictor of abundance, with 95% confidence intervals large, but not overlapping zero, for 7 out of 9 species. The interaction terms between urbanization proportion and edge distance were less robust under resampling trials, with parameter estimates significantly different from zero for only 3 out of 5 species. The resampling estimates for urban edge distance and trail density were each significant for 1 out of 2 species. Although the effect of census year on per site abundance was highly significant ($p < 0.01$) for most species, the bootstrap parameter estimates varied widely and were not significantly different from zero for any species.

Overall, urbanization models for the Ash-throated Flycatcher, Bewick's Wren, Blue-gray Gnatcatcher, Black-headed Grosbeak, California Towhee, Northern Mockingbird, Phainopepla, Spotted Towhee and Wrentit were validated with the bootstrap resampling trials (Table 1.3). Species whose models didn't withstand the resampling pseudovalidation included the California Thrasher, Rufous-crowned Sparrow and Western Scrub-Jay.

1.4. Discussion

1.4.1. Urbanization-Sensitive Species

The primary objectives of this study were to determine which, if any, chaparral bird species were associated with levels of urbanization in the surrounding landscape and to identify common characteristics of these species. Thirteen of 18 species exhibited

significant responses ($p < 0.05$) to at least one measure of urbanization. Most chaparral specialists examined (8 of 10) were negatively affected by surrounding urbanization, while most of the remaining species either increased or exhibited no significant response (6 of 8), suggesting chaparral habitat degradation as a mechanism for decline with increasing urbanization. However, differential responses among species with similar habitat requirements, as well as significant responses by non-chaparral specialists, indicated that reduced habitat quality was not the only mechanism for decline.

Chaparral Specialists

Eight out of ten “chaparral specialists” exhibited significant negative responses to at least one measure of urbanization in the surrounding landscape. Exceptions to this trend were not difficult to explain. The California Quail, which exhibited no significant response to urbanization measures, tends to utilize grassy, open areas, and may be found in residential neighborhoods and golf courses (Ehrlich et al. 1988, Blair 1996). The Orange-crowned Warbler, which exhibited increased abundance near urban development, is known to prefer mixed chaparral/woodland habitats (Sogge et al. 1994), and may actually prefer oak and walnut woodlands to chaparral in the Santa Monica Mountains (personal observation), where breeding density is low (Yeaton 1974). Thus, neither of these species are true chaparral specialists, despite their primary affinities for chaparral.

For the remaining chaparral-associated species, urbanization-associated declines in abundance may be attributable to factors like habitat degradation, predation and stochastic demographic effects (Soulé et al. 1988, Bolger et al. 1991). The biggest anomaly was the California Thrasher, which despite its high predation rate and strong shrub dependence (Cody 1998), was only weakly negatively associated with urban edge proximity and trail density.

In a San Diego County study similar to mine, but with more habitat fragmentation and a greater diversity of habitat types, Bolger et al. (1997) found the Rufous-crowned Sparrow to be edge/fragmentation-sensitive, but not the Wrentit, Spotted Towhee, Bewick’s Wren,

California Thrasher or California Towhee—all of which were found to be negatively affected by urbanization in my study. Bolger et al. (1997), found that most of these “insensitive” species *are* significantly associated with various landscape characteristics (e.g., level of fragmentation), but not when habitat characteristics (e.g., shrub coverage) were entered in the models first.

While associations with surrounding urbanization levels detected in my study may also be due to local habitat differences, these habitat variations are likely to be confounded with landscape configuration. Disturbed areas such as roadcuts and clearings, which Sauvajot (1997) found to support fewer resident bird species, are more likely to occur in highly fragmented, urbanized landscapes. Increases in surrounding urbanization and resulting human disturbances may also reduce shrub density, a measure of habitat quality and determinant of population density for several chaparral species (Miller 1951, Small 1974).

Three species in particular—the Wrentit (Erickson 1938), California Thrasher (Cody 1998) and Spotted Towhee (Jones and Diamond 1976)—are known to depend on dense, shrubby vegetation, which provides cover from predators. For the Wrentit, Erickson (1938) found an inverse relationship between territory size and brush density, with interior territories smaller than territories bordering on roads, clearings, or non-scrub vegetation. Although Erickson attributes the larger territories near edges to the corresponding reduction in territory boundary to be defended, it may also be an indication of poorer habitat quality near roads and clearings. I found the Wrentit and towhee to be negatively associated with surrounding urbanization proportion, as expected, although the Spotted Towhee was also positively associated with urban edge length, or degree of fragmentation (Table 1.2). Surprisingly, however, the thrasher was not significantly associated with surrounding urbanization proportion, although it did exhibit weak negative associations with urban edge proximity and trail density (Table 1.2). Of these three species, the Wrentit is the only one not found in residential areas (Blair 1996), which may explain its comparatively strong urbanization response.

Other species are less shrub-dependent, utilizing a wider range of vegetation densities. The Rufous-crowned Sparrow, which has been officially designated a conservation priority (Federal “Special Concern Species” and State of California “Species of Special Concern” [California Department of Fish and Game 1998]), seems to prefer areas with sparser vegetation coverage—usually “dry, rocky slopes with scattered scrub and patches of grass and forbs” (Ehrlich et al. 1988, p.584). The Bewick’s Wren may be found in sparse sagebrush and desert scrub, as well as suburban gardens (Blair 1996, Kennedy and White 1997), while the California Towhee, despite its primary affinity for chaparral, is often considered an edge-exploiting species (Ehrlich et al. 1988, Sisk et al. 1997) and has been demonstrated to *increase* with fragmentation (Bolger et al. 1997). The Ash-throated Flycatcher and Phainopepla are primarily desert scrub species that also breed in the chaparral (Miller 1951). Thus, factors other than shrub coverage may be more important in regulating abundances of these species.

Ash-throated Flycatchers are long-distance migrants, wintering in Central America, while the Phainopepla is a local migrant, breeding first in the inland desert and later that year along the coast, in chaparral scrub. While their habitat requirements are less strict than those of other “chaparral specialists,” these wide-ranging, relatively mobile species may cue in on larger landscape patterns, preferring less urbanized areas. Indeed, the Ash-throated Flycatcher has been characterized as an “urban avoider,” and is generally absent in urban/suburban areas (Blair 1996).

All of the chaparral specialists examined, except the Ash-throated Flycatcher and Bewick’s Wren, are open cup nesters and therefore more vulnerable to nest predation (Martin and Li 1992), which may increase near urban areas if scrub-jays and other corvid nest predators are more abundant (Wilcove 1985, Cody 1998). Ground-nesting species, such as the Rufous-crowned Sparrow and Spotted Towhee are also highly susceptible to mammalian predation (Martin and Li 1992), which may increase near urban development, due to the presence of human-introduced domestic cats (*Felis catus*) and dogs (*Canis domesticus*) (Soulé et al. 1988). In addition, these mammalian predators

may be responsible for higher adult mortality rates among ground-foraging species, including the Rufous-crowned Sparrow, California Thrasher and both towhees (Cody 1998).

Oak Woodland Species

Two of the oak woodland species examined—the Oak Titmouse and Nuttall's Woodpecker—exhibited no significant urbanization response. This may be due to the spatial habitat arrangement in this study area, and the tendency for oak woodlands to occur near development, especially in the eastern portion of the study area (see Figure 1.3), or to the cavity-nesting habits of these species, and their consequent lower rates of nest predation (Martin and Li 1992). Furthermore, these species are considered edge-exploiting (woodpecker) or edge-neutral (titmouse) (Sisk et al. 1997) and may be found in suburban areas (Blair 1996).

The Blue-Gray Gnatcatcher, the only urbanization-sensitive oak woodland species identified, may actually be better characterized as chaparral-associated in the Santa Monica Mountains (personal observation), and may also be detrimentally affected by changes in shrub cover. Although this species does not appear especially sensitive to human activity near the nest, it is highly susceptible to nest predation, which accounts for the large majority of nest failures (Root 1969, Ellison 1992). The gnatcatcher may also have specific microhabitat requirements, such as riparian corridors and canopy openings (Ellison 1992), which may be limited in urbanized landscapes. It is generally not present in urban or suburban areas (Blair 1996).

Riparian Woodland Species

Of the two riparian woodland species, only the Black-headed Grosbeak was negatively affected by urbanization. Grosbeak reproductive opportunities are thought to be limited by availability of suitable habitat, which is primarily a factor of jay abundance and predation threat (Hill 1995). The negative association with urbanization in this species may also be related to riparian habitat requirements, as riparian corridors in more

urbanized areas have often been channelized, highly modified and/or replaced entirely by housing developments. Finally, this grosbeak is migratory, wintering in Central America, and may respond to large-scale landscape structure more readily than some of the resident species, as has previously been noted (Hansen and Urban 1992).

The Northern Flicker, which exhibits no significant relationship with urbanization measures, is a widespread generalist in many respects, with three subspecies occurring across North America. It prefers open woodlands, savannas and forest edges, but is well-adapted to human habitats and commonly breeds in urban and suburban environments (Moore 1995).

Suburban-Associated Species

The species that exhibited the strongest positive association with urbanization was the Northern Mockingbird, a common suburban bird whose preferred breeding habitat is mowed lawns interspersed with trees and ornamental bushes (Arnold 1980, David et al. 1990, Derrickson and Breitwisch 1992). This result was expected, given the virtual absence of mockingbirds in chaparral and woodland interiors (Derrickson and Breitwisch 1992, Blair 1996, Cody 1998). The Mourning Dove, however, showed no detectable association with surrounding urbanization, which is consistent with other studies that found this species to be insensitive to land cover type (Germaine et al. 1998) and landscape characteristics (Bolger et al. 1997).

The Western Scrub-Jay, which is more abundant in urban and suburban settings than in native oak woodlands (Blair 1996), exhibited a weakly significant ($p > 0.01$) association with large-scale surrounding urbanization (Table 1.2). Nests of several species examined in this study, including the Wrentit (Geupel and DeSante 1990), California Thrasher (Cody 1998), Black-headed Grosbeak (Hill 1995) and Blue-gray Gnatcatcher (Ellison 1992), are known to suffer significant losses from scrub-jay predation. Thus enhanced scrub-jay abundance near urban edges could detrimentally affect songbird reproductive success, as has been demonstrated with the related Blue Jay and Golden-cheeked

Warblers in Juniper woodlands near urban developments (Engels and Sexton 1994). Although Langen et al. (1991) actually found higher overall rates of predation on artificial nests in the chaparral interior than at highly disturbed sites, they suggest that avian predators, which are visually cued, may have been underestimated, particularly at disturbed sites.

Summary

These results suggest that, although chaparral specialists seem most susceptible to landscape changes, individual species respond differently to urbanization for multifaceted reasons. The abundance of certain common, yet “shy,” cover-dependent chaparral specialists like the Wrentit and Spotted Towhee may directly track habitat quality, perhaps measured by shrub density. Less common species with specialized habitat requirements, such as the Rufous-crowned Sparrow, may suffer from a lack of suitable nest sites.

Other species with broader habitat associations, such as the Blue-gray Gnatcatcher and Black-headed Grosbeak, may be sensitive to urbanization and landscape changes due to possible related increases in nest predation, or a reduction in preferred breeding habitat, such as riparian corridors. Highly mobile migratory species, such as the Black-headed Grosbeak and Ash-throated Flycatcher, may respond to large-scale landscape patterns, selecting areas with less overall urbanization in which to breed.

1.4.2. Scale of Urbanization Influence

My secondary interest was in the spatial extent of urbanization influence for each of the species exhibiting a significant urbanization response. This varied according to species, and cannot be precisely determined, due to the coarseness of the intervals examined. For all species examined, however, responses to urbanization were consistent across scales—i.e., there was no sign reversal (positive/negative) as scale increased. This may be due in part to the relatively narrow range of scales examined, such that this study is best suited

for identifying ranges of urbanization influence, or ecological neighborhoods, rather than specific scale thresholds.

Landscape-scale responses (i.e., greater than 250m) were recorded for all urbanization-sensitive species except the Rufous-crowned Sparrow and California Thrasher, suggesting that responses to surrounding urbanization are occurring at the level of the population, rather than the individual, and on an intermediate, rather than short-term time scale (see Wiens 1981). Temporal lags in population responses to environmental change may also result in spatial lags in the relationship between bird abundance and characteristics of the surrounding landscape. Alternatively, these large-scale responses may indicate the presence of a habitat gradient coinciding with the urbanization gradient, or other large-scale variations in bird abundance. This seems particularly likely for species such as the Blue-gray Gnatcatcher, which was virtually absent from counts conducted in the eastern portion of the study area, and is negatively associated with surrounding urbanization proportion at distances up to 4000m.

Conversely, the Wrentit, which was highly urbanization-sensitive, in terms of both model fit and magnitude of urbanization effects, was affected only at distances up to 500m. This species is “extremely sedentary” (Ehrlich et al. 1988, p. 420) and may not be affected by habitat configuration at such large scales. Furthermore, its small territory size (Erickson 1938) and adherence to chaparral, the primary vegetation type within the study area, may ensure continued dispersal and habitat occupation, even in narrow habitat corridors.

Highly mobile migratory species, such as the Black-headed Grosbeak, Ash-throated Flycatcher and Phainopepla, may have a greater range of potential urbanization influence, as well as a greater awareness of large-scale landscape change. But these species were urbanization-sensitive only up to 1000m, suggesting that the larger-scale responses observed in the Northern Mockingbird and Blue-gray Gnatcatcher may have been artifacts of large-scale distribution patterns.

Finally, for some species, such as the Black-headed Grosbeak, local chaparral habitat may have been less important than the availability of suitable riparian or other woodland habitat in the surrounding area. The parallel north-south running canyons in this study area are separated by distances of approximately 1000m, such that, where canyon bottoms are not urbanized, most sampling sites are within 1000m of seasonal streams and associated riparian vegetation (Figure 1.3).

1.4.3. Landscape Pattern vs. Composition

Until recently, most studies of habitat fragmentation in urbanized landscapes have focused on distinct habitat islands (e.g., Soulé et al. 1988, Tilghman 1987, Dickman 1987, Friesen et al. 1995), rather than largely contiguous habitat interspersed with urban development (but see Sauvajot and Beuchner 1991, Bolger et al. 1997). The results of this study suggest that the effects of habitat fragmentation may be manifest before the traditional fragmentation scenario—habitat islands in a sea of inhospitable environment—is reached. In other words, urban encroachment may cause population declines in areas that aren't yet completely isolated by urbanization or other “inhospitable” land uses.

With respect to landscape pattern, however, my results indicate that fragmentation *per se*, as measured by total urban edge length within the maximum response radius, does not contribute to additional declines in the abundance of urbanization-sensitive species. For all species except the Spotted Towhee, the amount of urban edge present within the maximum urbanization response radius did not significantly improve the abundance model. The towhee's positive association with fragmentation, controlling for the negative effect of urbanization proportion, may indicate an attraction to suburban food and water resources, as this species is often found in suburban gardens with sufficient cover (Blair 1996, Greenlaw 1996).

These results should be interpreted with caution, however, given the narrow range of urbanization conditions available (high correlation between fragmentation and

urbanization proportion). In this study area, most highly urbanized areas were also highly fragmented; thus little of the variation in abundance not explained by urbanization proportion could be explained by the fragmentation index. The variation in bird abundance across presumably-equivalent suitable habitat within the same landscape indicates that landscape configuration is influential, but cannot be distinguished from the effects of landscape composition at the local level.

Furthermore, most remaining chaparral habitat in this study area is still interconnected, and very few of the true habitat islands were sampled due to logistical constraints. The primary exception, Griffith Park (approximately 2000ha), is much larger than the home ranges of the species under study (e.g. ~9ha for the gnatcatcher [Ellison 1992]). As long as habitat patches are larger than the minimum area requirements of a species, landscape configuration is less likely to affect species abundance (Andr n 1992). Birds, in particular, may be less sensitive to spatial landscape configuration due to their relative mobility (Wiens 1981).

1.4.4. Urban Edge Proximity and Human Use

With respect to the effects of proximity to urban development, this study suggests that certain species are urban edge-averse or edge-affiliated, but that the relationship may depend upon the level of surrounding urbanization. Only the California Thrasher, a chaparral specialist, exhibited a weakly ($p < 0.05$) positive association with distance to urban development (natural log-transformed), independent of urbanization proportion (Table 1.2). This species was not significantly associated with surrounding urbanization proportion, but was expectedly edge-sensitive, given its specialized habitat requirements and susceptibility to nest predation. Its eggs and nestlings are susceptible to scrub-jay and raven predation, and juveniles are often taken by domestic cats (*Felis catus*) near urban fringes (Murphy and Fleischer 1986). Furthermore, thrashers are thought to compete with mockingbirds, which are similar in diet and foraging behavior, near urban areas (Cody 1998).

As also expected, the Northern Mockingbird, an abundant urban-associated species that is virtually absent in chaparral and forest interiors (Derrickson and Breitwisch 1992, Cody 1998), exhibited a negative relationship with distance to urban development. The Orange-crowned Warbler was also found to be negatively associated with distance to urban development, perhaps due to its preference for mixed chaparral/woodland habitat (Sogge et al. 1994), and the tendency for walnut woodlands, in particular, to occur near development in this study area (see Figure 1.3).

Species that exhibited a significant positive response to the interaction between urban edge distance and urbanization proportion included the Wrentit, Bewick's Wren, Blue-gray Gnatcatcher and Northern Mockingbird. For the Wrentit, Blue-gray Gnatcatcher and Bewick's Wren, which exhibited negative responses to surrounding urbanization, this suggests a dampened positive influence of urban edge distance, which becomes less important as urbanization proportion decreases. This may be due to the habitat saturation that must occur at higher abundances, and the "carrying capacity" of this environment. In more urbanized parts of the landscape, there may also be more opportunities for predation and other urban-associated influences from several directions, rather than from just one edge in the large chaparral tracts. Furthermore, since individuals counted were not necessarily on breeding territories, or may have had territories extending farther than 100m from the point count locations, maximum density may be lower near the chaparral/urban interface, and even less so where urbanization is encroaching from many sides.

For the Northern Mockingbird, which was positively associated with surrounding urbanization proportion, the positive interaction effect is reinforcing, in that mockingbirds are even less abundant (nonexistent) in chaparral interior when surrounding urbanization proportion is low. Mockingbirds apparently penetrate farther into the chaparral in highly urbanized and fragmented landscapes, whereas they are rarely found more than 100m from urban development that borders on large, contiguous chaparral areas (personal observation).

The limited influence of urban edge proximity in this study is generally consistent with Sauvajot (1997), who, in a less urbanized portion of this same study area, found no significant relationships between proximity to urban development and resident bird species richness or abundance. Edge-insensitivity in largely unfragmented areas may be due to the hardiness of chaparral vegetation, and its resistance to invasion by non-native plant species (Knops et al. 1995), as well its relative impenetrability to humans (Sauvajot 1997). Indeed, much of the chaparral-development interface appears to be characterized by a distinct "edge," rather than transitional vegetation, although chaparral vegetation in more fragmented areas may become degraded and invaded by exotic plant species over time (Alberts et al. 1993). Furthermore, recent studies (e.g. Hansen and Urban 1992, Tewksbury et al. 1998) suggest that western bird species may be less sensitive than eastern species to landscape fragmentation and edge effects, based on differences in life-history traits and predation pressures. These studies examined forested, rather than urban landscapes, however, and may therefore be influenced by quite different edge-associated pressures.

Another possible explanation is that reproductive success is indeed lower near urban development, but source-sink dynamics keep abundances high. Previous studies have suggested that habitat fragmentation reduces reproductive success of migratory songbirds, resulting in source-sink dynamics that may not be detected in simple surveys of species abundance (Donovan et al. 1995, Brawn and Robinson 1996).

Hiking Trail Density

In terms of surrounding trail density, only three species exhibit significant responses (all negative) after accounting for other urbanization factors: the California Thrasher, Rufous-crowned Sparrow and Wrentit. Other studies have also recorded a reduced probability of nesting near trails in some species, as well as increased rates of nest predation and occurrence of "edge" species (Zande et al. 1984, Hickman 1990, Miller et al. 1998).

Of all species examined, the Wrentit and thrasher are probably the most sedentary and cover-dependent, the Wrentit so much so that it often refuses to cross firebreaks and trails (Small 1974). It follows, therefore, that these species respond negatively to trail density, even after factoring in urban edge proximity and surrounding urbanization proportion, which are correlated with this variable. The Rufous-crowned Sparrow, however, nests primarily on dry, rocky open slopes (Ehrlich et al. 1988), which actually tend to be located near hiking trails, firebreaks and roadcuts in this study area. Thus the relationship found in this species is initially surprising, although given its relatively low density and patchy distribution (Ehrlich et al. 1988), this species may be particularly sensitive to human disturbance.

1.4.5. Caveats

The increase in urbanization from west to east within the study area (Figure 1.1) complicates the interpretation of my results. Although I kept vegetation cover constant to the extent possible, the effects of urbanization and fragmentation are difficult to disentangle from the effects of geographic location, given the potential variations in climate generated by proximity to the Pacific Ocean. The vegetation in the eastern end of the study area tended to be patchier and drier in general. The extent to which this is a function of increased urbanization, as opposed to natural microclimate conditions, is uncertain. Furthermore, small-scale variations in vegetation, and interactions among sites that are close in spatial proximity may result in spatial dependence among sampling locations.

For this study, I ignored potential clinal and local variations in vegetation, assuming that vegetation is constant across the sampling locations. Given the lack of variation in avifauna among scrub vegetation types in southern California (Small 1974), this assumption may indeed be reasonable. If there is considerable spatial dependence among sampling locations, however, and model residuals are autocorrelated, conclusions about urbanization may be biased (see Chapter 2).

1.4.6. Research Recommendations

This observational study examines relationships between a set of independent urbanization-related variables and abundance of several common chaparral birds.

Without experimental manipulation, causal relationships can only be inferred, and the mechanisms responsible for these patterns remain speculative. Given the difficulties of conducting experimental studies at such a large scale, the development and testing of predictive models can produce results valuable to land-use planners and researchers alike. In order to better formulate specific policy recommendations, however, more research on underlying mechanisms should be conducted.

Most important for future research is the study of breeding biology and factors influencing mortality and reproductive success in urbanization-sensitive species. While many species examined here are known to be susceptible to nest predation, studies monitoring individual pairs and territories, their breeding behavior, and reproductive success, could illuminate population dynamics with respect to various landscape and habitat features. In particular, data on predation pressures should be collected at various sites throughout the landscape to confirm or refute the findings of Langen et al. (1991), who did not find nest predation to increase near urban areas. Furthermore, long-term studies would help determine if populations are stable and to what extent source-sink dynamics are occurring.

