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Source: *Conservation Biology*, Apr., 1997, Vol. 11, No. 2 (Apr., 1997), pp. 406-421

Published by: Wiley for Society for Conservation Biology

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Breeding Bird Abundance in an Urbanizing Landscape in Coastal Southern California

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Abstract: *The relative influence of local versus landscape heterogeneity on species abundance is an important consideration in the design and management of nature reserves in heterogeneous landscapes. We described the spatial patterns of resident breeding bird abundance at a landscape scale in an urbanizing landscape gradient in coastal San Diego County, California (USA). The gradient spanned approximately 260 km² and included a large, mostly contiguous block of undeveloped shrub habitat mosaic which graded into an area of internally fragmented habitat and finally into an area characterized by discrete patches of habitat in an urban matrix. We quantified the distribution of resident bird species in this landscape with point counts and used stepwise logistic regression and canonical correspondence analysis to explore the relative strengths of association between bird abundance and local habitat variation versus landscape variation for the 20 most common bird species. We measured local habitat conditions in a 100-m radius around each point count station. Landscape variables were extracted from a GIS database of this region and included habitat patch size, distance to developed edge, and two indices of urban exposure. The addition of landscape variables to stepwise logistic regression analyses substantially improved the predictive power of the resulting models in 14 of 20 species. Model concordance (the ability of the model to correctly classify all pairs of divergent sites) increased from a mean of 56% without landscape variables to 76% when one or more landscape variables were selected for inclusion in the final model. Response of the 20 focal species to the landscape gradient differed markedly among species. Canonical correspondence analysis was used to rank species along a landscape response gradient from edge/fragmentation reduced species to edge/fragmentation enhanced species. The four species exhibiting the most edge/fragmentation reduced pattern were sparrows: Sage (Amphispiza belli), Rufous-crowned (Aimophila ruficeps), Lark (Chondestes grammacus), and Black-chinned sparrows (Spizella atrogularis). Costa's Hummingbird (Calypte costae) also showed a pattern of edge/fragmentation reduction. The opposite end of the gradient was occupied by species whose densities are elevated near edges and in fragmented areas. The middle of the gradient was occupied by species that were abundant, widely distributed, and showed no sensitivity to landscape position or shrub habitat type. The abundance of edge/fragmentation reduced species appears to be depressed within 200 to 500 m of an edge and the abundance of the edge/fragmentation enhanced species is elevated up to 1000 m from an edge, depending on the species. Conservation analyses, including GAP analysis, often assume that the relationship between species abundance and habitat is invariant with landscape position. In heterogeneous landscapes these analyses may underestimate the conservation risk to species in the edge/fragmentation sensitive category because their abundance varies strongly with landscape location.*

Abundancia de Aves Reproductoras en un Paisaje Urbanizado en la Costa Sur de California

Resumen: *La influencia relativa de heterogeneidad local y de paisaje en abundancia de especies es de importante consideración en el diseño y manejo de reservas naturales en paisajes heterogéneos. Describimos los patrones espaciales de aves reproductoras residentes a escala de paisaje en un paisaje con gradiente de ur-*

Paper submitted January 11, 1996; revised manuscript accepted November 14, 1996.

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Conservation Biology, Pages 406–421
Volume 11, No. 2, April 1997

banización en la costa del municipio de San Diego, California (USA). El gradiente se extiende por aproximadamente 260 km² e incluye un bloque grande casi contiguo de mosaicos de hábitat arbustivo poco desarrollado que atravieza un área de hábitat internamente fragmentado y finaliza en un área caracterizada por parches discretos de hábitat en una matriz urbana. Cuantificamos la distribución de especies de aves residentes en este paisaje con puntos de conteo y usamos una regresión logística por pasos y un análisis de correspondencia canónica para explorar el grado relativo de asociación entre la abundancia de aves y la variación local del hábitat contra la variación del paisaje para las 20 especies de aves mas comunes. Medimos las condiciones locales de hábitat en un radio de 100 m alrededor de cada estación de conteo. Las variables de paisaje fueron extraídas de una base de datos del Sistema de Información Geográfico (GIS) de la región y que incluye el tamaño del parche, distancia hasta el borde desarrollado y dos índices de exposición urbana. La adición de variables del paisaje al análisis de regresión logística por pasos mejoró sustancialmente el poder predictivo de los modelos resultantes en 14 de las 20 especies. La concordancia del modelo (habilidad del modelo para clasificar correctamente todos los pares de sitios divergentes) incrementó de un promedio de 56% sin variables del paisaje a un 76% donde una o mas variables del paisaje fueron seleccionadas para su inclusión en el modelo final. La respuesta de las 20 especies al gradiente del paisaje varió considerablemente entre especies. El análisis de correspondencia canónica fue usado para ubicar las especies en rangos a lo largo de un gradiente de respuesta al paisaje a partir de especies con reducido borde/fragmentación hasta especies con mayor borde/fragmentación. Las cuatro especies que exhibieron los patrones de reducción de borde/fragmentación mas fuerte fueron: *Amphispiza belli*, *Aimophila ruficeps*, *Chondestes grammacus* y *Spi-zella atrogularis*. *Calypte costa* también mostró un patron de reducción de borde/fragmentación. El sitio opuesto del gradiente fue ocupado por especies cuyas densidades son elevadas cerca de los bordes y en áreas fragmentadas. El punto medio del gradiente fue ocupado por especies que son abundantes, ampliamente distribuidas y no muestran sensibilidad a la posición del paisaje o tipo de hábitat arbustivo. La abundancia de especies reducidas en borde/fragmentación aparentemente disminuye dentro de los 200 y 500 m de un borde y la abundancia de las especies con mejor borde/fragmentación se eleva mas alla de los 1000 m de un borde, dependiendo de la especie. Análisis de conservación, incluyendo GAP análisis frecuentemente asumen que la relación entre abundancia de especies y hábitat no cambia con la posición del paisaje. En paisajes heterogeneos estos análisis pueden desestimar el riesgo de conservación para especies en una categoria sensitiva de borde/fragmentación debido a que su abundancia varía fuertemente con la ubicación del paisaje. Modelo de metapoblación basado en el hábitat de *Polioptila c. californica*.