Another approach to determining mechanisms for decline is to quantify more specifically the factors associated with increased urbanization and fragmentation. For example, measuring shrub density, vegetation structure and diversity, leaf litter characteristics, and invertebrate abundance might indicate whether there is indeed a decrease in habitat quality with increased urbanization. Quantifying urban-associated predators, such as dogs and cats, as well as human activities, such as mountain biking and hiking, may also be informative.

Finally, the examination of a broader range of habitats, including urban areas, may help complete a spatial picture of species distributions. It would be useful to quantify how far, if at all, birds of the chaparral penetrate into urbanized areas, what habitat characteristics are necessary, and whether these results are constant across space, or differ according to overall landscape matrix characteristics.

1.5. Conclusion

The eastern Santa Monica Mountains are unique in representing an intermediate stage of habitat fragmentation. The associated declines in abundance of common chaparral and woodland species may not be immediately apparent in the field, as the species are all still relatively common. But Poisson regression models helped detect these not-so-obvious patterns. The results of this study suggest that several chaparral bird species may decline in abundance as surrounding urbanization increases, even when apparently suitable habitat is present.

Some species, including the Wrenit, Spotted Towhee, Black-headed Grosbeak and Blue-Gray Gnatcatcher, appear particularly vulnerable to urbanization, and may serve as indicators for chaparral quality and/or landscape integrity. Furthermore, certain urban-associated species, such as the Northern Mockingbird and Western Scrub-Jay, appear increase in abundance as surrounding urbanization increases, and may contribute to declines of other songbirds, through competition and nest predation, respectively.

Scale of urbanization influence can be quite large for some species, indicating the importance of population responses to landscape-level urbanization processes. In the case of the Blue-gray Gnatcatcher, additional declines in abundance were detected with changes in urbanization up to 4000m from census locations.

Although urbanization extent was shown to be a significant predictor of abundance for several species, urbanization pattern did not explain significant additional declines or increases. This does not mean that the birds studied are not affected by habitat fragmentation, only that the total proportion of available habitat is an adequate measure

of fragmentation, and that, in this largely interconnected landscape, birds do not appear to distinguish between different habitat configurations when urbanization extent is constant.

Urban edge aversion and/or affinity varied, depending on levels of urbanization in the surrounding landscape. Within less urbanized parts of the chaparral, few species were sensitive to urban development proximity, and weakly so. Distance from the urban/chaparral edge does appeared to be important in highly urbanized landscapes, however.

Urban expansion is largely inevitable in the Greater Los Angeles area, where rapid population growth and high property values have placed tremendous pressure on remaining undeveloped lands. While much of the remaining natural habitat in this area is protected in Federal and State public parkland, development has continued at a rapid pace on privately owned lands. The influence of surrounding landscape urbanization on chaparral bird abundance suggests that conservation and land use planning efforts would benefit by incorporating regional and landscape, as well as local perspectives, to help ensure that sufficiently large, intact areas of chaparral are maintained. Such planning is possible because chaparral habitat still remains largely unfragmented throughout large sections of the Santa Monica Mountains, and elsewhere in southern California. The relationships observed in this study highlight that planning and forethought will help preserve chaparral habitat before crisis proportions are reached.

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Table 1.1. Results from nested Poisson regression analyses. Sequential score tests were used to evaluate the contribution of urbanization proportion and fragmentation at increasing radius distances (see Figure 1.4). Overall models include urbanization proportion at the maximum significant radius and urban edge length at the same radius when applicable. Chi-square (p) values are displayed in bold when significant ($p < 0.05$).

Species†	Urbanization Proportion -- Radius Distance					Urban Edge Length*	Overall Sign
	0-250m	250-500m	500-1000m	1000-2000m	2000-4000m		
<i>Chaparral Specialists</i>							
ATFL	4.23 (0.040)	1.56 (0.21)	4.28 (0.039)	0.16 (0.69)	0.90 (0.34)	0.57 (0.45)	13.52 (0.0002)
BEWR	5.26 (0.022)	0.76 (0.38)	6.75 (0.0094)	0.66 (0.42)	2.11 (0.15)	0.06 (0.81)	8.47 (0.014)
CAQU	1.39 (0.24)	0.92 (0.34)	0.72 (0.40)	0.85 (0.36)	0.41 (0.52)		
CATH	1.22 (0.27)	0.08 (0.77)	0.51 (0.48)	0.00 (0.95)	0.00 (0.97)		
CATO	2.39 (0.12)	0.06 (0.81)	6.56 (0.010)	0.03 (0.86)	0.50 (0.48)	1.13 (0.29)	8.48 (0.0036)
OCWA	0.46 (0.50)	1.17 (0.28)	0.35 (0.55)	0.01 (0.91)	0.95 (0.33)		
PHAI	3.26 (0.071)	0.68 (0.41)	7.59 (0.0059)	2.33 (0.13)	1.62 (0.20)	0.49 (0.49)	12.12 (0.0005)
RCSP	7.20 (0.0073)	0.42 (0.52)	0.29 (0.60)	0.60 (0.44)	0.30 (0.58)	3.26 (0.071)	7.20 (0.0073)

† See Appendix 1.1 for full species names and scientific names.

* Evaluated at maximum significant radius of urbanization proportion.

Table 1.1. (continued)

Species†	Urbanization Proportion -- Radius Distance						Urban Edge Length*	Overall	Sign
	0-250m	250-500m	500-1000m	1000-2000m	2000-4000m				
<i>Chaparral Specialists</i>									
SPTO	3.44 (0.064)	0.10 (0.75)	2.71 (0.10)	8.15 (0.0043)	2.86 (0.091)	9.55 (0.0020)	13.93 (0.0023)	-,+	
WREN	9.44 (0.0021)	4.02 (0.045)	0.38 (0.54)	3.63 (0.057)	0.83 (0.36)	2.04 (0.15)	11.12 (0.0009)	-	
<i>Riparian Species</i>									
BHGR	9.11 (0.0025)	0.02 (0.88)	4.27 (0.039)	2.08 (0.15)	0.05 (0.83)	0.85 (0.36)	12.18 (0.0005)	-	
NOFL	0.03 (0.87)	0.43 (0.51)	0.47 (0.49)	0.76 (0.38)	2.20 (0.14)				
<i>Oak Woodland Species</i>									
BGGN	9.11 (0.0025)	0.05 (0.82)	8.98 (0.0027)	2.57 (0.11)	5.73 (0.0167)	3.13 (0.077)	19.67 (<0.0001)	-	
NUWO	0.04 (0.84)	3.56 (0.06)	0.98 (0.32)	0.06 (0.81)	0.29 (0.59)				
OATI	0.16 (0.69)	0.10 (0.75)	0.00 (0.94)	0.80 (0.37)	1.22 (0.27)				

† See Appendix 1.1 for full species names and scientific names.

* Evaluated at maximum significant radius of urbanization proportion.

Table 1.1. (continued)

Species† (per site abundance)	Urbanization Proportion -- Radius Distance					Urban Edge Length*	Overall	Sign
	0-250m	250-500m	500-1000m	1000-2000m	2000-4000m			
<i>Suburban Species</i>								
MODO	0.00 (0.98)	0.63 (0.43)	2.23 (0.14)	0.11 (0.74)	3.12 (0.08)			
NOMO	7.60 (0.0058)	5.96 (0.015)	4.66 (0.031)	3.86 (0.050)	0.98 (0.32)	0.33 (0.57)	12.07 (0.0005)	+
WESJ	3.16 (0.076)	2.59 (0.11)	0.02 (0.88)	1.80 (0.18)	4.33 (0.037)	1.00 (0.32)	5.93 (0.015)	+

† See Appendix 1.1 for full species names and scientific names.

* Evaluated at maximum significant radius of urbanization proportion.

Table 1.2. Final GEE Poisson regression models: significant ($p < 0.05$) parameter estimates and score tests for significance of combined urbanization variables and overall models.

Species†	Year	Urban Edge Distance (ln)	Trail Density (250m buffer)	Urbanization Proportion (buffer distance)	Fragmentation Index (buffer distance)	Urbanization Proportion x Edge Distance*	Urbanization Score Test (p-value)	Total Model Score Test (p-value)
<i>Chaparral Specialists</i>								
ATFL (Std. Error)	0.42 (0.13)			-1.80 (0.43)			14.57 (0.0001)	18.77 (<0.0001)
	1997 > 1996			(1000m)				
BEWR (Std. Error)	0.23 (0.07)			-6.93 (1.78)		1.30 (0.35)	7.59 (0.023)	17.91 (0.005)
	1997 > 1996			(1000m)				
CALT (Std. Error)				-0.75 (0.25)			8.48 (0.0036)	8.48 (0.0036)
				(1000m)				
CAQU (Std. Error)								
CATH (Std. Error)	0.24 (0.08)	0.11 (0.05)	-0.025 (0.01)				7.11 (0.029)	12.71 (0.0053)
	1997 > 1996							
OCWA (Std. Error)	1.06 (0.43)	-0.48 (0.19)					9.90 (0.0071)	9.90 (0.0071)
	1997 > 1996							

† See Appendix 1.1 for full species names and scientific names.

* Urbanization proportion evaluated at maximum significant radius.

Table 1.2. (continued)

Species†	Year	Urban Edge Distance (ln)	Trail Density (250m buffer)	Urbanization Proportion (buffer distance)	Fragmen-tation Index (buffer distance)	Urbanization Proportion x Edge Distance*	Urbanization Score Test Chi-Square (p-value)	Total Model Score Test Chi-Square (p-value)
<i>Chaparral Specialists</i>								
PHAI		-1.19				-0.93	11.50	20.47
(Std. Error)		(0.23)				(0.31)	(0.0007)	(<0.0001)
	1996 > 1997							
RCSP		0.96	-0.10	-12.29	1.86		11.85	16.15
(Std. Error)		(0.35)	(0.040)	(4.725)	(0.42)		(0.0027)	(0.0011)
	1997 > 1996			250m	(2000m)			
SPTO		0.14		-2.91	1.86		10.77	12.65
(Std. Error)		(0.06)		(0.58)	(0.42)		(0.0046)	(0.0054)
	1997 > 1996			(2000m)	(2000m)			
WREN		0.07	-0.02	-5.76		0.85	13.93	16.57
(Std. Error)		(0.03)	(0.007)	(1.96)		(0.38)	(0.003)	(0.0023)
	1997 > 1996			(500m)				
<i>Riparian Species</i>								
BHGR		0.43		-2.79			13.19	18.53
(Std. Error)		(0.14)		(0.77)			(0.0003)	(<0.0001)
	1997 > 1996			(1000m)				
NOFL								
(Std. Error)								

† See Appendix 1.1 for full species names and scientific names.

* Urbanization proportion evaluated at maximum significant radius.

Table 1.2. (continued)

Species†	Year	Urban Edge Distance (ln)	Trail Density (250m buffer)	Urbanization Proportion (buffer distance)	Fragmen-tation Index (buffer distance)	Urbanization x Edge Distance*	Urbanization Score Test Chi-Square (p-value)	Total Model Score Test Chi-Square (p-value)
<i>Oak Woodland Species</i>								
BGN				-12.47		1.50	21.50	21.50
(Std. Error)				(4.29)		(0.73)	(<0.0001)	(<0.0001)
				(4000m)				
NUWO								
(Std. Error)								
OATI								
(Std. Error)								
<i>Suburban Species</i>								
MODO								
(Std. Error)								
NOMO		0.47	-1.02			0.44	22.25	24.79
(Std. Error)		(0.19)	(0.16)			(0.14)	(<0.0001)	(<0.0001)
		1997 > 1996						
WESJ		0.28		0.38			4.02	19.42
(Std. Error)		(0.08)		(0.19)			(0.045)	(<0.0001)
		1997 > 1996		(4000m)				

† See Appendix 1.1 for full species names and scientific names.

* Urbanization proportion evaluated at maximum significant radius.

Table 1.3. Mean parameter estimates and 95% confidence intervals from bootstrap resampling ($k=50$) of repeated measures Poisson models. Parameter estimates in bold are robust (significantly different from zero). Scaled-down models are also shown when original models are not robust.

Species†	Year	Urban Edge Distance (ln)	Trail Density (250m buffer)	Urbanization Proportion (buffer distance)	Fragmentation Index (buffer distance)	Urbanization Proportion x Edge Distance*
<i>Chaparral Specialists</i>						
ATFL (95% CI)	0.22 (-0.30, 0.73)			-1.89 (-3.26, -0.51) (1000m)		
BEWR (95% CI)				-7.92 (-13.08, -2.75) (1000m)		1.50 (0.50, 2.51)
CALT (95% CI)				-0.78 (-1.534, -0.026) (1000m)		
CATH - 1 (95% CI)	0.11 (-0.17, 0.38)	0.11 (-0.021, 0.246)	-0.03 (-0.06, 0.005)			
CATH - 2 (95% CI)	0.11 (-0.17, 0.38)	0.11 (-0.03, 0.25)				
PHAI (95% CI)	-0.62 (-1.96, 0.71)					-1.03 (-2.03, -0.02)

† See Appendix 1.1 for full species names and scientific names.

* Urbanization proportion evaluated at maximum significant radius.

Table 1.3. (continued)

Species†	Year	Urban Edge Distance (ln)	Trail Density (250m buffer)	Urbanization Proportion (buffer distance)	Fragmentation Index (buffer distance)	Urbanization Proportion x Edge Distance*
<i>Chaparral Specialists</i>						
RCSP - 1 (95% CI)	0.46 (-0.70, 1.2)		-0.10 (-0.22, 0.02)	-14.04 (-31.96, 3.89) (250m)		
RCSP - 2 (95% CI)	0.50 (-0.74, 1.75)			-15.22 (-33.25, 2.80) (250m)		
SPTO (95% CI)	0.07 (-0.11, 0.25)			-3.23 (-4.96, -1.50) (2000m)	2.05 (0.79, 3.31) (2000m)	
WREN - 1 (95% CI)	0.03 (-0.06, 0.13)		-0.02 (-0.04, 0.0002)	-6.13 (-14.09, 1.82) (500m)		0.91 (-0.62, 2.43)
WREN - 2 (95% CI)	-0.03 (-0.12, 0.06)		-0.02 (-0.04, -0.0005)	-1.54 (-2.18, -0.89) (500m)		
<i>Riparian Species</i>						
BHGR (95% CI)	0.23 (-0.30, 0.75)			-2.87 (-5.06, -0.67) (1000m)		

† See Appendix 1.1 for full species names and scientific names.

* Urbanization proportion evaluated at maximum significant radius.

Table 1.3. (continued)

Species†	Year	Urban Edge Distance (ln)	Trail Density (250m buffer)	Urbanization Proportion (buffer distance)	Fragmentation Index (buffer distance)	Urbanization Proportion x Edge Distance*
<i>Oak Woodland Species</i>						
BGGN - 1 (95% CI)				-12.09 (-24.17, -0.003) (4000m)		1.40 (-0.72, 3.53)
BGGN - 2 (95% CI)				-4.03 (-6.04, -2.01) (4000m)		
<i>Suburban Species</i>						
NOMO (95% CI)	0.25 (-0.39, 0.89)	-1.15 (-1.64, -0.67) (2000m)				0.40 (0.003, 0.79)
WESI (95% CI)	0.14 (-0.19, 0.47)			0.34 (-0.15, 0.84) (4000m)		

† See Appendix 1.1 for full species names and scientific names.

* Urbanization proportion evaluated at maximum significant radius.

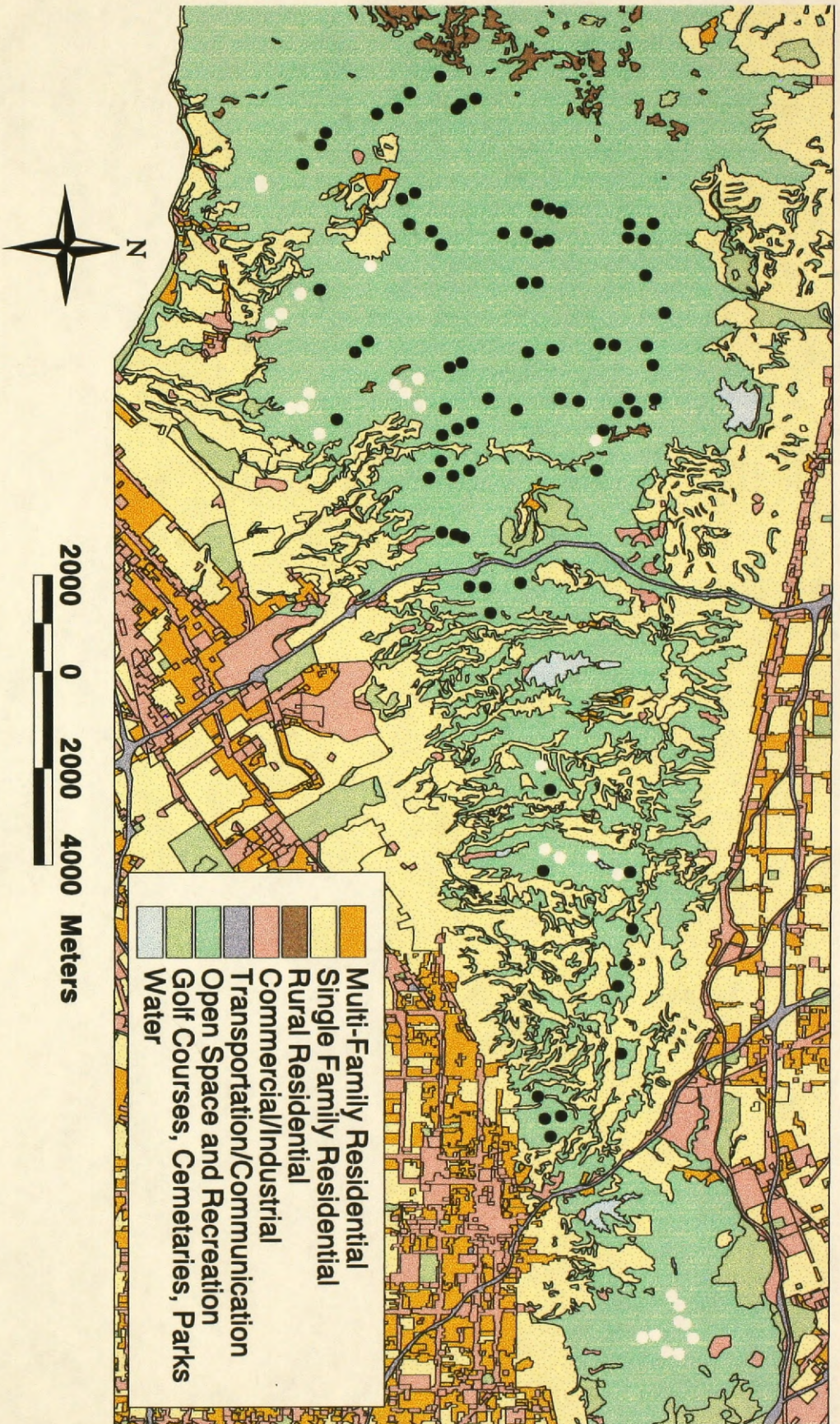


Figure 1.1. Study Area Land Uses. Green areas contain chaparral and other native vegetation types. Point count locations censused in 1996 and 1997 are shown in black; locations in white were added in 1997.

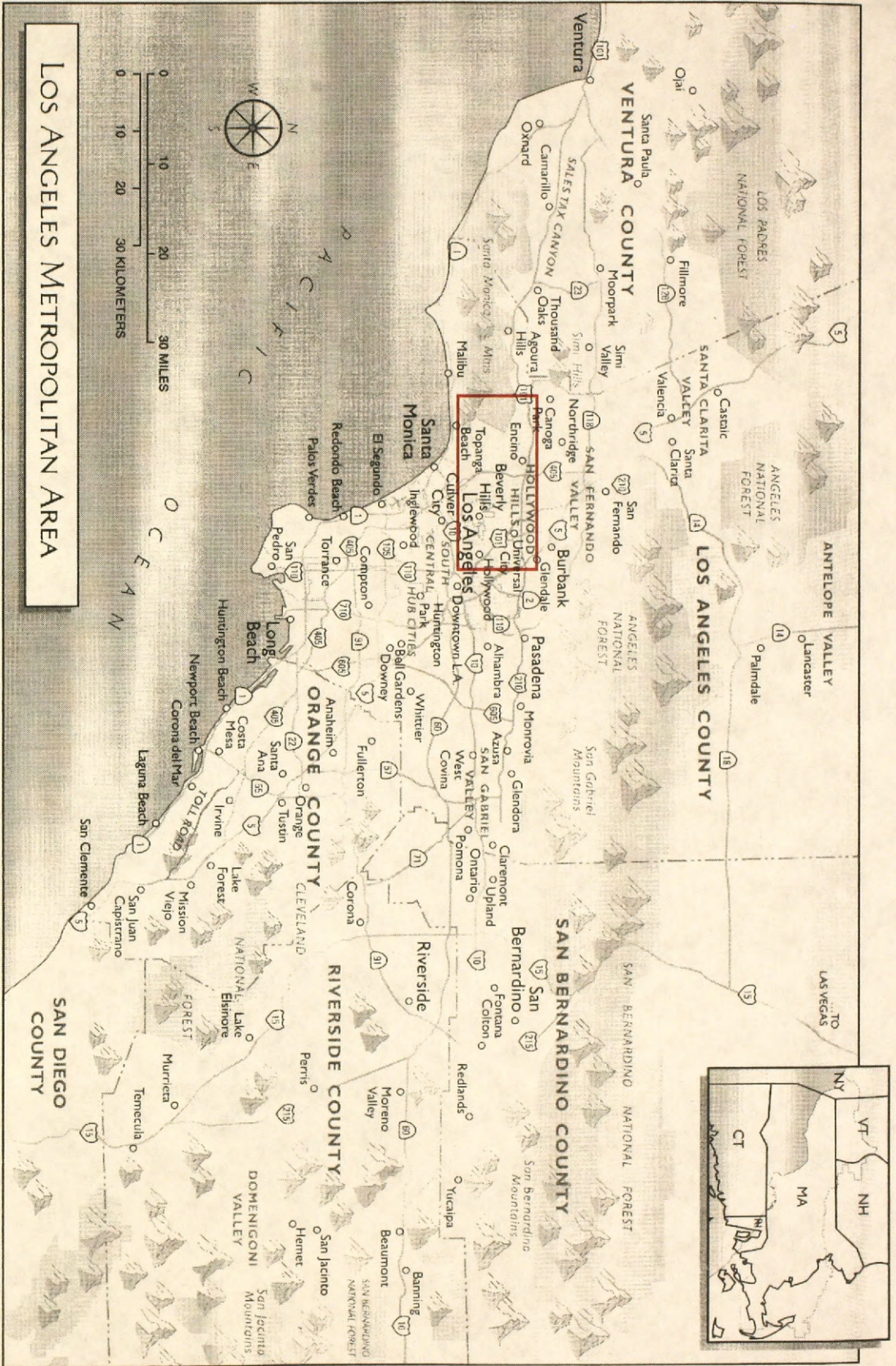


Figure 1.2. Los Angeles Metropolitan Area (from Fulton 1997). Study area outlined in red.

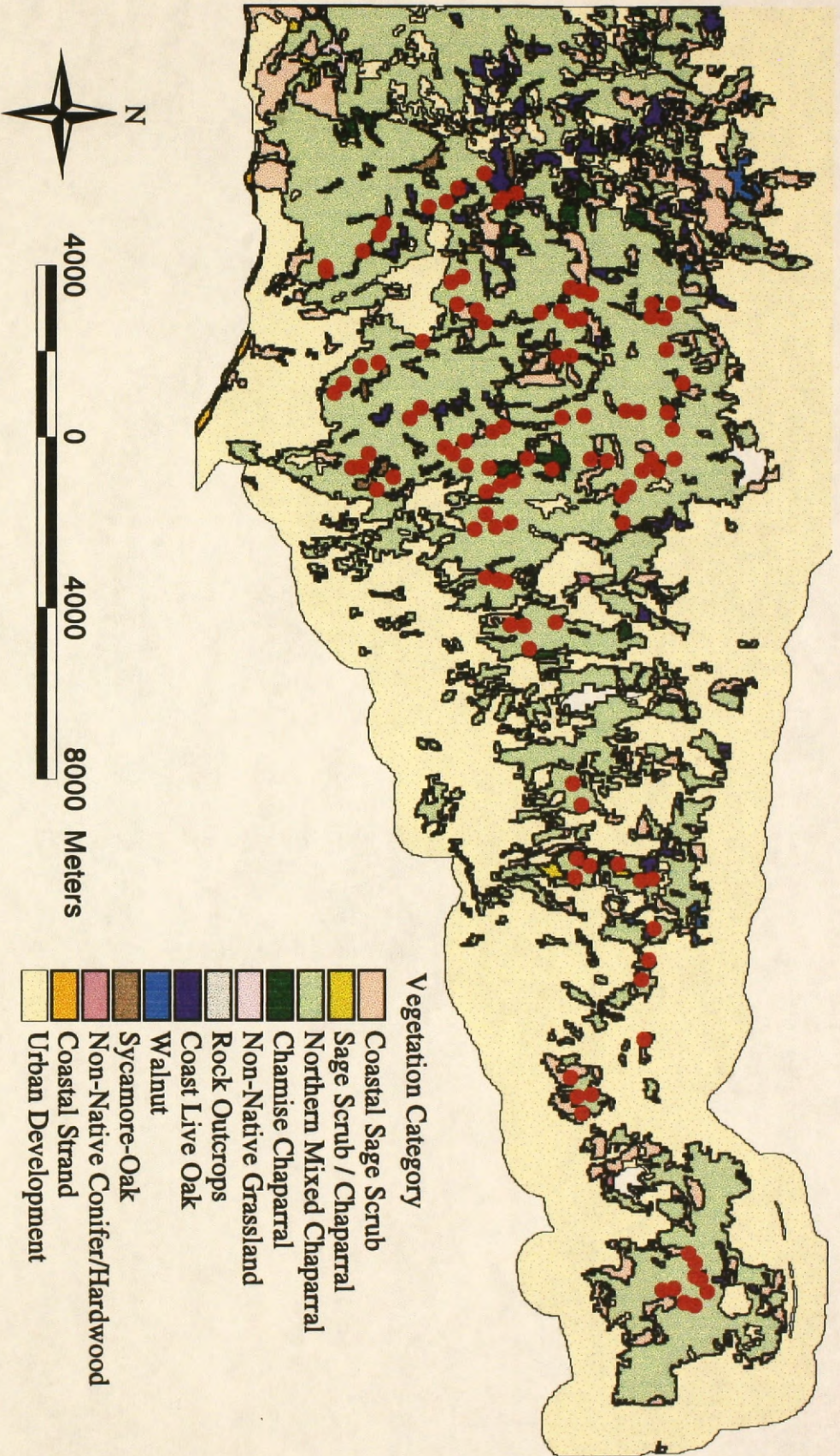


Figure 1.3. Vegetation classification within study area. Point count locations indicated in red.

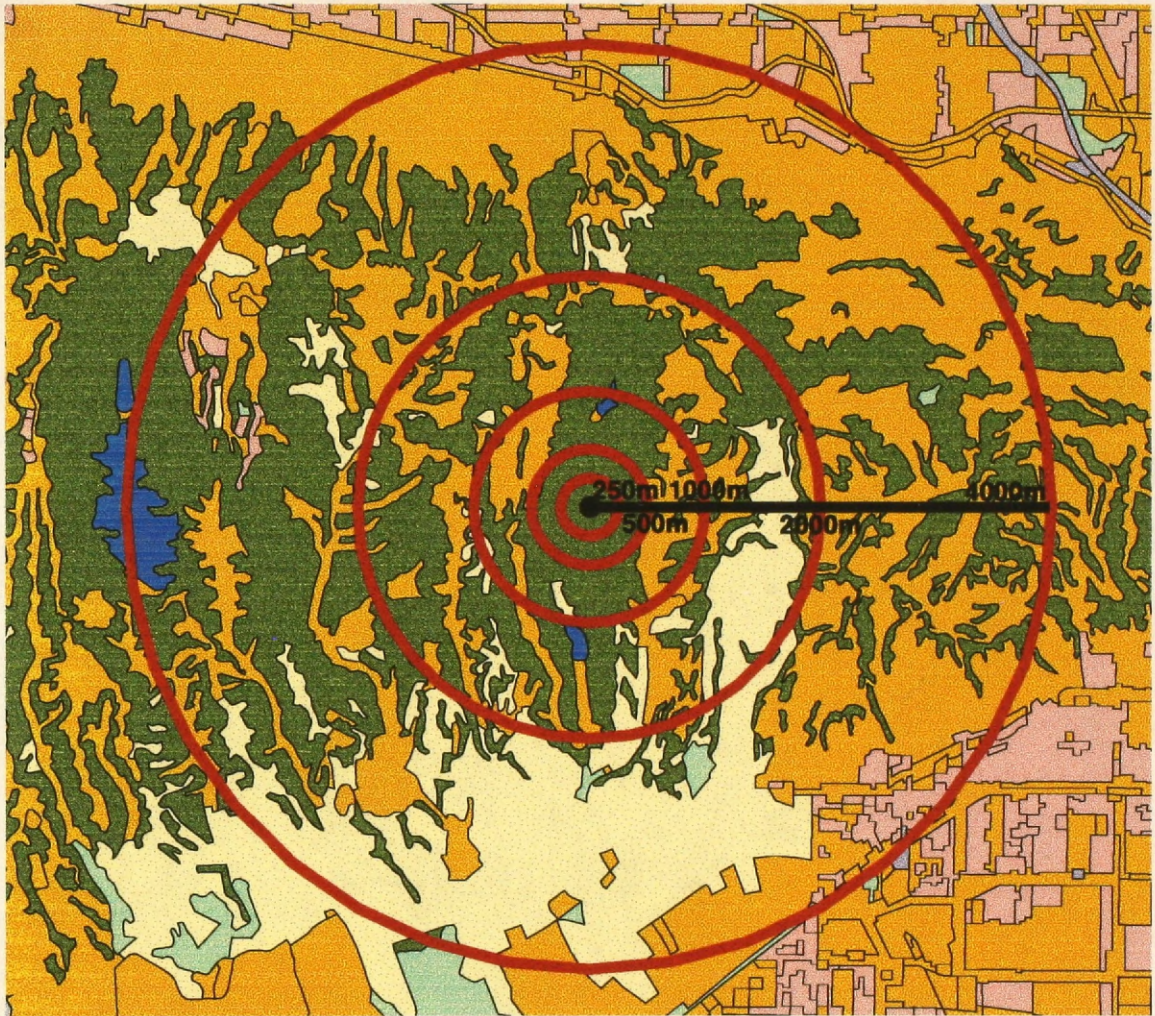


Figure 1.4. 250m-500m-1000m-2000m-4000m buffer rings used to calculate urbanization proportion and fragmentation index.

Appendix 1.1. Avian species recorded during study (swifts, swallows and raptors not included), in alphabetical order, according to AOU code.

AOU Code	Common Name (<i>Scientific Name</i>)	Migratory Status	Years Observed	Years Counted	Groups Counted*
ALHU	Allen's Hummingbird (<i>Selasphorus sasin</i>)	Long-distance migrant	1996, 1997	1997	T
AMCR	American Crow (<i>Corvus brachyrhynchos</i>)	Resident	1996, 1997	1996, 1997	T
ANHU	Anna's Hummingbird (<i>Calypte anna</i>)	Resident	1996, 1997	1997	T
ATFL	Ash-Throated Flycatcher (<i>Myiarchus cinerascens</i>)	Long-distance migrant	1996, 1997	1996, 1997	T, S
BCHU	Black-Chinned Hummingbird (<i>Archilochus alexandri</i>)	Long-distance migrant	1996, 1997	1997	T
BEWR	Bewick's Wren (<i>Thryomanes bewickii</i>)	Resident	1996, 1997	1996, 1997	T, S
BGGN	Blue-Gray Gnatcatcher (<i>Polioptila caerulea</i>)	Resident	1996, 1997	1996, 1997	T
BHGR	Black-Headed Grosbeak (<i>Pheucticus melanocephalus</i>)	Long-distance migrant	1996, 1997	1996, 1997	T, S
BLPH	Black Phoebe (<i>Sayornis nigricans</i>)	Resident	1996, 1997	1996, 1997	T
BUSH	Bushtit (<i>Psaltriparus minimus</i>)	Resident	1996, 1997		N/A
CAQU	California Quail (<i>Callipepla californica</i>)	Resident	1996, 1997	1996, 1997	S
CATH	California Thrasher (<i>Toxostoma redivivum</i>)	Resident	1996, 1997	1996, 1997	T, S
CALT	California Towhee (<i>Pipilo crissalis</i>)	Resident	1996, 1997	1996, 1997	T

* T = total individuals, S = singing males.

Appendix 1.1. (continued)

AOU Code	Common Name (<i>Scientific Name</i>)	Migratory Status	Years Observed	Years Counted	Groups Counted
CANW	Canyon Wren (<i>Catherpes mexicanus</i>)	Resident	1996, 1997	1996, 1997	T, S
CORA	Common Raven (<i>Corvus corax</i>)	Resident	1996, 1997	1996, 1997	T
COYE	Common Yellowthroat (<i>Geothlypis trichas</i>)	Long-distance migrant	1997	1997	T, S
HOFI	House Finch (<i>Carpodacus mexicanus</i>)	Resident	1996, 1997	1996, 1997	S
HOOR	Hooded Oriole (<i>Icterus cucullatus</i>)	Long-distance Migrant	1996, 1997	1996, 1997	T, S
HOWR	House Wren (<i>Troglodytes aedon</i>)	Resident	1996, 1997	1996, 1997	T, S
HUVI	Hutton's Vireo (<i>Vireo huttoni</i>)	Long-distance migrant	1996, 1997	1996, 1997	T, S
LEGO	Lesser Goldfinch (<i>Carduelis psaltria</i>)	Resident	1996, 1997		N/A
LOSH	Loggerhead Shrike (<i>Lanius ludovicianus</i>)	Long-distance migrant	1996	1996	T
MODO	Mourning Dove (<i>Zenaida macroura</i>)	Resident	1996, 1997	1996, 1997	T
NOFL	Northern Flicker (<i>Colaptes auratus</i>)	Resident	1996, 1997	1996, 1997	T
NOMO	Northern Mockingbird (<i>Mimus polyglottos</i>)	Resident	1996, 1997	1996, 1997	T, S
NUWO	Nuttall's Woodpecker (<i>Picoides nuttallii</i>)	Resident	1996, 1997	1996, 1997	T
OATI	Oak Titmouse (<i>Baeolophus inornatus</i>)	Resident	1996, 1997	1996, 1997	T

* T = total individuals, S = singing males.

Appendix 1.1. (continued)

AOU Code	Common Name (<i>Scientific Name</i>)	Migratory Status	Years Observed	Years Counted	Groups Counted
OCWA	Orange-Crowned Warbler (<i>Vermivora celata</i>)	Resident	1996, 1997	1996, 1997	T, S
PHAI	Phainopepla (<i>Phainopepla nitens</i>)	Resident / Local migrant	1996, 1997	1996, 1997	T, S
PSFL	Pacific Slope Flycatcher (<i>Empidonax difficilis</i>)	Long-distance migrant	1996, 1997	1996, 1997	T, S
RCSP	Rufous-Crowned Sparrow (<i>Aimophila ruficeps</i>)	Resident	1996, 1997	1996, 1997	T, S
SOSP	Song Sparrow (<i>Melospiza melodia</i>)	Resident	1996, 1997	1996, 1997	T, S
SPTO	Spotted Towhee (<i>Pipilo maculatus</i>)	Resident	1996, 1997	1996, 1997	T, S
WEKI	Western Kingbird (<i>Tyrannus verticalis</i>)	Long-distance migrant	1997	1997	T
WESJ	Western Scrub-Jay (<i>Aphelocoma californica</i>)	Resident	1996, 1997	1996, 1997	T
WETA	Western Tanager (<i>Piranga ludoviciana</i>)	Long-distance migrant	1996	1996	T
WREN	Wrentit (<i>Chamaea fasciata</i>)	Resident	1996, 1997	1996, 1997	T, S
YEWA	Yellow Warbler (<i>Dendroica petechia</i>)	Long-distance migrant	1997	1997	T

* T = total individuals, S = singing males.

Appendix 1.2. Commonly-Occurring Species, in Order of Total Abundance. Summary Statistics.

Species*†	Total (all counts)	1996 (n = 78)										1997 (n = 107)									
		Count 1	Count 2	Total abundance	# of sites	Site occupancy	Mean per site	Std. Error	Median	Max. per site	Total abundance	# of sites	Site occupancy	Mean per site	Std. Error	Median	Max. per site				
WREN (S)	1821	327	409	78	100%	4.19	0.19	4	8	490	107	100%	4.58	0.17	5	9					
		Count 2		77	99%	5.24	0.22	5	10	595	106	99%	5.56	0.20	6	10					
		Maximum		78	100%	5.68	0.19	6	10		107	100%	5.99	0.19	6	10					
SPTO (S)	898	254	71	74	96%	3.26	0.19	3	9	385	106	99%	3.60	0.16	3	9					
		Count 2		61	79%	0.91	0.14	0	6	188	95	89%	1.76	0.14	2	6					
		Maximum		75	97%	3.31	0.20	3	9		106	99%	3.70	0.16	4	9					
CALT (T)	740	129	181	0.9	95%	1.65	0.15	1	5	176	92	86%	1.64	0.12	1	5					
		Count 2		66	85%	2.32	0.19	2	6	254	95	89%	2.37	0.17	2	9					
		Maximum		74	95%	2.69	0.18	2	6		103	96%	2.79	0.15	3	9					
CATH (T)	600	52	150	35	45%	0.67	0.10	0	3	150	83	78%	1.40	0.11	1	5					
		Count 2		63	81%	1.92	0.17	2	6	248	96	90%	2.32	0.14	2	7					
		Maximum		71	91%	2.13	0.15	2	6		104	97%	2.64	0.13	3	7					
WESJ (T)	584	87	107	53	68%	1.12	0.12	1	3	178	88	82%	1.66	0.11	2	5					
		Count 2		58	74%	1.37	0.13	1	5	212	92	86%	1.98	0.13	2	6					
		Maximum		71	91%	1.81	0.12	2	5		104	97%	2.45	0.12	2	6					

* T = total individuals, S = singing males.

† See Appendix 1.1 for full species names and scientific names.

Appendix 1.2. (continued)

Species*†	Total (all counts)	1996 (n = 78)										1997 (n = 107)									
		Total abundance	# of sites	Site occupancy	Mean per site	Std. Error	Median	Max. per site	Total abundance	# of sites	Site occupancy	Mean per site	Std. Error	Median	Max. per site						
BEWR (S)	571	Count 1	103	65	84%	1.32	0.12	1	4	219	105	98%	2.05	0.12	2	5					
		Count 2	108	70	91%	1.38	0.14	1	5	141	101	94%	1.32	0.11	1	4					
		Maximum		77	100%	1.96	0.12	2	5		107	100%	2.49	0.10	2	5					
ATFL (S)	167	Count 1	30	25	32%	0.38	0.07	0	2	38	53	50%	0.49	0.08	0	3					
		Count 2	38	36	47%	0.49	0.08	0	3	61	63	59%	0.57	0.07	0	3					
		Maximum		47	61%	0.72	0.09	1	3		82	77%	1.07	0.08	1	3					
BHGR (S)	160	Count 1	45	42	55%	0.58	0.07	0.5	2	86	65	61%	0.80	0.08	1	3					
		Count 2	4	8	10%	0.05	0.03	0	2	25	28	26%	0.23	0.04	0	2					
		Maximum		45	58%	0.60	0.07	1	2		73	68%	0.90	0.08	1	3					
MODO (T)	143	Count 1	33	25	32%	0.42	0.08	0	4	41	33	31%	0.38	0.07	0	4					
		Count 2	22	15	19%	0.28	0.09	0	5	47	32	30%	0.44	0.07	0	3					
		Maximum		35	45%	0.64	0.11	0	5		53	50%	0.70	0.08	0	4					
NOMO (S)	127	Count 1	21	16	21%	0.27	0.07	0	4	51	32	30%	0.48	0.09	0	5					
		Count 2	16	13	17%	0.21	0.06	0	3	39	27	25%	0.36	0.07	0	4					
		Maximum		19	25%	0.35	0.09	0	4		39	36%	0.58	0.09	0	5					

* T = total individuals, S = singing males.

† See Appendix 1.1 for full species names and scientific names.

Appendix 1.2. (continued)

Species*†	1996 (n = 78)										1997 (n = 107)						
	Total (all counts)	Total abundance	# of sites	Site occupancy	Mean per site	Std. Error	Median	Max. per site	Total abundance	# of sites	Site occupancy	Mean per site	Std. Error	Median	Max. per site		
PHAI (T)	117	57	30	38%	0.73	0.13	0	5	17	12	11%	0.16	0.05	0	3		
	Count 1	29	16	21%	0.37	0.10	0	5	14	12	11%	0.13	0.04	0	2		
	Maximum		42	39%	0.72	0.11	0	5		20	19%	0.24	0.05	0	3		
NOFL (T)	95	19	12	15%	0.24	0.08	0	4	22	21	20%	0.21	0.04	0	2		
	Count 1	25	22	28%	0.32	0.06	0	2	29	28	26%	0.27	0.05	0	2		
	Maximum		28	36%	0.49	0.09	0	4		42	39%	0.41	0.05	0	2		
RCSP (T)	83	7	6	8%	0.09	0.04	0	2	38	28	26%	0.36	0.08	0	6		
	Count 1	10	6	8%	0.13	0.06	0	3	28	21	20%	0.26	0.06	0	2		
	Maximum		12	15%	0.22	0.09	0	6		39	36%	0.51	0.08	0	6		
NUWO (T)	78	9	9	12%	0.12	0.04	0	1	21	20	19%	0.20	0.04	0	2		
	Count 1	21	15	19%	0.27	0.07	0	3	27	26	24%	0.25	0.04	0	2		
	Maximum		22	28%	0.36	0.07	0	3		39	36%	0.38	0.05	0	2		
BGGN (T)	67	19	17	22%	0.24	0.06	0	2	17	14	13%	0.16	0.04	0	2		
	Count 1	11	9	12%	0.14	0.05	0	2	20	18	17%	0.19	0.04	0	2		
	Maximum		25	32%	0.37	0.03	0	1		29	27%	0.32	0.05	0	2		

* T = total individuals, S = singing males.

† See Appendix 1.1 for full species names and scientific names.

Chapter 2:
Examination and Modeling of Spatial Structure
in Selected Chaparral Bird Species

2.1. Introduction

Increasingly, many large-scale ecological studies involve an explicit spatial component. With the growing availability and sophistication of Geographic Information Systems (GIS), as well as portable, inexpensive Geographic Positioning Systems (GPS), ecologists can now georeference their sampling locations relatively easily and accurately.

Oftentimes, however, this extra information is not used to its full potential. In ecology, GIS has been used primarily as a map presentation tool, facilitating the visualization of spatial variables and relationships among them. Commonly, spatial data are analyzed using simple statistical methods that ignore the underlying spatial structure and often improperly assume independence among sampling locations. This tendency is likely due to the statistical complexity and computation-intensiveness of many spatial statistical techniques, as well as their lack of widespread acceptance. But the omission of spatial dependence in statistical analyses can be problematic for the interpretation of results, and may result in biased model parameter estimates (Robertson 1987, Anselin 1989) and false detection of significant relationships (Legendre 1993).

This is not to say that spatial patterns in nature have not been widely studied. Indeed, there is a long history of quantitative spatial analysis in ecology, with the description and explanation of regional and continent-wide vegetation distributions dating at least back to Von Humboldt (1807). Large-scale biogeographic vegetation trends have been explained largely by variation in soils, topography, and especially climate (e.g., DeCandolle 1874, Warming 1895, Merriam 1898, Gleason 1917, Whittaker 1956, Peet and Loucks 1977, Delcourt and Delcourt 1988, Davis and Zabinski 1992, Holling 1992). Factors controlling the distributions of animal species (Andrewartha and Birch 1954, Simpson 1964, MacArthur 1972, Bock 1984, Root 1988), and the relationships between distributions and

abundance (Cook 1969, Brown 1984, Bock 1987, Maurer 1990, Brown et al. 1995), have also been studied and modeled. Avian range distributions, in particular, have received considerable attention (Terborgh 1971, Bock 1984, Root 1988, Maurer and Heywood 1993, Lawton et al. 1994).

At the local scale, spatial dependence in the distribution of plants and other sessile organisms is well recognized by theoretical ecologists. A variety of heterogeneity- and aggregation-promoting mechanisms have been proposed, modeled and field-tested, including disturbance-recovery dynamics (Paine and Levin 1981), dispersal limitation (Levin et al. 1984), spatially subdivided resource competition (Roughgarden 1974, Tilman 1994), and predator-prey dynamics (Levin 1976, 1978). Mobile organisms are, almost by definition, more difficult to describe spatially. With the increasing speed and power of raster GIS technology, however, spatially-explicit population models (SEPMs), incorporating (cell-based) movement as well as spatial location of individuals, are becoming more sophisticated and useful (e.g., Pulliam et al., 1992, Turner et al. 1993, Dunning et al. 1995, Holt et al. 1995).

Until recently, however, there has been little focus on intermediate scales—those much smaller than a species range, yet large enough that individual dynamics become obscured by aggregate patterns (but see Watt 1947). For many species, this intermediate scale occurs at the landscape level—an admittedly broad term, with different definitions in different contexts. The landscape scale has significance, however, because it is inherently human-defined, and often coincides with the scale of anthropogenic land-use change. Within the last decade, often with the help of GIS technology, greater efforts have been made to describe the spatial patterning of organisms across landscapes (e.g., Swanson et al. 1988, O'Neill et al. 1991, Ward and Saltz 1994, Cherrill et al. 1995, Fortin et al. 1996) and the processes driving those patterns (e.g., Kareiva and Wennergren 1995, Turner et al. 1997). When spatial pattern is not the primary focus, however, it is often ignored altogether. This is especially true of studies examining the effects of human disturbance.

This study addresses some of the above-named shortcomings in the analysis of spatial ecological data. My primary goal is to determine how selected passerine bird species respond to increasing levels of urbanization (residential development) in a mountain landscape facing encroachment on three sides by metropolitan Los Angeles. Previously, I used standard statistical analyses to answer this question (Chapter 1). Here I also examine large-scale spatial trends and small-scale heterogeneity in a landscape-level spatial statistical analysis of avian responses to urbanization. Most of the bird species under study are particularly well-suited to this type of analysis, as they are year-round residents with low vagility and high territoriality (Soulé et al. 1988), and can therefore be modeled as fixed points in space.

2.1.1. Types and Sources of Spatial Dependence in Animal Populations

Spatial dependence can occur at different scales, which may be indicative of the process(es) driving the observed spatial patterns. Generally speaking, however, spatial autocorrelation in a data set indicates the presence of small-scale spatial dependence due to the interdependence of neighboring sites (Cressie 1991, MathSoft 1996). Small-scale spatial dependence is generally stochastic in origin and therefore difficult to predict. Conversely, large-scale spatial dependence refers to a predictable pattern or spatial trend (Cressie 1991), also known as “structural” spatial dependence (Rossi et al. 1992), which is often related to underlying physiographic features.

Large-scale spatial dependence in a species’ distribution and abundance may reflect “continuous biogeographical dispersion routes” (Carroll and Pearson 1998), as well as underlying trends in the abiotic environment (e.g., topography, substrate, climate) that are generated slowly over geologic time (Brown 1984). Small-scale dependence tends instead to reflect patchiness in the biotic environment, stemming from stochastic disturbance events or complex species interactions that occur on an ecological time scale (O’Neill et al. 1991, Wiens 1981). Adding to the complexity of spatial dependence are intraspecific factors like non-selective dispersal, time lags in population dynamics, and density-dependent behaviors (e.g., territoriality, flocking) (Brown et al. 1995). These small-scale

biological interactions may introduce temporal and/or spatial lags, decoupling a system from underlying geophysical factors (Wiens 1989) and making spatial variability difficult to predict. At large scales, however, physical processes often overshadow the biological (Wiens 1989).

As a result of these and other sources of spatial dependence, animal populations are likely to be non-uniformly distributed across a landscape, and may contain variations in abundance that are not easily explained by environmental factors. The existence of spatial heterogeneity suggests that sampling locations across a landscape may not be equally independent of one another. Rather, sites that are closer in spatial proximity are likely to be more similar in species abundance (Brown 1984, Rossi et al. 1992). Thus, a fundamental statistical assumption is violated when populations exhibit significant spatial dependence. This leads to an over-specification of degrees of freedom, and an increased probability of rejecting a valid null hypothesis (type I or α error), meaning that results may too often be declared significant (Legendre 1993).

One must therefore control for spatial location when analyzing relationships between spatially distributed ecological variables. The detection of spatial autocorrelation in model residuals indicates the presence of an additional explanatory variable, which may or may not be measurable. When this variable is not measurable, the spatial autocorrelation may instead be explicitly modeled. Spatial regression models eliminate correlation in the residuals, so that assumptions are met and significance tests are valid. Large-scale trends, which are easily misinterpreted as autocorrelation, should be investigated before spatial autocorrelation is modeled (Legendre and Fortin 1989). Semivariograms, correlograms, and other “structure functions” (Yaglom 1957) can help identify these trends.

The purpose of this study is to investigate the importance of both small- and large-scale spatial dependence in a landscape-level spatial data set, thereby providing an example of how simple spatial statistics may be used to construct improved models of species abundance.

2.1.2. Tools for Investigating Spatial Structure and Autocorrelation

Several methods have been used to examine spatial structure and detect scales of influence in ecological data. Scale detection has received particular attention among landscape ecologists (e.g., Carlile et al. 1989, Turner 1989, Wiens 1989, Moloney et al. 1991, O'Neill et al. 1991, Cullinan and Thomas 1992, Levin 1992), with respect to both simulated and actual landscapes. Methods used to examine scales of spatial pattern include spectral analysis (Ripley 1978), variance ratio analysis (Carlile et al. 1989), Hill analysis (Hill 1973), and fractal dimension (Sugihara and May 1990), each of which has its strengths and weaknesses. No one method seems to provide consistently good estimates of scale, and consequently the use of more than one method is recommended (O'Neill et al. 1991, Cullinan and Thomas 1992).

Another class of tools for analyzing spatial structure comes from the field of geostatistics and the generalized regional variable model (Matheron 1963). Geostatistics theory is most commonly used in "kriging," a method for interpolating the values of a variable over the geographic area from which the sample was taken by incorporating a semivariogram model for spatial correlation. Related to the semivariogram are the covariogram and the correlogram. Each of these "structure functions" may be used to describe the spatial dependence between sampling points at various "lag distances" or distance classes, and to detect spatial trends in the data.

The Semivariogram

The semivariance function $\gamma(h)$ (Matheron 1963) is estimated by one-half the average squared difference between points separated by a distance h , calculated as:

$$\gamma(h) = \frac{\sum_{i=1}^{|N(h)|} \sum_{j=1}^{|N(h)|} (z_i - z_j)^2}{2 |N(h)|}, \quad (2.1)$$

where $N(h)$ is the set of all pairwise Euclidean distances $i - j = h$, $|N(h)|$ is the number of distinct pairs in $N(h)$, and z_i and z_j are data values at spatial locations i and j , respectively (Cressie 1991, MathSoft 1996).

A semivariogram is a plot of the semivariance function for increasing lag distances.

Standard semivariograms are omnidirectional, but directional semivariograms, where γ is a function of the direction as well as magnitude of h , may also be examined if the spatial autocorrelation of a variable changes with direction—a property referred to as “anisotropy” (lack of “isotropy”). In this case, the set of data pairs, $N(h)$ is defined by direction as well as distance.

The semivariance represents the portion of the population variance that is not explained by spatial autocorrelation. Thus in a system with no spatial dependence, the semivariance is constant and equal to the population variance (σ^2). For most spatial data, however, the semivariogram increases with distance until it converges at a “sill,” which corresponds to the population variance. The distance at which the sill is reached and data are no longer autocorrelated is called the “range” (Cressie 1991; see Figure 2.1). The range may be interpreted as a *maximum* autocorrelation distance, while autocorrelation is generally *strongest* at the distance for which the semivariogram slope is steepest (Robertson 1987). A semivariogram that fails to converge to a sill indicates that the variable of interest is non-stationary (non-constant mean and variance) and exhibits a large-scale trend over the area of interest (Legendre and Fortin 1989). The “nugget” of a semivariogram represents all unaccounted-for spatial variability at distances smaller than the smallest sampling distance, which may be due to micro-scale variation and/or measurement error (Rossi et al. 1992; see Figure 2.1). Several functions are typically used to model theoretical semivariograms, depending on the spatial structure of the variable. Some of the more commonly used functions are the spherical, exponential, linear and Gaussian models (see Figure 2.2).

An empirical semivariogram provides a graphical description of the autocorrelation structure in a sample of a particular variable, and can be used to estimate the theoretical semivariogram for the entire population, which is required for kriging. It does not lend itself to statistical hypothesis testing, however; nor is it standardized, so comparison of different models may be difficult. In addition, the semivariogram is sensitive to local mean and variance differences and is strongly affected by outliers, so it may provide an incomplete picture of spatial pattern (Rossi et al. 1992). Meisel and Turner (1998) found that the semivariogram acts best as a “high pass filter,” detecting coarse but not necessarily fine scale patterns, and that it is not particularly well-suited to the study of multiple scales of pattern. They also found it to be highly sensitive to data gaps.

Despite a relatively long kriging tradition in the mining and geology fields (e.g., David 1977, Journel and Huijbregts 1978), semivariograms have only recently been applied to ecological studies, where they have been useful for describing spatial structure and interpolating the values of ecological variables over space (e.g., Grieg-Smith 1983, Taylor 1984, Villard and Maurer 1996, Robertson et al. 1997, Meisel and Turner 1998).

The Covariogram and Correlogram

The empirical covariance function, $C(h)$, represents the portion of the population variance that is explained by spatial autocorrelation at lag distance h . It is defined by:

$$C(h) = \text{cov}(z_i, z_j) = \frac{\sum_{i=1}^{|N(h)|} \sum_{j=1}^{|N(h)|} (z_i - \bar{z})(z_j - \bar{z})}{|N(h)|} \quad (2.2)$$

When the population mean and variance are constant over the sampling space (i.e., the second-order stationarity assumption is met), then for any lag distance h , the semivariance, $\gamma(h)$, and the covariance, $C(h)$, add up to the population variance, σ^2 (Rossi et al. 1992). Thus the semivariogram and the covariogram (a plot of the covariance function against increasing lag distances) are inversely related. Under these same

conditions, the correlogram, $\rho(h)$, or standardized covariogram ($C(h)/\sigma^2$), is also directly related to the semivariogram (Rossi et al. 1992).

The term “correlogram” may also be used to refer to any plot of autocorrelation versus spatial lag distance (or temporal lags, in the case of time-series analysis). Thus correlograms for spatial data may also be constructed using other standardized measures of autocorrelation. A commonly used autocorrelation index, related to $\rho(h)$, is Moran’s I statistic (Moran 1950). Moran’s I, which generally ranges from -1 to 1, is similar in interpretation to a Pearson’s Product Moment correlation statistic, with the numerator consisting of a sum of cross-products (Legendre and Fortin 1989). For a given distance class h , Moran’s statistic, $I(h)$, is defined as:

$$I(h) = \frac{\left[n \sum_{i=1}^n \sum_{j=1}^n w_{ij} (z_i - \bar{z})(z_j - \bar{z}) \right]}{\left[\sum_{i=1}^n \sum_{j=1}^n w_{ij} \sum_{i=1}^n (z_i - \bar{z})^2 \right]}, \quad (2.3)$$

where w_{ij} takes on the value 1 when the pair (i,j) pertains to distance class h , and 0 otherwise; n is the number of sampling locations (Fortin 1989). Because they are standardized, correlograms may easily be compared. A Moran’s I correlogram can also be tested for statistical significance, making it less subjective than the semivariogram for describing spatial structure and detecting autocorrelation.

In terms of large-scale patterns, positive autocorrelation at small distances coupled with negative autocorrelation at large distances indicates the presence of a gradient, or large-scale trend. Negative values at large distances result from distant points being less similar than average, so that the semivariance is greater than the population variance (covariance = population variance - semivariance). Aggregated data may exhibit positive autocorrelation at distances corresponding to the gaps between patches or data clusters (Legendre and Fortin 1989), and zero or negative autocorrelation in between.

Correlograms for variables containing only small-scale spatial autocorrelation will quickly decrease and converge to or oscillate around zero.

With respect to small-scale patterns, the evaluation of autocorrelation statistics at various lag distances in a correlogram may be useful in determining the maximum scale of significant spatial autocorrelation. This may indicate the size of the “ecological neighborhood” for the species or phenomenon being investigated (Addicott et al. 1987), or the range of interaction between sites (Cressie 1991). This information can also be ascertained from a semivariogram, but not with any statistical certainty.

Recently, several ecological studies have made use of correlograms and spatial autocorrelation statistics for examining large- and small-scale spatial patterns (e.g., Legendre and Fortin 1989, Carroll and Pearson 1998, Koenig 1998, Koenig and Knops 1998).

2.1.3. Spatial Covariance Models

Ordinary least-squares regression analysis requires that model residuals are independent (Neter et al. 1989). When this assumption is violated, model parameter estimates may be biased (Robertson 1987, Anselin 1989), and confidence intervals too small (Legendre 1993). Upon detection of spatial dependence in regression model residuals using tests for spatial autocorrelation (e.g., Moran’s I), the spatial covariance structure of the residuals can be specified and modeled explicitly. Provided the residuals are stationary (i.e., no trend), then semivariograms and/or covariograms may be used to define the nature of spatial dependence in the residuals and estimate the appropriate spatial parameters.

One approach to spatial covariance modeling is based on geostatistical principles integrated with a mixed model framework (Zimmerman and Harville 1991, Littell et al. 1996). The regression model is of the form $y_i = \mu_i + e_i$, where y_i is the i^{th} observation and e_i is the corresponding error. If y_i occurs at location s_i , then the covariance structure is defined by assuming that the covariance of two locations, s_i and s_j , is a function of the distance between them (d_{ij}). The covariance model then takes on the general form:

$$\text{Cov}(e_i, e_j) = \sigma^2 [f(d_{ij})], \text{ with } \text{Var}(e_i) = \sigma^2 = \sigma_1^2 + \sigma_2^2 \quad (2.4)$$

Since the covariance and semivariance are directly related (under the assumption of stationarity), these parameters can be expressed in terms of semivariogram parameters: d is the range, σ^2 is the sill, σ_1^2 is the nugget, and σ_2^2 is the remaining variance, or partial sill (see Figure 2.1). The function $f(d_{ij})$ depends on the shape of the semivariogram, and is generally specified according to one of the models in Figure 2.2.

2.1.4. Objectives

In 1996, I initiated a study to assess the effects of landscape-level urbanization patterns on breeding-bird abundance in the Santa Monica Mountains of southern California. In recent decades, chaparral and other native communities within the Santa Monica Mountains have been experiencing urban encroachment from the surrounding Los Angeles metropolitan area. Currently, the area contains a mosaic of interspersed suburban development and native chaparral vegetation (see Figure 1.1). It presents a unique opportunity to study the effects of urban encroachment at its intermediate stage, before the native habitat is severely fragmented.

In my study area, the abundances of several chaparral- and woodland-associated bird species were negatively associated with levels of surrounding urbanization, while the abundances of two urban-associated species exhibited positive associations with surrounding urbanization (Chapter 1). Significant responses to large-scale landscape characteristics (i.e., surrounding urbanization proportion within radii up to 4000m) were observed in most of these species.

Because the bird census locations used in this study were distributed over a large (~17,000 ha) geographic area, they are unlikely to be completely independent. Small-scale spatial heterogeneity may result in spatially autocorrelated abundance. In addition, urbanization within the study area follows an east-west gradient. To better understand the relationship between urbanization and bird abundance, I posed the following research questions:

1. What is the nature of the spatial structure that characterizes the abundances of these chaparral birds?
2. Controlling for spatial structure, does surrounding urbanization affect breeding bird abundance?

2.2. Field Methods and Previous Results

Bird abundance data were collected during the summers of 1996 and 1997. A stratified random sample totaling 79 chaparral-vegetated sites was censused for birds in 1996 using 100-meter fixed radius point counts, and georeferenced with GPS readings (detailed field methods are given in Chapter 1). Twenty-eight sites were added in 1997 (totaling 107) and the same bird census procedures were repeated (Figure 1.1). Using this sample of 107 sites, I modeled the effect of surrounding urbanization on maximum-per-site abundance of each species, using Poisson regression with a repeated measures covariance structure (1997 data + 1996 data where available). Several measures of surrounding urbanization were examined, including the proportion of the surrounding area (within a circle of a specified radius) contained in urban land uses (including golf courses, urban parks and other human-constructed green spaces). GIS land use data were obtained from a 1:24000 Arc/Info polygon coverage, constructed from 1990 aerial photos by the Southern California Association of Governments. Scales of urbanization ranged from 250m to 4000m radius buffer distances (Chapter 1). Sequential score tests (Tarone 1988) were used to determine the largest measure of surrounding urbanization proportion contributing significantly to each species abundance model.

2.3. Spatial Statistics Methods and Results

Of the thirteen species exhibiting significant responses to some measure of surrounding urbanization in 1997 (Table 1.3), four were selected for further analysis in this study, due to the relative robustness of their models, and the small departures from normality in their model residuals: the Wrentit (*Chamaea fasciata*), Northern Mockingbird (*Mimus polyglottos*), Black-headed Grosbeak (*Pheucticus melanocephalus*) and Blue-gray

Gnatcatcher (*Polioptila caerulea*). To confirm the validity of these non-spatial urbanization models, I looked for spatial structure in the abundance of each of the species and modeled it explicitly as needed.

This analysis included four major steps:

1. Investigation of large- and small-scale spatial dependence in bird abundance, urbanization proportion and vegetation cover, using semivariograms and correlograms.
2. Regression of bird abundance on surrounding urbanization levels using (non-spatial) ordinary least squares (OLS) regression, and investigation of spatial dependence in model residuals.
3. Removal of large-scale spatial trends in bird abundance (regression of bird abundance on spatial coordinates), regression of trend model residuals on surrounding urbanization levels, and investigation of spatial structure in detrended model residuals.
4. Construction of spatial covariance models for bird abundance, using spatial covariance structures suggested by semivariogram and correlogram analyses, in order to statistically incorporate small-scale spatial dependence.

Semivariogram and correlogram generation were performed using S-Plus 4.5 (MathSoft 1997), S+SpatialStats (MathSoft 1996), and S-Plus for ArcView GIS (MathSoft 1998). SAS Systems' version 6.12 mixed models procedure (SAS 1997, Littell et al. 1996) was used for spatial covariance modeling.

2.3.1. Investigating Spatial Structure in Bird Abundance

Upon visual inspection of distribution maps for each species examined, they all appear to vary along the east-west urbanization gradient, to some degree (Figure 2.3). The Northern Mockingbird (2.3b) seems to increase in abundance from west to east, while the other three species decrease. The Wrentit (2.3a) and Blue-gray Gnatcatcher (2.3d) may also

exhibit north-south variation, with the Wrentit more abundant in the south, and the gnatcatcher more abundant in the north. The latter trends are less clear, however, due perhaps to the general lack of north-south variation among sampling locations, especially in the eastern section of the study area.

Using two related structure functions, the semivariogram and the correlogram, I examined the spatial covariance structure of the sampling locations with respect to bird abundance, as well as urbanization proportion. For each variable, I examined large-scale trends, and determined the effective range of spatial autocorrelation (if any).

For maximum 1997 abundance of each of the four species and urbanization proportion within a 2000m radius, I constructed an omnidirectional semivariogram, as well as directional semivariograms in the east-west (90° azimuth) and north-south (0° azimuth) directions (using a 45° tolerance), based on the 107 sampled locations. Fourteen lag distances, at 1000m intervals, were used for the omnidirectional and east/west semivariograms; nine 1000m lag distances were examined in the north/south direction. Semivariograms were generated using the variogram function in S+SpatialStats (MathSoft 1996).

I also constructed an omnidirectional correlogram for each of the above variables using Moran's I statistic. Correlograms were constructed from Moran's I autocorrelation values individually calculated for each 1000m lag distance (e.g., 0-1000m, 1000-2000m), also using S+SpatialStats (MathSoft 1996). In calculating Moran's I values, point pairs within the given interval were considered to be spatial neighbors, and assigned a spatial weight (w_{ij}) of 1; all other point pairs were assigned a spatial weight of 0. I tested for overall significance of each correlogram using a Bonferroni-adjusted significance level ($\alpha = 0.01$) to account for multiple comparisons, as well as for significance of individual correlation values ($\alpha = 0.05$), as suggested by Legendre and Fortin (1989).

Semivariogram Results – Original Variables

The overall trend apparent in the omnidirectional semivariogram for urbanization (Figure 2.4a) was driven primarily by east-west variation, as supported by the 90° directional semivariogram (2.4b), in which the variation among points increases almost monotonically with distance, particularly at lag distances of 7000m or larger. The north-south (0°) semivariogram (2.4c) exhibited a similar trend between 0-8000m, but stops there, constrained by the dimensions of the study area.

Three of the bird species examined—the Wrentit, Northern Mockingbird and Blue-gray Gnatcatcher—exhibited distinct large-scale spatial trends (Figure 2.5a,d,j) that appear to follow the urbanization trend (2.4a-c). These trends occurred primarily in the east-west direction (2.5b,e,k), as suggested by their distribution maps (2.3a,b,d), and slightly in the north-south direction (2.5c,f,l). The semivariograms did not increase monotonically, however, suggesting the presence of additional spatial structure not related to the east-west or north-south gradients. The semivariograms for the Black-headed Grosbeak were fairly constant, but with a small increase in the very largest distance classes, suggesting a slight spatial trend (2.5g-i).

In general, the omnidirectional semivariograms for each of the species resembled the east-west semivariograms, indicating that large-scale spatial trends were driven primarily by the east-west gradient (perhaps resulting from urbanization). The north-south semivariograms were most likely constrained by the configuration of the study area (long and narrow); thus they were based on fewer point pairs within each lag interval, and may be less reliable than the other semivariograms. The east-west semivariograms are most suspect at the shorter lag distances (<1000m) due to fewer point pairs, while both directional and omnidirectional semivariograms should be interpreted with caution at the larger lag distances (>8000m) (see sample sizes for each lag distance in Figure 2.5).

Correlogram Results – Original Variables

The omnidirectional Moran's I correlogram for urbanization proportion displayed a nearly linear decrease in autocorrelation (covariance) with increasing lag distance (Figure 2.6). It demonstrated overall significance ($p < 0.01$), as well as significant autocorrelation values for almost all distance classes. This indicates a clear, large-scale gradient, supporting the conclusions of the semivariogram analysis (Figure 2.4a-c).

Correlograms also confirmed that all four species were distributed along a spatial gradient, based on the steady (if not monotonic) decrease from positive to negative autocorrelation and overall significance ($p < 0.01$) of each correlogram (Figure 2.7). All species exhibited significant positive autocorrelation ($p < 0.05$) in more than one of the closer distance classes, while only the mockingbird and grosbeak also showed significant negative autocorrelation ($p < 0.05$) at greater distance classes. Autocorrelation ranges suggested by the correlograms are approximately 7000m for the Wrenit (2.7a), 5000m for the Northern Mockingbird (2.7b), 6000m for the Black-headed Grosbeak (2.7c), and 4000m for the Blue-gray Gnatcatcher (2.7d).

2.3.2. Non-Spatial Modeling of Bird Responses to Urbanization

Results from the previous section indicate large-scale trends in the abundances of all four bird species examined, which could invalidate tests for spatial autocorrelation (Legendre 1993). That is, the similarity between sites that are close in spatial proximity may be due to their position on a gradient, rather than some intrinsic heterogeneity-producing spatial process. To obtain a reliable picture of small-scale autocorrelation, large-scale trends must first be removed.

Because similar trends were also observed in landscape urbanization proportion (within a 2000m radius of each point), I suspected that these large-scale trends were actually products of the urbanization gradient. Thus I modeled the effects of surrounding urbanization levels on bird abundance and examined the resulting model residuals for remaining spatial autocorrelation, using the same tools as in the previous section.

Previous analyses indicated that the Wrentit is sensitive to urbanization up to 500m away, the Black-headed Grosbeak up to 1000m, Northern Mockingbird up to 2000m, and the Blue-gray Gnatcatcher up to 4000m away (Chapter 1). Based on these results, and ignoring other significant urbanization-related predictors of bird abundance, I regressed maximum-per-point abundance on surrounding urbanization proportion at the appropriate scale, using ordinary least squares (OLS) regression.

OLS regression models (rather than Poisson maximum likelihood) were used to facilitate comparison with the Gaussian mixed models used in spatial covariance modeling (Littell et al. 1996). Model residuals did not exhibit major departures from normality, and non-spatial OLS model results were not found to differ markedly from those of the Poisson-based models.

Effects of Urbanization on Bird Abundance

As demonstrated previously, the level of surrounding urbanization was a significant predictor of abundance for all four species examined (Table 2.1). Due to the high variation in the system, R^2 values are low, although regression coefficients (β) are generally highly significant. The mockingbird exhibited a positive response to surrounding urbanization proportion, while the other three species were negatively influenced.

Semivariogram Results – Urbanization Model Residuals

One species, the Black-headed Grosbeak, did not appear to exhibit any spatial dependence in its residuals, in that its omnidirectional and directional semivariograms were fairly flat, fluctuating around a population variance of approximately 0.5 (Figure 2.8g-i). For the three other species, omnidirectional semivariograms increased initially, but eventually reached a maximum, indicating the possible presence of spatial autocorrelation in model residuals up to the distance at which the sill is reached (range) (2.8a,d,j). Although the sill and range differed, these species all exhibited several small peaks and troughs, with maxima between 4000 and 10,000 meters. This type of semivariogram function may

indicate that several processes govern bird abundance, operating at different spatial scales. A sharp discontinuity in the semivariogram may represent a critical scale threshold (Turner et al. 1989), or change in the process driving variation. More likely, however, is that the peaks and dips reflect patchiness or aggregation in the sampling locations (Legendre and Fortin 1989, Meisel and Turner 1998). Particularly in the eastern portion of the study area, there were large data gaps resulting from the inaccessibility of certain chaparral areas, as well as urbanization-related habitat fragmentation (see Figure 2.3).

The omnidirectional semivariogram for Wrentit residuals reached a sill (~ 3) at 7000m (Figure 2.8a), indicating that this rather large distance was the maximum range of autocorrelation. This pattern appeared to be driven by north-south variation, as seen in the corresponding directional semivariogram, where the peak at 7000m was quite pronounced, suggesting possible outlier data (2.8c). The east-west semivariogram had a much smaller sill and range, peaking at a distance of 2000m (2.8b). These discrepancies suggest that autocorrelation in this species may be anisotropic (direction-dependent).

For Northern Mockingbird residuals, the omnidirectional semivariogram had an even larger range, reaching a sill (~ 0.8) at 10,000m (Figure 2.8d). Thus this species still appeared to exhibit a slight large-scale trend in its abundance, even after the effect of urbanization was removed. As with the Wrentit, this large-scale trend appeared to be driven by north-south variation (8f), while the east-west semivariogram (8e) was almost flat, suggesting anisotropic conditions. This remaining north-south dependence may be a product of topography, in that study area consists of many north-south running canyons. Within these canyons, bird abundance may be more similar than between sites in different canyons that are closer in a Euclidean sense. Both species may also vary with elevation, which generally increases from south to north in the study area.

The omnidirectional semivariogram for the Blue-gray Gnatcatcher reached a sill (~ 0.4) near 4000m, then decreased fairly rapidly, reaching a minimum near 10,000m (Figure 2.8j). This suggests a large-scale pattern, or similarity between the extreme ends of the

local population. Directional semivariograms (2.8k-l) were fairly similar, indicating isotropic (non direction-dependent) autocorrelation.

The presence of a sill in each semivariogram indicates that the residuals were stationary over the study area, which in turn suggests that large-scale trends in bird abundance were primarily explained by variations in urbanization (although causality cannot be determined). However, the large autocorrelation ranges revealed by the semivariograms (4000-10,000m) indicated that model residuals still contained large-scale spatial dependence. This may have been due to the influence of other large-scale patterns (smaller than the size of the study area), such as patterns of variation in vegetation or elevation, in determining bird abundance.

Correlogram Results – Urbanization Model Residuals

Examination of omnidirectional Moran's I correlograms (Figure 2.9) provided a more complete picture of spatial structure in urbanization model residuals. Correlograms were overall significant ($p < 0.01$) for all species but the Grosbeak, with spatial autocorrelation generally declining with distance and oscillating around zero (Figure 2.9). What the correlograms suggested, beyond the semivariograms, was a maximum range of "small-scale" autocorrelation (when the correlogram first reaches zero). Three of the four species exhibited significant small-scale spatial autocorrelation ($p < 0.05$), with maximum autocorrelation ranges apparently near 2000m for the Wrentit (2.9a) and mockingbird (2.9b), and 4000m for the gnatcatcher (2.9d). Additional autocorrelation beyond these ranges may represent remaining large-scale trends and/or patchiness in the sampling sites.

Again, all species exhibited somewhat periodic dips and crests in the correlograms for their model residuals. For the Wrentit, significant positive spatial autocorrelation occurred at 1000m and 5000m; negative autocorrelation was present at the 7000m and 9000m lag distances (Figure 2.9a). The mockingbird was positively autocorrelated at 1000m and 12,000m, and negatively autocorrelated at 6000m and 10,000m (2.9b). The grosbeak was positively autocorrelated at 11,000m (2.9c). The gnatcatcher exhibited

significant positive autocorrelation at 1000m and 2000m, and negative autocorrelation at 7000m (2.9d). Negative autocorrelation in the middle distances (i.e. 6000m-10,000m) most likely indicates the influence of spatial patchiness in the sample. The positive autocorrelation at large distances exhibited in grosbeak and mockingbird residuals may represent similarities at extreme ends of the study area, caused by large-scale processes, but more plausible is the influence of outliers, given the high variability and large gaps in the data.

2.3.3. Modeling large-scale spatial trends

Because the east-west trend in urbanization was so prominent, teasing apart the effects of urbanization and spatial location on bird abundance was difficult. Results from the previous section suggested that large-scale trends in bird abundance are largely a reflection of variations in urbanization, but that additional large-scale spatial dependencies may have been present, primarily in the north-south direction. The question remained as to whether these trends indicated non-stationarity over the study area (a "true gradient"), or intrinsic autocorrelation among sampling locations separated by large distances (a "false gradient") (Legendre 1993). If the former is true, then bird abundance should vary as a function of spatial location, and residuals should be uncorrelated once the trend is removed (Legendre 1993).

To statistically remove the large-scale trend, I separately regressed the abundance of each species on the x - y coordinates of the sampling locations and the interaction between them ($z \sim x + y + x*y$). I then regressed the trend model residuals on urbanization proportion, and compared the significance of the parameter estimates and overall predictive ability with the original urbanization models for each species. Finally, I looked for remaining spatial dependence in the residuals of the de-trended urbanization models for each species, using semivariograms and correlograms.

Results of trend models

For the Blue-gray Gnatcatcher and Wrentit, spatial location explained a greater portion of the variation in abundance than urbanization proportion—25% vs. 12% for the gnatcatcher and 35% vs. 23% for the Wrentit (Table 2.1). For the Northern Mockingbird and Black-headed Grosbeak, however, surrounding urbanization levels explained more of the variance than spatial location (41% vs. 24% and 14% vs. 12%, respectively). Over 50% of the variation in urbanization (at the 2000m radius) was explained by spatial location, which means that the two effects are difficult to separate.

After removing the large-scale spatial trend, urbanization proportion was still a significant predictor of mockingbird, Wrentit and grosbeak abundance, although the explanatory power of these models was generally low, compared with the initial OLS models (i.e., lower R^2 and p-values) (Table 2.1). These results indicate that urbanization, in and of itself, did explain a significant portion of the variation in abundance of these species, even under the most conservative assumptions.

For the Blue-gray Gnatcatcher, urbanization proportion was no longer a significant predictor of abundance when the spatial trend was removed. Thus the effects of spatial location and urbanization were difficult to separate in this case, suggesting that gnatcatcher abundance may have been distributed along a large-scale gradient determined by something other than urbanization.

Semivariogram and Correlogram Results – Detrended Model Residuals

Semivariogram (Figure 2.10) and correlogram (Figure 2.11) analyses suggest that all species but the Northern Mockingbird may have followed a “true” gradient, in that detrended model residuals appeared to be uncorrelated. The extent to which these large-scale trends in abundance were a product of urbanization remains unclear, however, especially since surrounding urbanization proportion at a particular scale may not describe all of the variation in urbanization. Because urbanization may have been driving the observed trends, it is not necessarily helpful to conservatively attribute bird responses to

spatial location. It may be more appropriate to assume that all spatial variation not attributable to urbanization is autocorrelation resulting from interactions between sites, and incorporate this dependence into the urbanization model.

2.3.4. Modeling small-scale spatial autocorrelation

Spatial dependence detected in the residuals from non-spatial regression models means that the models were improperly specified (Anselin 1989). If this autocorrelation represents positive, small-scale autocorrelation, rather than large-scale trends, then a spatial covariance model can be used to adjust for the spatial dependence. By constructing a spatial covariance model for the residuals, the autocorrelation structure can be explicitly defined, so that independence assumptions are met and significance tests are valid.

For spatial covariance models to be appropriate, the residuals should exhibit second order stationarity (constant mean and variance over sampling area) and isotropy (covariance independent of direction) (Littell et al. 1996). Based on the apparent convergence of the semivariograms to a sill, I assumed that the stationarity assumption was met in all cases, despite irregularities and large autocorrelation ranges in the semivariograms and correlograms. I also assumed isotropic behavior, despite differences in east/west and north/south semivariograms.

For each of the three species with autocorrelated residuals according to semivariograms and Moran's I correlograms (mockingbird, Wrentit and gnatcatcher), I fit a spatial covariance model (Littell et al. 1996) corresponding to the non-spatial model. The model was fit using mixed model regression in SAS version 6.12 with REML (restricted maximum likelihood) estimation of model parameters (SAS 1997). Based on the shapes of the semivariogram for non-spatial model residuals, I used an exponential model for the covariance function:

$$f(d_{ij}) = e^{\left(-d_{ij}/\rho\right)} \quad (2.5)$$

The range parameter (ρ) was fixed at a value consistent with the empirical semivariogram for non-spatial model residuals, and the partial sill (σ_2^2) and nugget (σ_1^2) values were estimated simultaneous with estimation of regression coefficients (β). Using the maximum values of the empirical semivariograms, the approximate ranges determined for the Northern Mockingbird, Wrentit and Blue-Gray Gnatcatcher were 9000m, 7000m, and 4000m, respectively. These range estimates are rather large, however, and the spatial covariance model is only intended for positive, small-scale dependence (Littell et al. 1996). Thus I also used correlograms to determine more appropriate ranges for comparison. I used as a second range estimate the approximate distance at which the correlogram for non-spatial model residuals first reached zero: 2000m for the Wrentit and mockingbird and 4000m for the gnatcatcher (same as semivariogram estimate). For the Wrentit, this smaller range also corresponded with the range suggested by the east-west directional semivariogram. The use of two different ranges (small vs. large) also provided a sensitivity analysis for the regression parameters.

Likelihood ratio χ^2 tests were used to determine the significance of the spatial (vs. non-spatial) models. The "best" covariance model could not be determined statistically, but was evaluated by comparing log likelihood values and significance of individual spatial parameter estimates. Regression coefficients and standard errors were also compared between spatial and non-spatial models to determine whether modeling of spatial structure in the residuals changed the substantive interpretations of the regression analysis.

Results of spatial covariance models

For all species, the spatial models exhibited significantly better fit than the corresponding non-spatial models (χ^2 likelihood ratio test, $p < 0.05$) (Table 2.2), indicating significance of the spatial covariance parameters. Overall, the inclusion of spatial parameters caused regression parameter estimates (β) to decrease, although not always substantially.

The Wrentit exhibited the largest variation in regression parameter estimates between the three models, with somewhat higher magnitude values estimated by the non-spatial model

than in either spatial covariance model, although confidence intervals for all parameter estimates were overlapping (Table 2.2). Spatial parameter estimates (σ_1^2 and σ_2^2) were larger in the large range (7000m) model, but the nugget effect was only significantly different from zero ($p < 0.05$) in the small range (2000m) model. The log likelihood value for the large-scale model was slightly higher, indicating that the incorporation of large-scale spatial structure (up to 7000m) improved model fit for this species, but with a consequent reduction in the urbanization parameter estimate. This suggests that part of the urbanization association may indeed be attributable to spatial autocorrelation. The most appropriate model depends on the range of autocorrelation assumed.

The Northern Mockingbird exhibited a slightly smaller relative reduction in regression parameter estimates with the inclusion of spatial parameters (Table 2.2). Spatial covariance parameter estimates were also significantly different from zero ($p < 0.05$) in both spatial models, but the nugget estimate was quite a bit larger in the large range model (9000m) than in the small range (2000m) model. For this species, the 2000m range distance appeared to generate the best-fitting model, based on the higher log likelihood value. Thus the incorporation of large-scale autocorrelation (above 2000m) was unnecessary and inappropriate for this species.

In the Blue-gray Gnatcatcher models, the effect of urbanization proportion was reduced enough that it is no longer significant in the spatial model (Table 2.2). The partial sill estimate in the spatial model (4000m range) was significantly different from zero ($p < 0.05$), but not the nugget. This indicates, as does the trend model from the previous section, that all of the urbanization-related variation in gnatcatcher abundance may also be described by spatial location.

2.4. Discussion

The four species examined in this study have demonstrated significant population responses to urbanization at large spatial scales. Abundance of the Wrentit, Black-headed Grosbeak and Blue-gray Gnatcatcher were negatively associated with high levels of

surrounding urbanization, while the Northern Mockingbird was positively associated with urbanization. These results suggested that chaparral bird populations may be affected by changes in landscape composition and pattern, even when apparently suitable habitat is present.

Using a variety of spatial statistics tools, I was able to consider the influence of spatial dependence in my analysis of landscape-level urbanization effects on chaparral birds, in order to verify and/or qualify these results. Equally important, these techniques also allowed a better understanding of the spatial structures of the bird populations under study, and the landscape mosaic that they inhabit. Different insights were gained for each of the species examined, while common spatial patterns were also illuminated.

All four species exhibited large-scale spatial trends in their abundance, primarily coinciding with the east-west urbanization gradient along which they were sampled (Figures 2.4-2.7). After accounting for urbanization effects, however, these trends were largely absent from model residuals (Figures 2.8-2.9), suggesting that urbanization explained most of the large-scale spatial structure in these species. Conversely, when the spatial trends were removed, three of these species (Black-Headed Grosbeak, Wrentit and Northern Mockingbird) still demonstrated significant responses to changes in urbanization (Table 2.1).

Abundance patterns for all four species exhibited additional spatial autocorrelation unrelated to urbanization (Figures 2.8-2.9). The use of spatial covariance models to incorporate this small-scale spatial dependence (where possible) allowed conclusions about urbanization effects to be more robust. In general, the observed relationships between urbanization and bird abundance hold, despite small-scale spatial structure (autocorrelation) in the data. Furthermore, the spatial covariance models had better predictive capabilities, indicated by the significant improvement in log likelihood statistics. If desired, the spatial and regression parameter estimates obtained in these analyses could be used to interpolate bird abundance at points between those sampled.

statistics. If desired, the spatial and regression parameter estimates obtained in these analyses could be used to interpolate bird abundance at points between those sampled.

2.4.1. Ranges of Spatial Autocorrelation

Ranges of small-scale spatial autocorrelation, as suggested by the correlogram analysis, can be interpreted as indications of the ecological neighborhoods for each species—that is, the “regions of activity or influence during periods of time appropriate to particular ecological processes” (Addicott et al. 1987, p.340). Depending on the process and time-scale, a mobile animal’s ecological neighborhood can be defined by factors like (in order of increasing spatial scale) breeding territory size, home range size, natal/adult dispersal distance, and spatial extent of a local population.

Territory sizes, home range sizes and dispersal distances vary widely among passerine species in general, as among the four species examined in this study. For the Wrentit, an “extremely sedentary” resident chaparral species (Ehrlich et al. 1988, p. 420), breeding territories average ~0.3ha in size (Erickson 1938), which is equivalent to a 30m x 30m area. Natal dispersal distance for this species averages 375m, with a maximum near 700m (Baker et al. 1995). The Blue-gray Gnatcatcher, also a year-round resident in the Santa Monica Mountains, has somewhat larger territories, averaging ~1.8ha, and may have winter home ranges up to 9ha in size (Ellison 1992). Natal dispersal distances are unknown for the gnatcatcher, but movements up to 75km between breeding sites have been recorded (Ellison 1992). The Black-headed Grosbeak, a long-distance migrant species, has similar territory sizes, averaging 0.7-2.7ha, and low natal philopatry, with no individuals returning to breed in one New Mexico study area (Hill 1995). For the urban-associated Northern Mockingbird, large movements (>300km) have also been recorded, although natal dispersal distances are typically much shorter (Derrickson and Breitwisch 1992). Thus, while chaparral bird species, in general, tend to be sedentary (Soulé et al. 1988), three of the four species examined in this study are known to move over large distances, possibly on the order of the autocorrelation ranges detected (2000-4000m).

The large autocorrelation distances found in this study—on the order of dispersal ranges and population sizes, rather than territory and home range sizes—may indicate the influence of population (vs. individual) dynamics, which is reasonable given the intermediate temporal and spatial scales of the urbanization processes being studied. Time lags may also result in a decoupling of ecological variables and responses in bird abundance (Wiens 1989). Given the coarse resolution of this analysis, however, autocorrelation at smaller scales, resulting from interactions among individuals, could not easily be detected.

Of the four species examined, the Northern Mockingbird demonstrated the strongest small-scale autocorrelation, even after large-scale trends were removed (Figures 2.9 and 2.11). This indicated a strong interdependence among sampling sites, independent of the location in the landscape, but may also have been due in part to the clustering of this species near urban developments. Based on correlograms for non-spatial model residuals, the range of small-scale autocorrelation appeared to be 2000m (Figure 2.9), although autocorrelation dropped off quickly, indicating that maximum autocorrelation occurred at a somewhat smaller distance.

Similar results were obtained for the Wrentit, a species that was negatively associated with surrounding urbanization, although for this species, residuals were longer correlated after large-scale trends were removed (Figure 2.11). The Wrentit also seemed to exhibit anisotropic variation in the shorter distance ranges (Figure 2.8), which likely explained the weaker overall autocorrelation values. Autocorrelation in the north-south, but not east-west, direction, after factoring out urbanization influences, may be due to the north-south orientation of the canyons and trails along which sampling sites were located. Given the sedentary nature of this species, a juvenile Wrentit may be more likely to disperse within a canyon than across a ridgetop to the next canyon, especially since many of the ridges have firebreaks, which this species may be reluctant to cross (Small 1974).

The comparatively large range of potential spatial autocorrelation (4000m) in the Blue-gray Gnatcatcher (Figure 2.9) seemed to indicate the presence of a large-scale trend in

abundance, rather than interaction among distant sites. This was also supported by the non-significant urbanization parameter in both the spatial covariance model and trend model for this species. Although the large-scale trend may have been urbanization-related, this could not be determined with certainty. In order to obtain more conclusive results for this species, a larger area should be studied, given that 4000m is nearly 20% of the length of the study area. Given the large movements documented in this species (Ellison 1992), the 4000m range of autocorrelation may indeed reflect dispersal distance and interaction among sites.

For the Northern Mockingbird and Blue-gray Gnatcatcher, the range of autocorrelation in model residuals, as determined by correlogram analyses (Figure 2.9), coincided with the maximum range of urbanization influence: 2000m and 4000m, respectively (Chapter 1). These “scale agreements” suggest that either (1) urbanization patterns (e.g., clustering of developments or recreational trails) were responsible for the observed spatial dependencies; or (2) autocorrelation in bird abundance due to other factors (e.g., dispersal limitations or social interactions) facilitated urbanization influences over larger distances. Indeed, this chaparral system is so integrated with the surrounding urbanized area that such interactions might be expected.

2.4.2. Large-scale Trends vs. Small-scale Autocorrelation

Spatial covariance modeling is most appropriate for small-scale spatial dependence resulting from the interactions among sites that are close in spatial proximity. Spatial autocorrelation can also occur at larger scales, when the influence of one site carries a long way through geographic space (Legendre 1993). But large-scale spatial dependence commonly reflects a spatial gradient, and if so, it should be removed before spatial autocorrelation is modeled, as it violates the stationarity assumption (Legendre 1993). The distinction between the two is subtle, and also depends upon the temporal scale and window of analysis (Wiens 1981). For example, a gradient at the landscape level may represent a mere blip of heterogeneity at the regional level. For the purpose of geostatistical analyses, a true gradient should encompass and extend beyond the study

area. Large-scale patterns that are smaller than this can be incorporated in a spatial covariance model.

In this study, large-scale spatial dependence in bird abundance was certainly present, but most of it was explained by the urbanization gradient. Remaining large-scale structure appeared to be operating on a smaller scale than that of the study area (as demonstrated by semivariograms in Figure 2.8) and may have followed patterns of variation in vegetation, topography, or other geophysical factors. It may also have been a product of aggregated sampling locations (Legendre and Fortin 1989), resulting from a combination of habitat fragmentation by urbanization, clustering of census sites along trails and fire roads, and gaps in census sites due to restricted or privately-owned areas. Regardless of the source, this large-scale spatial dependence appeared to be adequately described in the spatial covariance models. The similarity between large- and small-scale covariance models, however, in terms of regression parameter estimates and overall fit, indicated that small-scale autocorrelation is most important. The large-scale variations may have been too unpredictable to model accurately with the type of model used, which is only intended for positive, small-scale autocorrelation (Littell et al. 1996).

For all species but the Northern Mockingbird, residuals from the detrended models exhibited no spatial autocorrelation (Figure 2.11), suggesting that spatial covariance models may not be necessary to describe their abundance patterns if large-scale trends are removed. Here emerges a possible trade-off between describing the distribution of bird abundance and detecting urbanization-related changes. If the primary goal is to model the abundance of these species in this particular landscape, then factoring in spatial location, in addition to the effect of urbanization influence, may be adequate. The remaining residuals were uncorrelated, so the models should be appropriately specified. Given the distinct urbanization gradient, however, such a model diminishes the potential for detection of urbanization influences. If autocorrelation is thought to occur over large distances, than this spatial dependence can instead be explicitly incorporated in a spatial covariance model.

The decision to de-trend a variable, in cases such as this when the trend is not obvious, depends on the assumptions made about the system. Here, because the birds under study are fairly widespread and common throughout the Santa Monica Mountains, and the vegetation types in which I sampled were similar for all sites, I would expect urbanization and landscape pattern to cause more variation in abundance than spatial location *per se*.

Directional semivariograms indicated that trends in bird abundance were primarily driven by east-west variation (Figure 2.6), but after factoring out urbanization, north-south autocorrelation was responsible for remaining large-scale dependence in Wrentit, mockingbird and gnatcatcher abundance (Figure 2.8). These results suggest that east-west trends were primarily urbanization-related, while north-south trends were likely due to natural features. Anisotropic covariance models, explicitly incorporating direction, as well as distance, may therefore be more appropriate for these species. Furthermore, the use of local spatial statistics (Getis and Ord 1992, Anselin 1995, Bao and Henry 1996) may help identify specific regions of autocorrelation.

2.5. Conclusion

Fundamentally, spatial autocorrelation in nature is caused by unknown factors that could potentially be measured and modeled explicitly, as many have done, particularly in small-scale studies. Measuring these unknown variables is often infeasible or impractical, however, especially when they involve things like animal behavior, indirect effects of biotic interactions, and time lags. Furthermore, such “bottom-up” approaches may sacrifice generalizability for detail (Wiens 1989, Root and Schneider 1995).

In this study, landscape-level urbanization influences on bird abundance were the primary focus of interest, while habitat type (i.e., vegetation) were kept constant. Although other potential explanatory variables could certainly be measured (and some were, with no significant associations found), small-scale autocorrelation, which has a large stochastic component, is difficult to predict. Thus, in the absence of the elusive “right” variables,

This study provides an example of how spatial statistical methods can be used to control for spatial structure in analyzing relationships between spatially distributed variables. The methods used helped confirm my conclusions regarding the influence of urbanization on bird abundance, while also providing further insight into the spatial structure of the bird populations examined.

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Table 2.1. Non-spatial and detrended models for bird abundance. β is the regression coefficient for the effect of urbanization proportion within a surrounding radius (500m for Wrentit; 1000m for Black-headed Grosbeak; 2000m for Northern Mockingbird; 4000m for Blue-gray Gnatcatcher).

	OLS model: bird abundance ~ urbanization measures	Trend model residuals ~ urbanization measures	Trend model: bird abundance / urbanization measures ~ x,y coordinates (x = east/west, y =north/south)	
<i>Wrentit</i>				
$\beta \pm$ S.E. (<i>p-value</i>)	-7.83 \pm 1.41 (<i><0.0001</i>)	-3.82 \pm 1.24 (<i>0.003</i>)	Significant effects (<i>p<0.05</i>)	x, y, x*y
F-statistic (<i>p-value</i>)	30.61 (<i><0.0001</i>)	9.43 (<i>0.003</i>)	F-statistic (<i>p-value</i>)	18.36 (<i><0.0001</i>)
R ²	0.23	0.08	R ²	0.35
<i>Northern Mockingbird</i>				
$\beta \pm$ S.E. (<i>p-value</i>)	3.42 \pm 0.40 (<i><0.0001</i>)	1.65 \pm 0.43 (<i><0.0001</i>)	Significant effects (<i>p<0.05</i>)	x, y, x*y
F-statistic (<i>p-value</i>)	72.05 (<i><0.0001</i>)	14.89 (<i><0.0001</i>)	F-statistic (<i>p-value</i>)	10.67 (<i><0.0001</i>)
R ²	0.41	0.12	R ²	0.24
<i>Black-headed Grosbeak</i>				
$\beta \pm$ S.E. (<i>p-value</i>)	-1.98 \pm 0.48 (<i><0.0001</i>)	-0.97 \pm 0.47 (<i>0.042</i>)	Significant effects (<i>p<0.05</i>)	--
F-statistic (<i>p-value</i>)	17.33 (<i><0.0001</i>)	4.23 (<i>0.042</i>)	F-statistic (<i>p-value</i>)	4.57 (<i>0.005</i>)
R ²	0.14	0.04	R ²	0.12
<i>Blue-gray Gnatcatcher</i>				
$\beta \pm$ S.E. (<i>p-value</i>)	-0.89 \pm 0.24 (<i><0.0001</i>)	-0.04 \pm 0.22 (<i>0.86</i>)	Significant effects (<i>p<0.05</i>)	x, y, x*y
F-statistic (<i>p-value</i>)	14.31 (<i><0.0001</i>)	0.03 (<i>0.86</i>)	F-statistic (<i>p-value</i>)	11.49 (<i><0.0001</i>)
R ²	0.12	0.00	R ²	0.25

Table 2.2. Non-spatial vs. spatial covariance models for Bird Abundance. β is the regression coefficient for the effect of urbanization proportion within a surrounding radius (500m for Wrentit; 2000m for Northern Mockingbird; 4000m for Blue-gray Gnatcatcher).

	Non-Spatial Model	Spatial Covariance Models	
<i>Wrentit</i>			
$\beta \pm$ S.E.	-7.83 \pm 1.41	-6.16 \pm 1.78	-4.93 \pm 1.82
(<i>p</i> -value)	(<0.0001)	(0.0008)	(0.0078)
-2 Log Likelihood	400.93	384.34	382.59
Range (ρ) \pm S.E.		2000m	7000m
Nugget (σ_1^2) \pm S.E.		1.28 \pm 0.51	1.77 \pm 0.81
Partial Sill (σ_2^2) \pm S.E.		1.45 \pm 0.29	1.65 \pm 0.27
Model Likelihood Ratio		16.59	18.34
Chi-Square (<i>p</i> -value)		(0.0009)	(0.0004)
<i>Northern Mockingbird</i>			
$\beta \pm$ S.E.	3.43 \pm 0.41	3.23 \pm 0.74	2.96 \pm 0.90
(<i>p</i> -value)	(<0.0001)	(<0.0001)	(0.0014)
-2 Log Likelihood	241.85	204.84	210.39
Range (ρ) \pm S.E.		2000m	9000m
Nugget (σ_1^2) \pm S.E.		0.69 \pm 0.22	2.30 \pm 0.87
Partial Sill (σ_2^2) \pm S.E.		0.10 \pm 0.06	0.14 \pm 0.06
Model Likelihood Ratio		37.01	31.45
Chi-Square (<i>p</i> -value)		(<0.0001)	(<0.0001)
<i>Blue-gray Gnatcatcher</i>			
$\beta \pm$ S.E.	-0.89 \pm 0.23	-0.59 \pm 0.44	
(<i>p</i> -value)	(0.0003)	(0.19)	
-2 Log Likelihood	169.94	161.68	
Range (ρ) \pm S.E.		4000m	
Nugget (σ_1^2) \pm S.E.		0.09 \pm 0.06	
Partial Sill (σ_2^2) \pm S.E.		0.22 \pm 0.04	
Model Likelihood Ratio		8.27	
Chi-Square (<i>p</i> -value)		(0.016)	

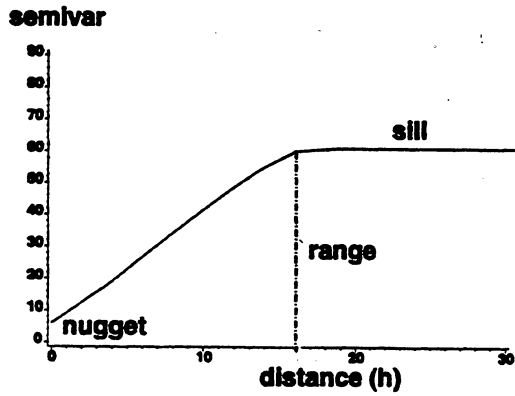


Figure 2.1. Idealized Semivariogram Function (from Littell et al. 1996).

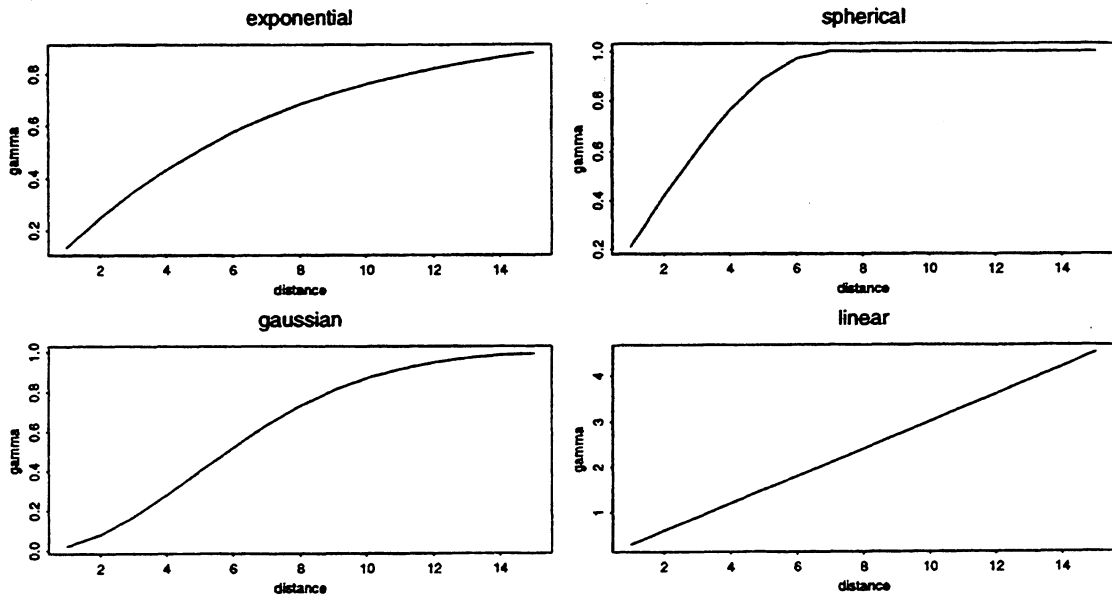


Figure 2.2. Theoretical Semivariogram Models (from MathSoft 1996).

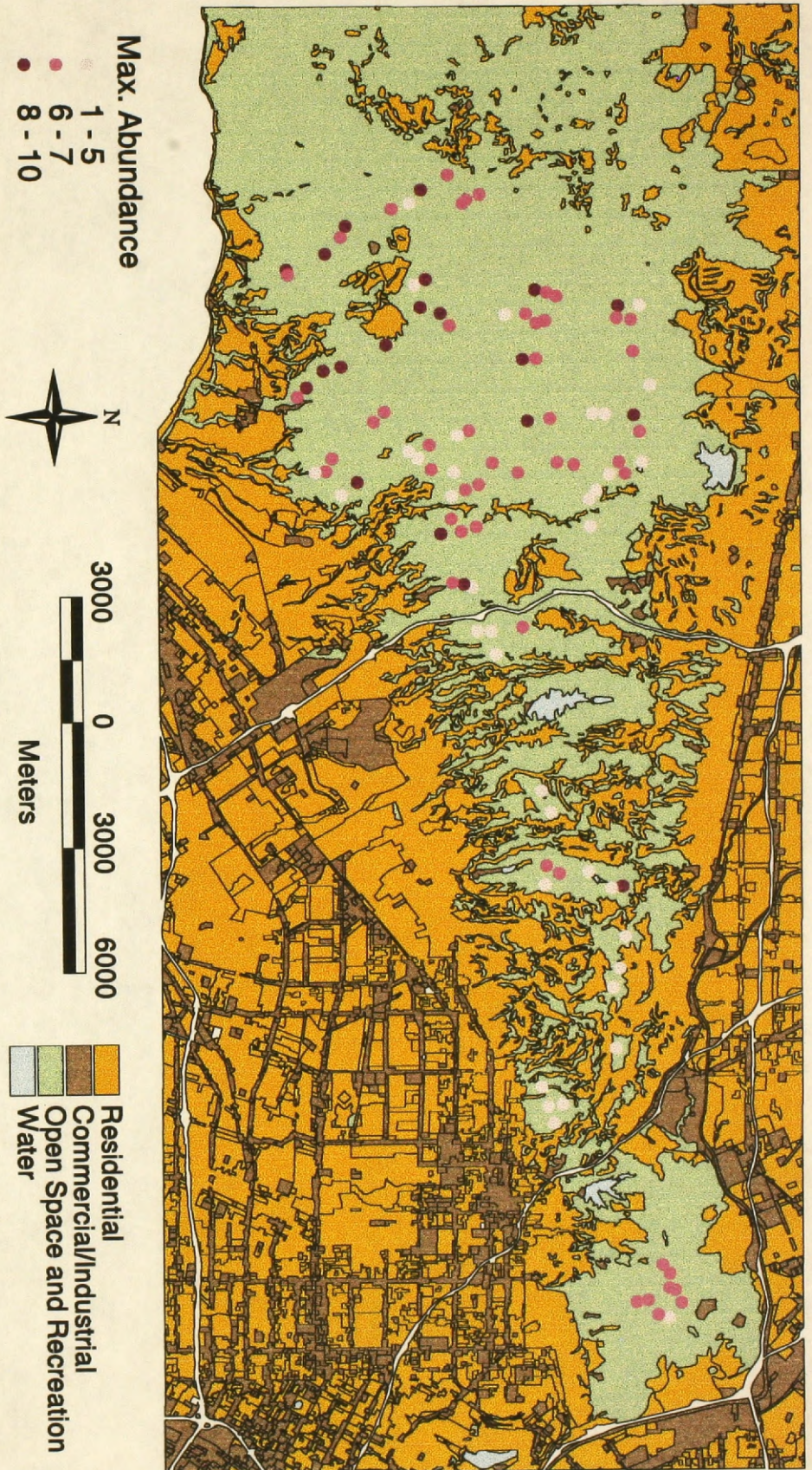


Figure 2.3a. Wren tit abundance. Maximum of two counts (1997). 107 sampling locations.

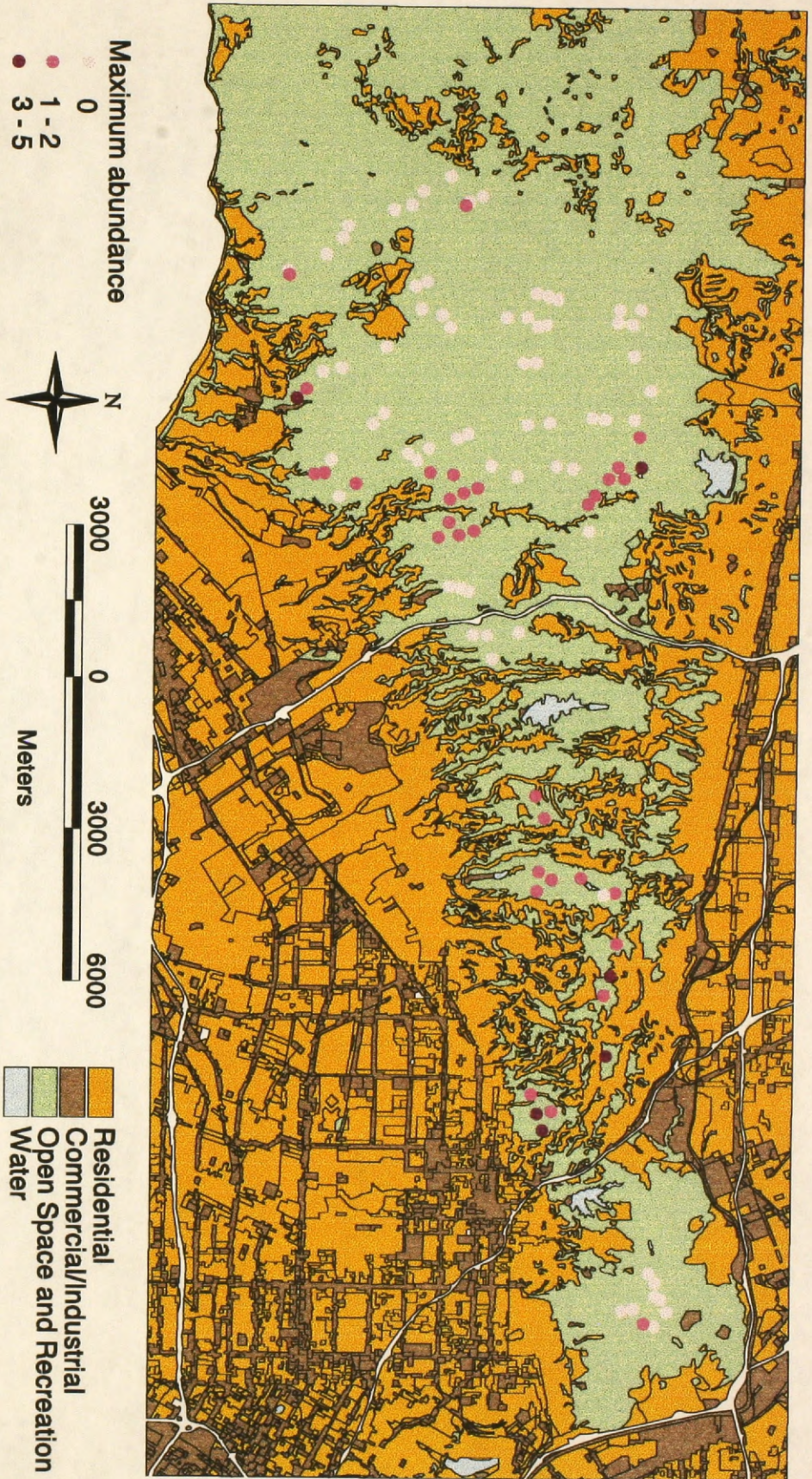


Figure 2.3b. Northern Mockingbird Abundance. Maximum of two counts (1997). 107 Sampling Locations.

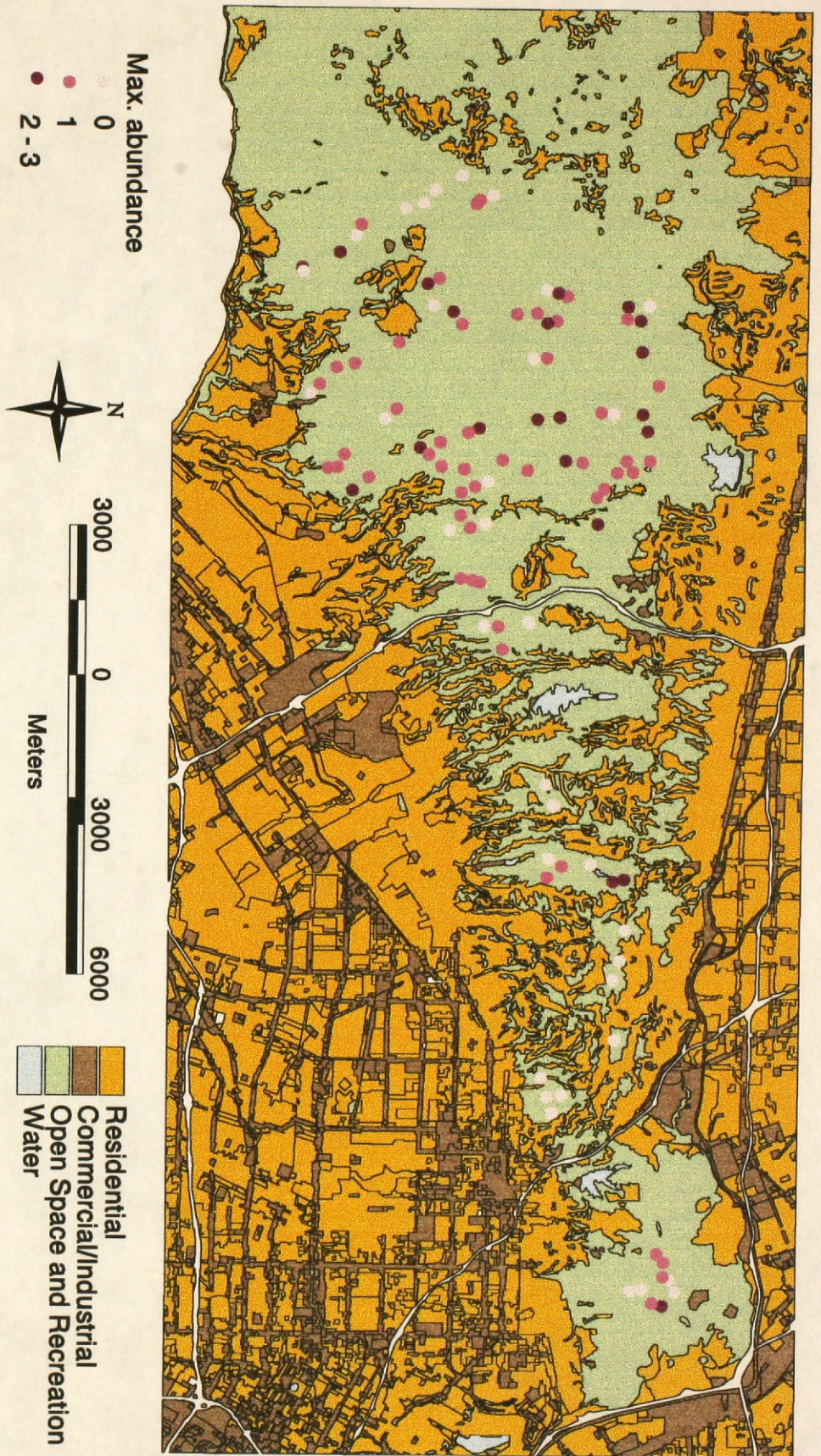


Figure 2.3c. Black-headed Grosbeak Abundance. Maximum of two counts (1997). 107 sampling locations

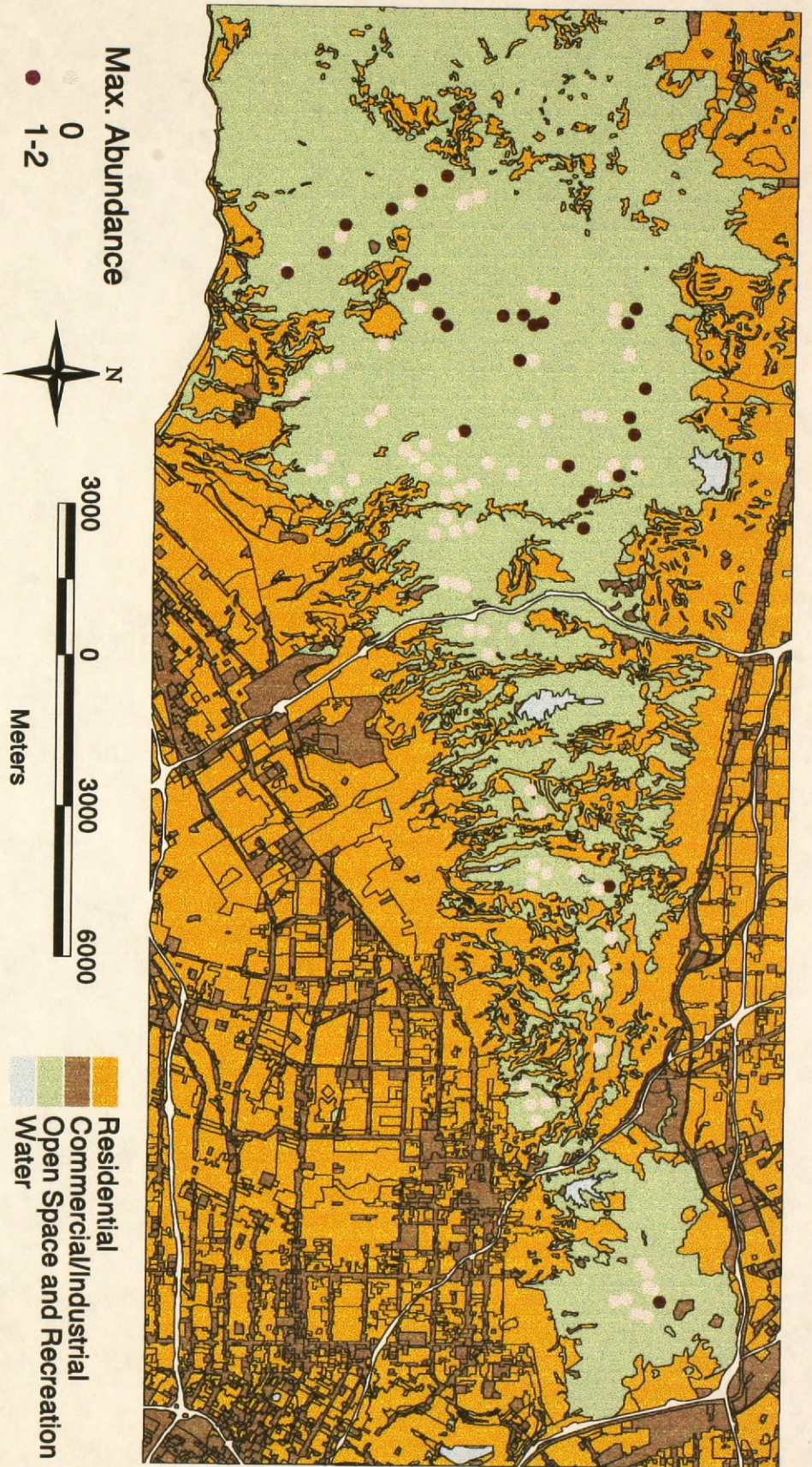


Figure 2.3d. Blue-gray Gnatcatcher Abundance. Maximum of two counts (1997). 107 Sampling Locations.

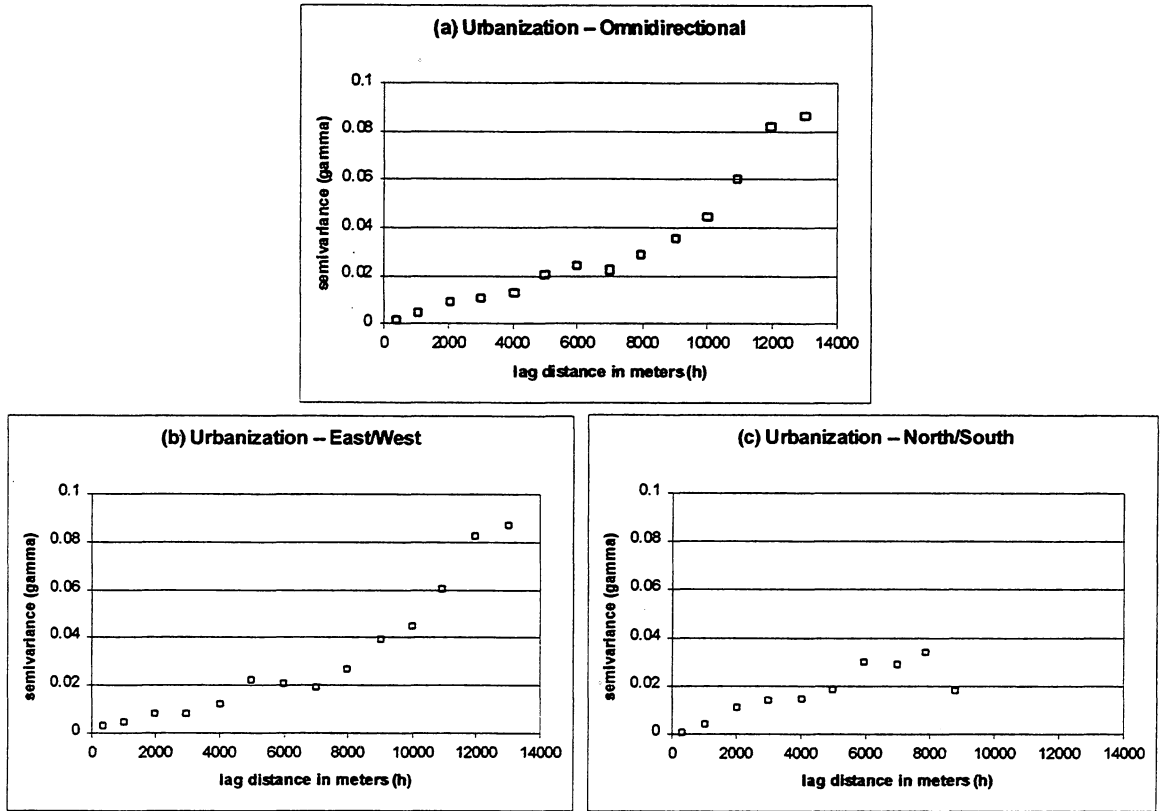


Figure 2.4. Empirical Semivariograms, $\gamma(h)$, for Urbanization Proportion (2000m radius). East/West = 90° azimuth, 45° tolerance; North/South = 0° azimuth, 45° tolerance. Lag distance values represent averages distances between pairs of points within each 1000m distance class.*

* Sample sizes for each distance class in omnidirectional semivariograms:

Avg.dist.	361	1044	2038	3010	4024	5011	5980	7013	7950	8987	9989	10939	11972	13041
# Pairs	72	282	357	567	580	582	504	388	287	158	158	151	110	137
East/West:														
Avg.dist.	379	1060	2033	3002	4024	5010	5994	7020	7973	9021	9989	10939	11972	13041
# Pairs	31	164	166	297	322	332	292	256	199	130	158	151	110	137
North/South:														
Avg.dist.	348	1021	2043	3018	4025	5012	5960	6999	7898	8832				
# Pairs	41	118	191	270	258	250	212	132	88	28				

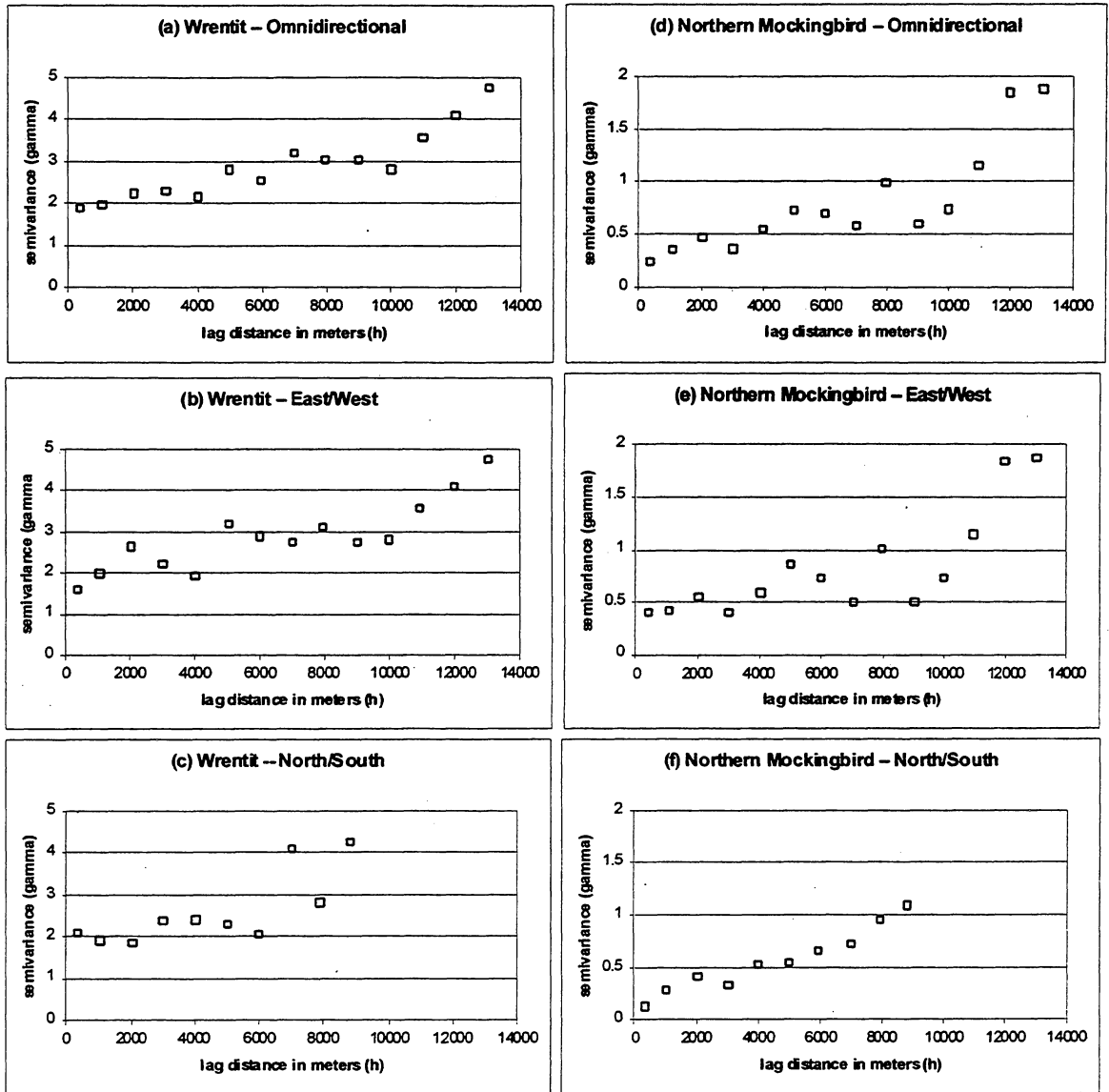


Figure 2.5. Empirical Semivariograms, $\gamma(h)$, for Maximum 1997 Bird Abundance. East/West = 90° azimuth, 45° tolerance; North/South = 0° azimuth, 45° tolerance. Lag distance values represent averages distances between pairs of points within each 1000m distance class.*

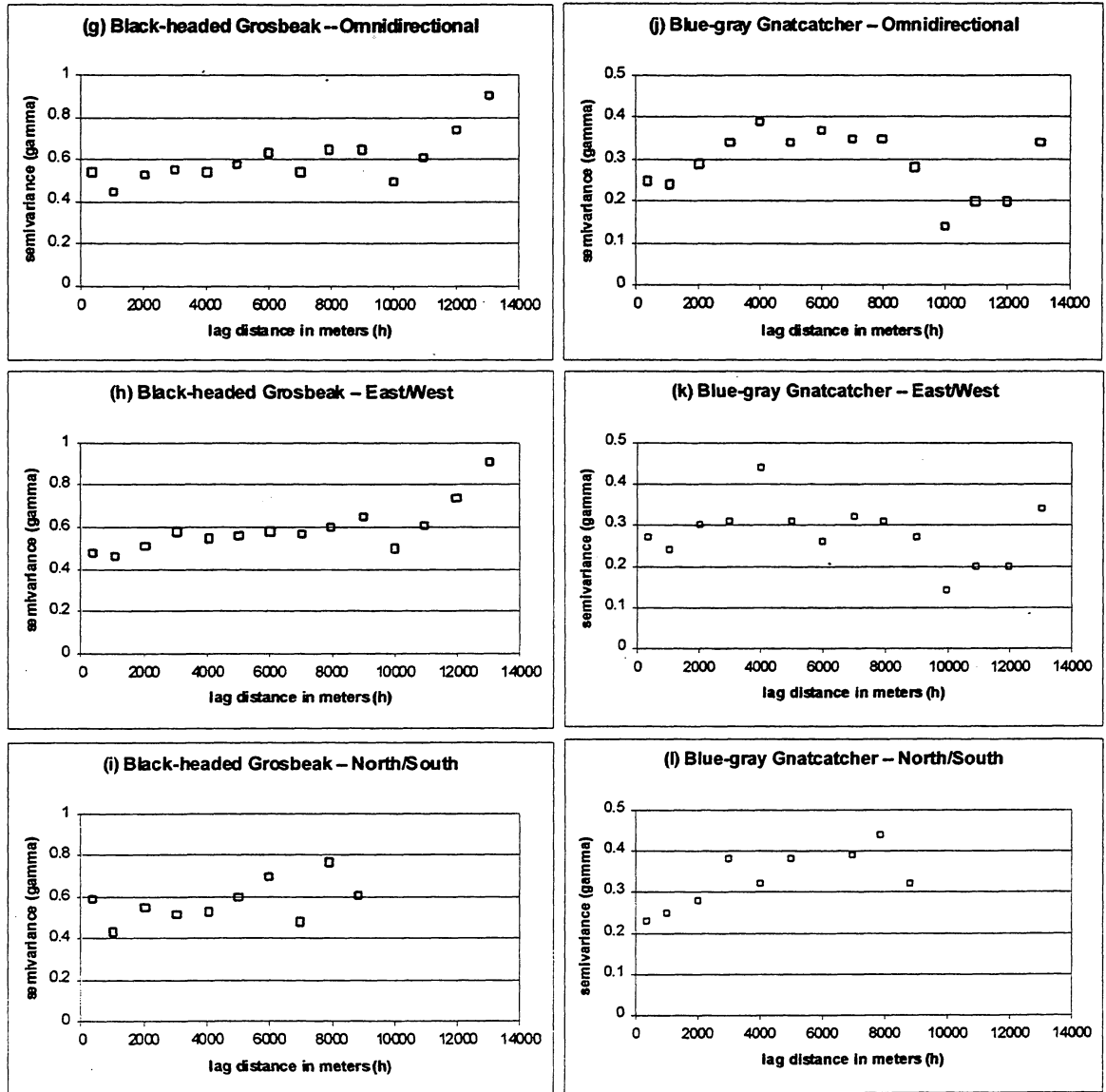


Figure 2.5. (continued)

* Sample sizes for each distance class in omnidirectional semivariograms:

Avg. dist.	361	1044	2038	3010	4024	5011	5980	7013	7950	8987	9989	10939	11972	13041
# Pairs	72	282	357	567	580	582	504	388	287	158	158	151	110	137
East/West:														
Avg. dist.	379	1060	2033	3002	4024	5010	5994	7020	7973	9021	9989	10939	11972	13041
# Pairs	31	164	166	297	322	332	292	256	199	130	158	151	110	137
North/South:														
Avg. dist.	348	1021	2043	3018	4025	5012	5960	6999	7898	8832				
# Pairs	41	118	191	270	258	250	212	132	88	28				

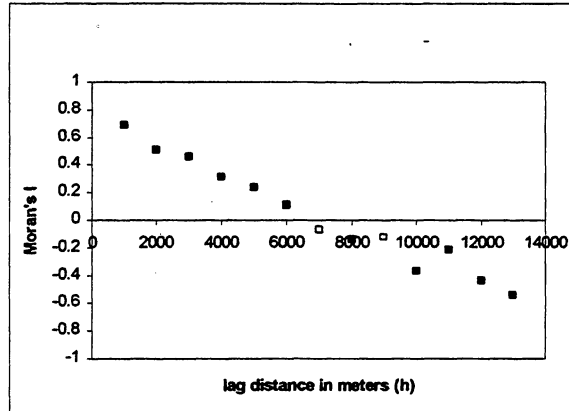


Figure 2.6. Moran's I correlogram for Urbanization Proportion (2000m radius). Shaded squares represent significant ($p < 0.05$) autocorrelation. Lag distance values represent maximum distances between pairs of points within each 1000m distance class.**

** Sample sizes for each distance class:

Maximum distance	1000	2000	3000	4000	5000	6000	7000	8000	9000	10000	11000	12000	13000
Number of Pairs	198	317	480	556	583	577	403	384	211	148	162	120	120

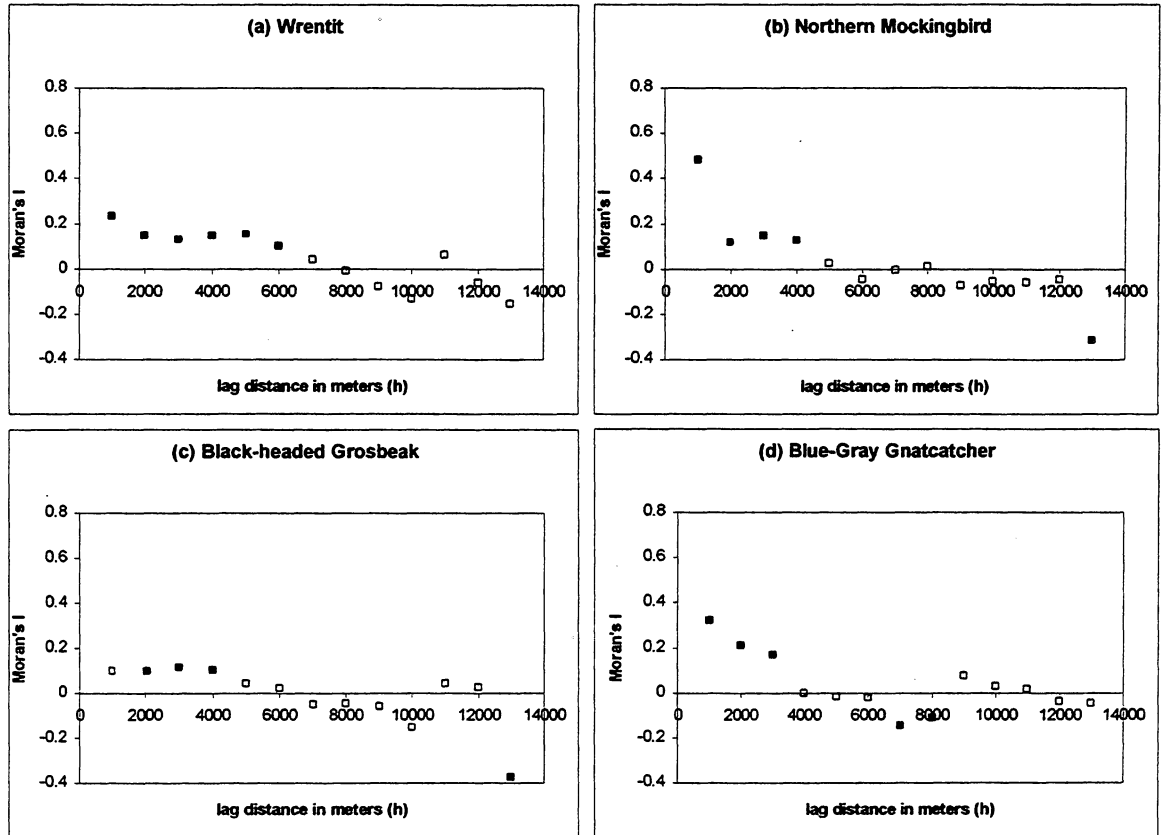


Figure 2.7. Moran's I correlograms for 1997 Maximum Bird Abundance. Shaded squares represent significant ($p < 0.05$) autocorrelation. Lag distance values represent maximum distances between pairs of points within each 1000m distance class.**

** Sample sizes for each distance class:

Maximum distance	1000	2000	3000	4000	5000	6000	7000	8000	9000	10000	11000	12000	13000
Number of Pairs	198	317	480	556	583	577	403	384	211	148	162	120	120

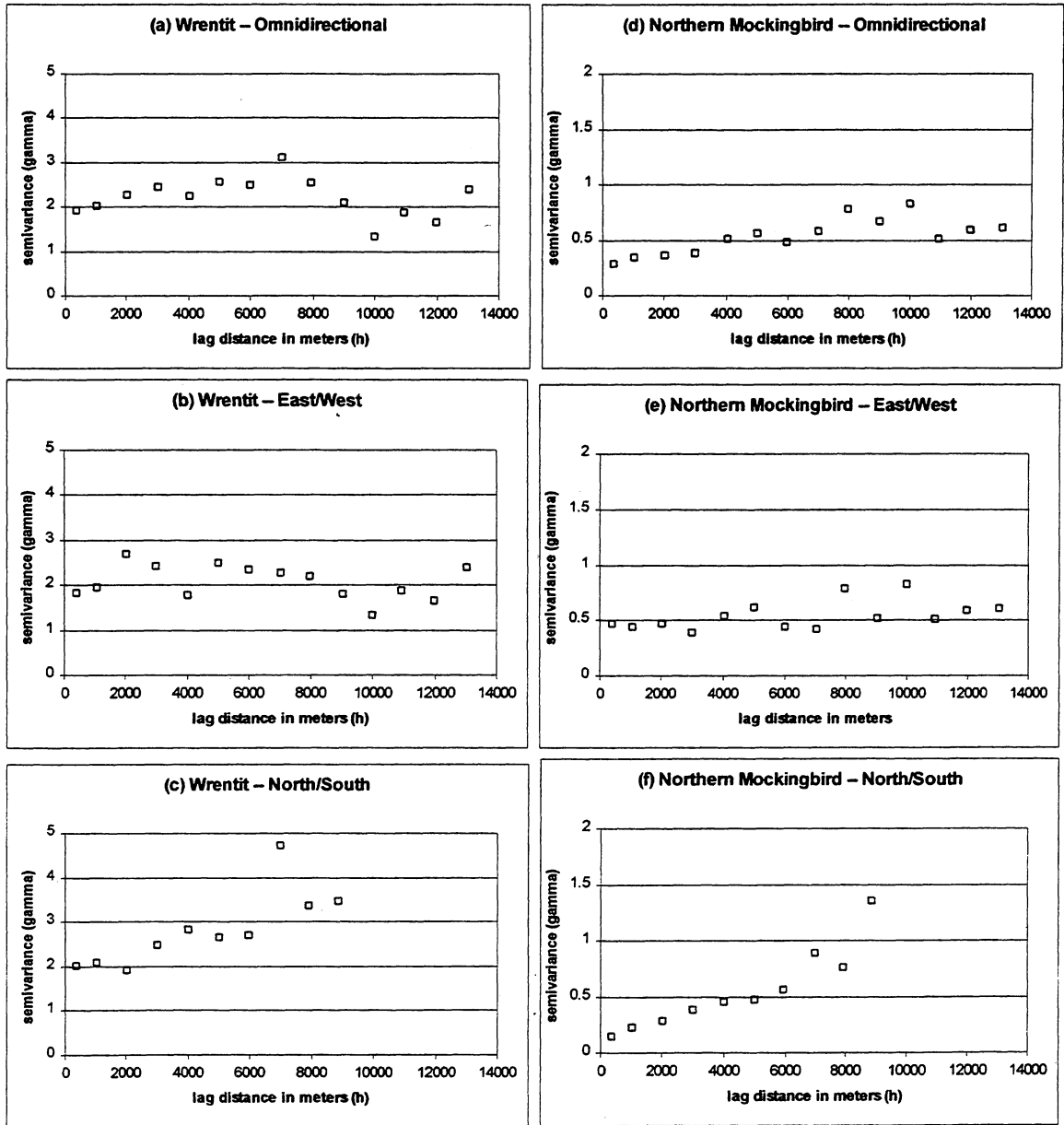


Figure 2.8. Empirical Semivariograms, $\gamma(h)$, for Non-Spatial Urbanization Model Residuals. East/West = 90° azimuth, 45° tolerance; North/South = 0° azimuth, 45° tolerance. Lag distance values represent averages distances between pairs of points within each 1000m distance class.*

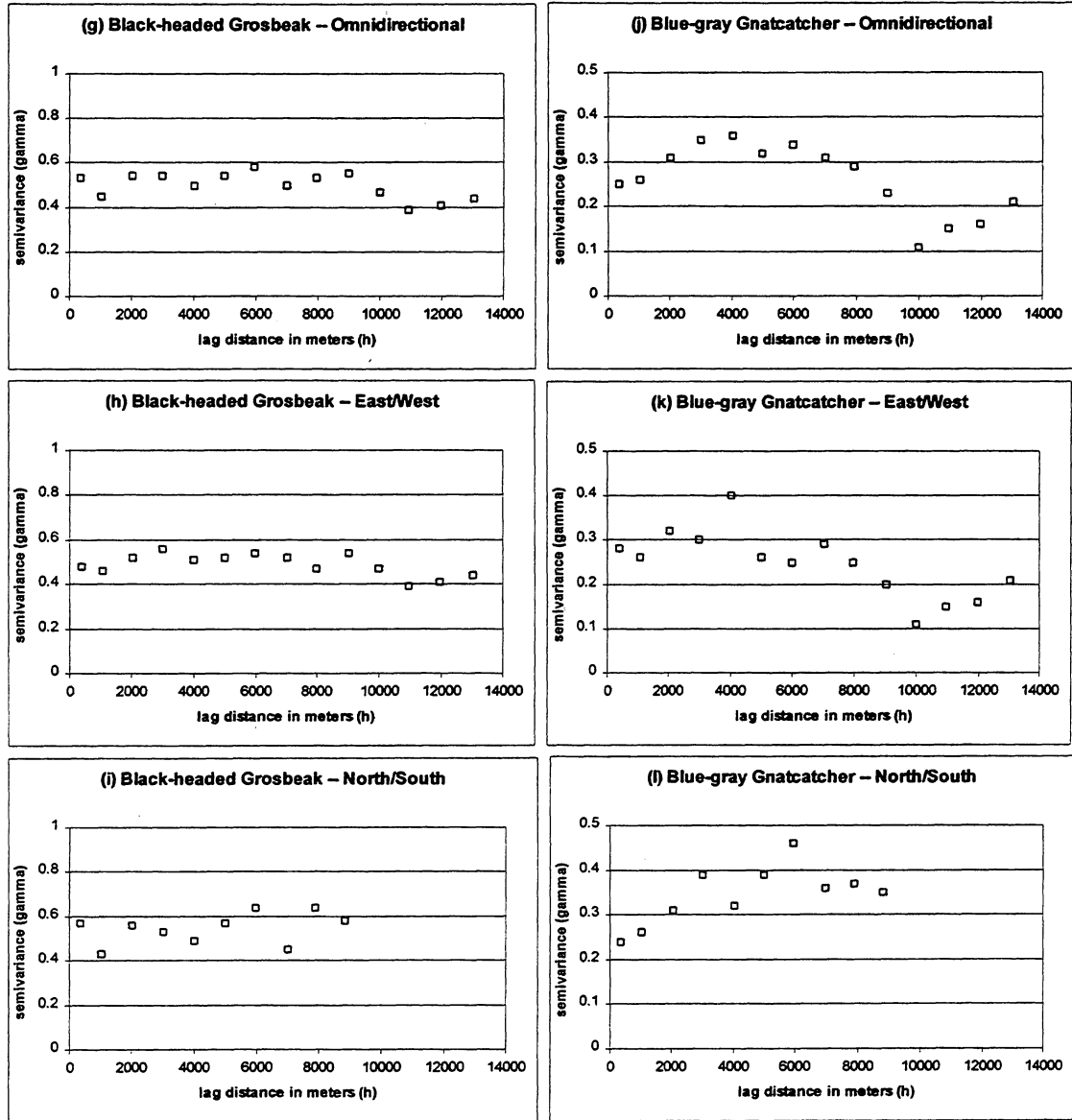


Figure 2.8. (continued)

* Sample sizes for each distance class in omnidirectional semivariograms:

Avg.dist.	361	1044	2038	3010	4024	5011	5980	7013	7950	8987	9989	10939	11972	13041
# Pairs	72	282	357	567	580	582	504	388	287	158	158	151	110	137
East/West:														
Avg.dist.	379	1060	2033	3002	4024	5010	5994	7020	7973	9021	9989	10939	11972	13041
# Pairs	31	164	166	297	322	332	292	256	199	130	158	151	110	137
North/South:														
Avg.dist.	348	1021	2043	3018	4025	5012	5960	6999	7898	8832				
# Pairs	41	118	191	270	258	250	212	132	88	28				

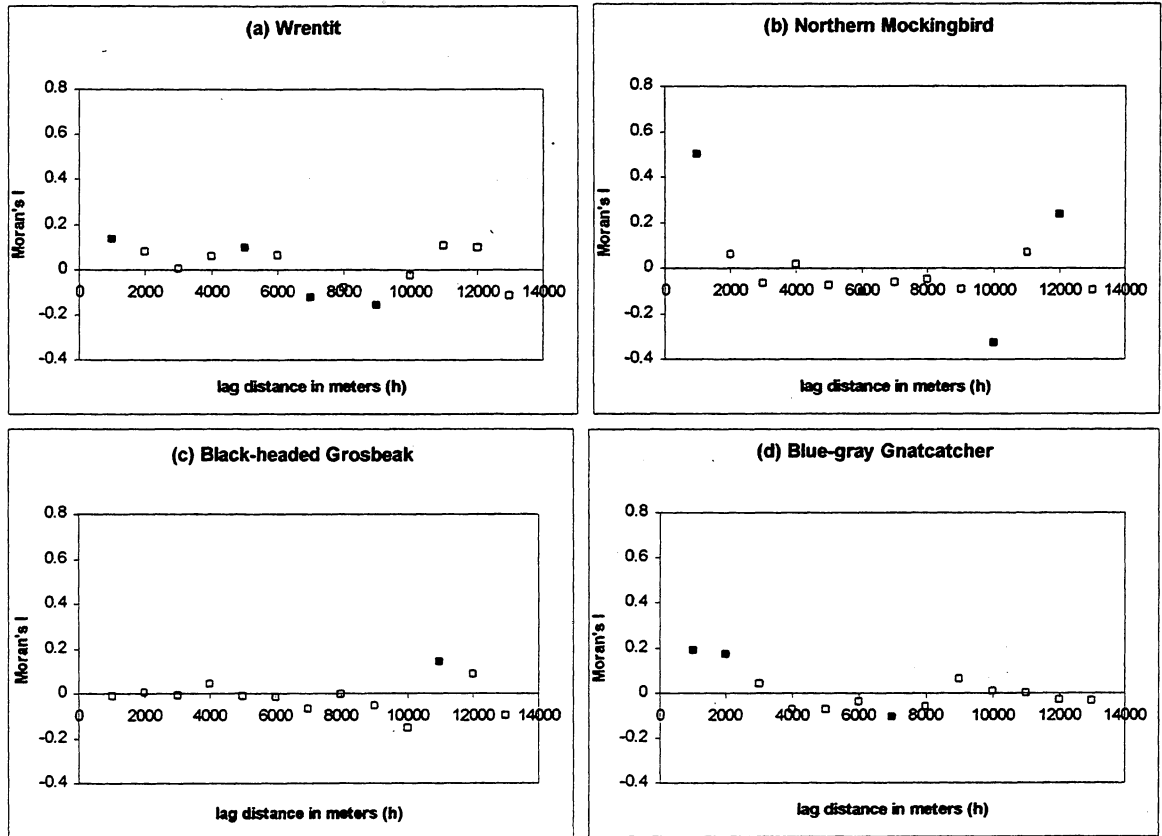


Figure 2.9. Moran's I correlograms for Non-Spatial Urbanization Model Residuals. Shaded squares represent significant ($p < 0.05$) autocorrelation. Lag distance values represent maximum distances between pairs of points within each 1000m distance class.**

** Sample sizes for each distance class:

Maximum distance	1000	2000	3000	4000	5000	6000	7000	8000	9000	10000	11000	12000	13000
Number of Pairs	198	317	480	556	583	577	403	384	211	148	162	120	120

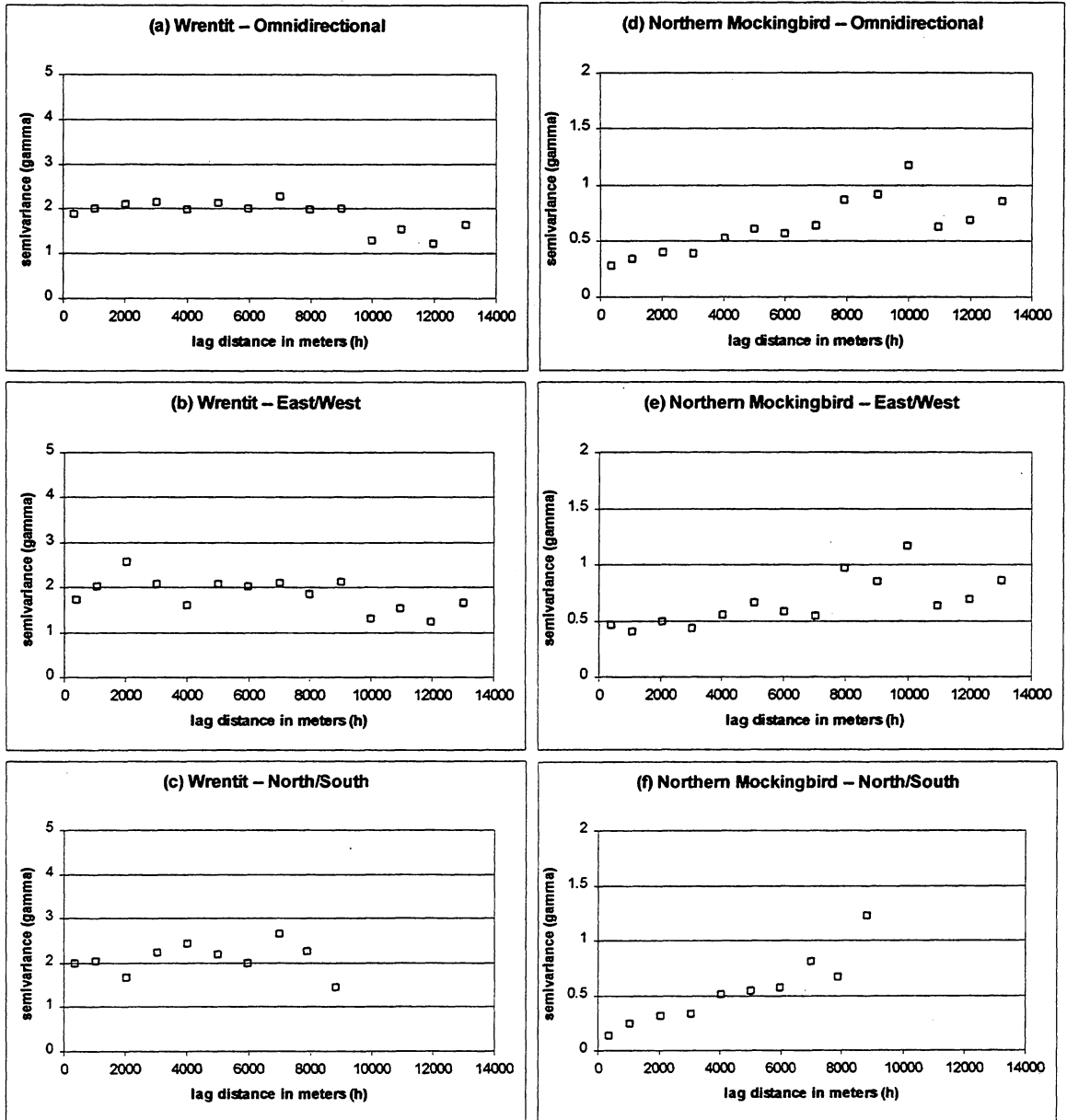


Figure 2.10. Empirical Semivariograms, $\gamma(h)$, for Detrended Urbanization Model Residuals. East/West = 90° azimuth, 45° tolerance; North/South = 0° azimuth, 45° tolerance. Lag distance values represent average distances between pairs of points within each 1000m distance class.*

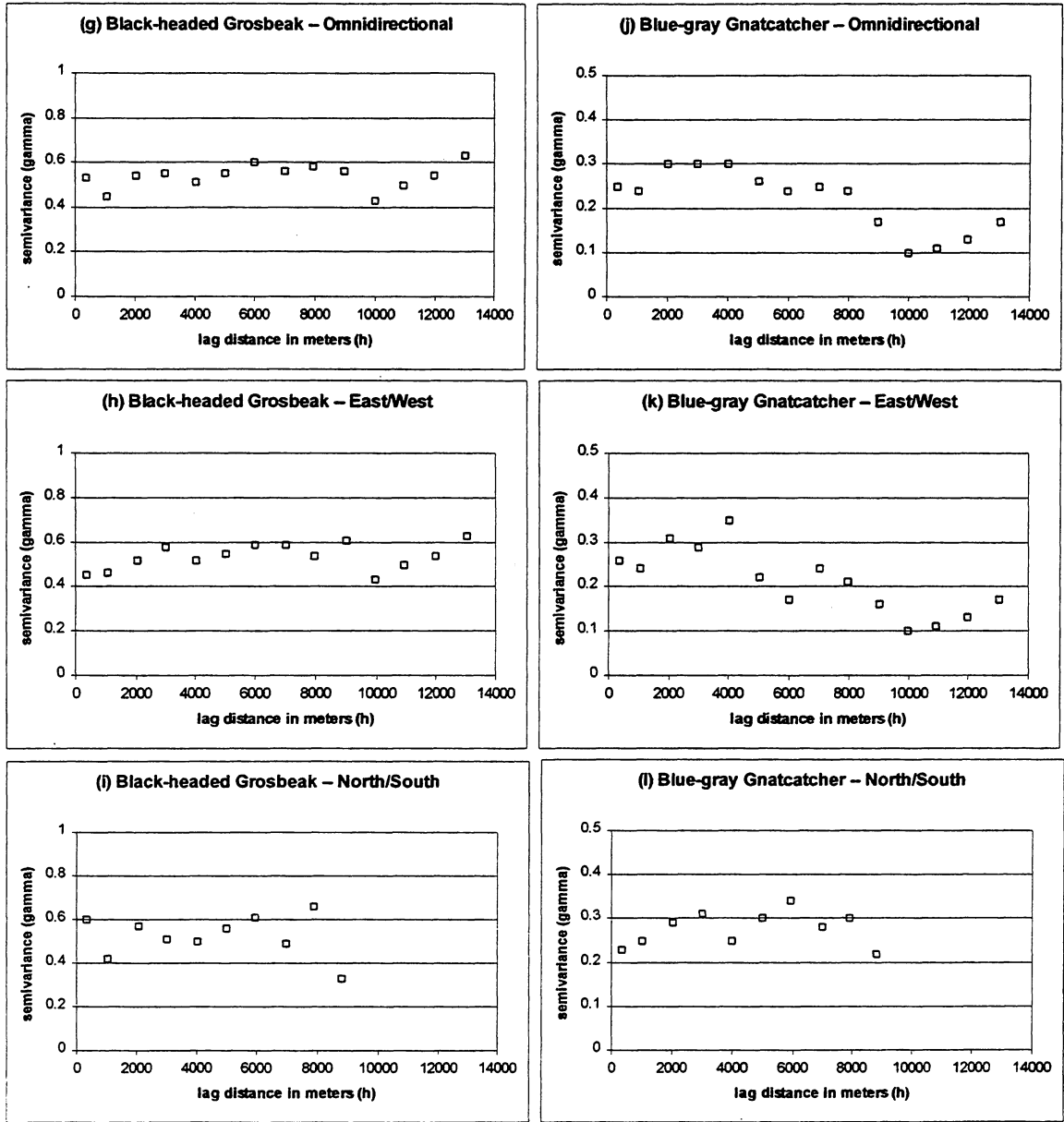


Figure 2.10. (continued)

* Sample sizes for each distance class in omnidirectional semivariograms:

Avg. dist.	361	1044	2038	3010	4024	5011	5980	7013	7950	8987	9989	10939	11972	13041
# Pairs	72	282	357	567	580	582	504	388	287	158	158	151	110	137
East/West:														
Avg. dist.	379	1060	2033	3002	4024	5010	5994	7020	7973	9021	9989	10939	11972	13041
# Pairs	31	164	166	297	322	332	292	256	199	130	158	151	110	137
North/South:														
Avg. dist.	348	1021	2043	3018	4025	5012	5960	6999	7898	8832				
# Pairs	41	118	191	270	258	250	212	132	88	28				

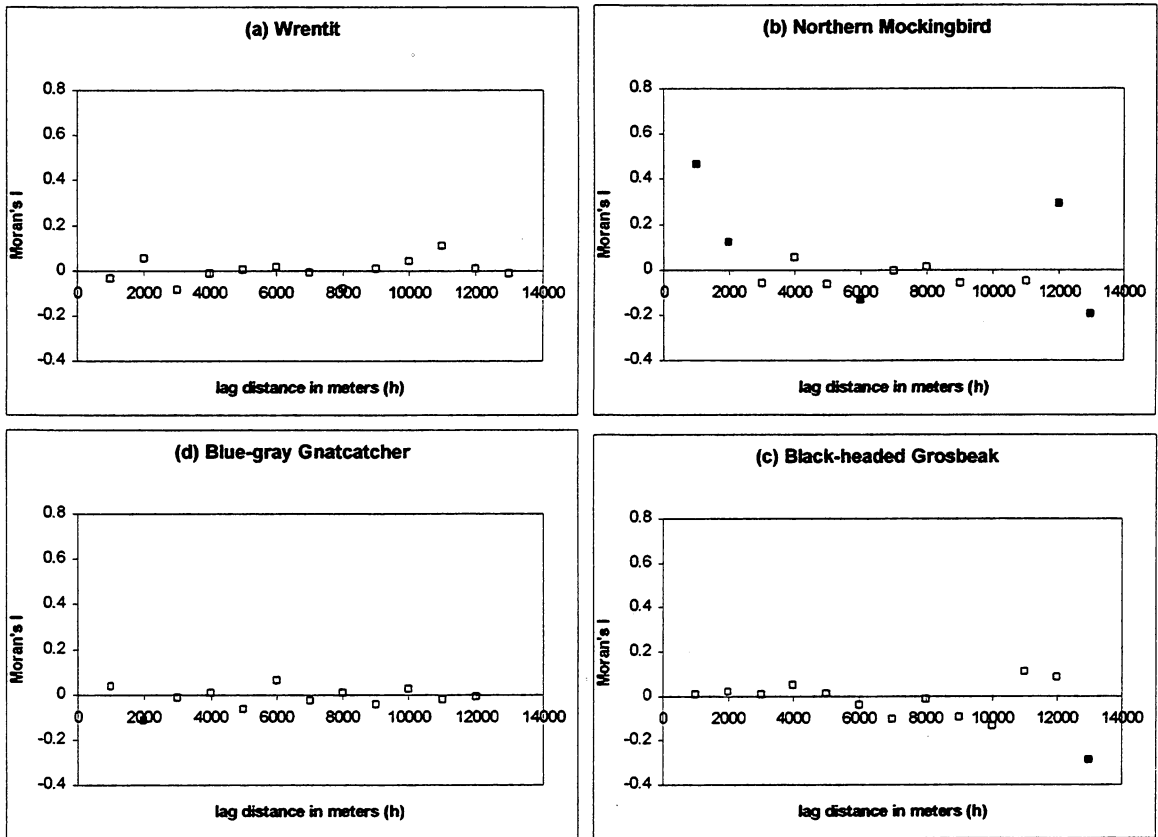


Figure 2.11. Moran's I correlograms for Detrended Urbanization Model Residuals. Shaded squares represent significant ($p < 0.05$) autocorrelation. Lag distance values represent maximum distances between pairs of points within each 1000m distance class.**

** Sample sizes for each distance class:

Maximum distance	1000	2000	3000	4000	5000	6000	7000	8000	9000	10000	11000	12000	13000
Number of Pairs	198	317	480	556	583	577	403	384	211	148	162	120	120

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