Introduction

In pure and applied ecology there has been a broadening of spatial scope from an emphasis on local-scale processes to a more explicit understanding that processes that regulate plant and animal populations occur at a variety of spatial scales. The field of landscape ecology (Forman & Godron 1986; Turner 1989) has focused attention on the influence of landscape-scale patterns of habitat heterogeneity on animal and plant species distributions. In avian ecology there has long been interest in the relationship between bird abundance and local habitat variation (Verner et al. 1986). Larger scale influences, such as patch size, were initially investigated in sets of isolated habitat fragments (Lynch & Whigham 1984; Blake & Karr 1987; Soulé et al. 1988). Until recently (Puliam et al. 1992; Pearson 1993; Knick & Rotenberry 1996), however, most studies of bird species habitat associations have not explicitly examined both local habitat variation and landscape-level variation. The change in spatial emphasis has been particularly relevant to conservation because conservation is often practiced at the landscape scale through the design and management of nature reserves. Effective design and management of reserves must incorporate consideration of these large-scale processes.

The focus of wildlife management research and practice has undergone a similar change from the local to the landscape scale. Since the 1970s there has been a great deal of interest in modeling the relationship between vertebrate abundance and the composition and structure of local habitat. Statistical wildlife-habitat relationship (WHR) models were developed to estimate quantitative relationships between habitat and species abundances. These models have been used to estimate total abundance of a species, predict abundance in unsurveyed areas, and predict changes in abundance that would result from potential habitat modifications (Verner et al. 1986; Morrison et al. 1992). More recently the GAP analysis project (Scott et al. 1993) has shifted management focus (in U.S. federal agencies) to the landscape and regional scale. In a GAP analysis vertebrate species protection status is assessed by combining WHR models derived from local data with regional-scale habitat maps to produce region-wide estimates of vertebrate species distribution and abundance (Scott et al. 1993; Edwards et al. 1996). This represents a mismatch between the scale at which the species-habitat relationships have been modeled and that at which they are being used to make predictions (Scott et al. 1993). Using WHR models based on local species-habitat relationships as part of a GAP analysis to make landscape and regional-scale predictions assumes

that the relationship between species abundance and local habitat variation is independent of landscape setting. This "coarse-filter approach" (Scott et al. 1993) may often be sufficient to the task at hand (Edwards et al. 1996); however, for certain applications or conditions this method may be seriously deficient. The predictions of vertebrate distribution and abundance arising from GAP analyses will be particularly inaccurate if landscape-scale patterns are important components of habitat suitability for the species modeled and if the landscapes of concern are highly heterogeneous.

Much of the heterogeneity in many landscapes is a result of the conversion of natural habitat to human land uses such as agriculture, forestry, and urban development. Habitat conversion has two effects on the spatial characteristics of natural landscapes: the reduction in total habitat area and the redistribution of the remaining habitat into disjunct fragments interspersed in a modified landscape matrix (Forman & Godron 1986; Wilcove et al. 1986). Particularly important landscape influences in these modified landscapes are patterns of habitat fragmentation (Wilcove et al. 1986; Robinson et al. 1992) and edge effects (Paton 1994). The effect of landscape patterns of edge and patch size on faunal communities may be mediated through changes in the abundance of predators, parasites, competitors, or resources.

The ecosystems of coastal southern California are marked by high habitat diversity, species diversity, and endemism (McCaull 1994). Conversion of habitat to human land uses is the major cause of the landscape-scale variation in these ecosystems. Regional-scale conservation planning efforts are now on-going in southern California with the stated objective of designing and implementing a nature reserve system to conserve biological diversity in the face of development pressure.

The State of California's Natural Communities Conservation Planning Program (NCCP) has focused its conservation planning on the coastal sage scrub habitat. This habitat has been reduced to 10–15% of its former extent and supports the California Gnatcatcher (*Poliioptila californica*), listed as threatened by the U.S. Fish and Wildlife Service, and approximately 100 other animal and plant species considered rare, sensitive, threatened, or endangered by California or federal wildlife agencies (McCaull 1994). Coastal sage scrub habitat occurs only in the densely populated, low elevation coastal areas of southern California (Davis et al. 1995).

In coastal southern California it is particularly important to consider the effects of landscape-scale heterogeneity on species abundance. Although the design of the NCCP reserve system is not complete, it seems inevitable that it will include areas where there is extensive interface between urban development and natural habitat. Conserving species in these landscapes will be challenging, particularly those species that respond negatively to the interdigitation of habitat and development. Previous

research on habitat fragmentation in this region has focused on relatively small (1–100 ha), isolated patches of habitat (Soulé et al. 1988, 1992; Bolger et al. 1991, in press; Alberts et al. 1993). We have little understanding of the response of individual bird species to landscape heterogeneity at the larger scale that will be encompassed in a reserve system. It seems important at this juncture to identify those species that respond strongly to landscape-scale patterns of development and habitat. These are the species for which a regional-scale conservation assessment might not adequately represent the risk to the species or the management challenge the species poses.

We describe the spatial patterns of breeding bird abundance in a partially urbanized landscape mosaic in coastal San Diego County, California. One objective was to determine the relative strengths of association of bird abundance with local habitat conditions versus landscape-scale variation due to patterns of land development. We test the hypothesis that for some species, local abundance will be significantly associated with landscape-scale patterns of interspersed natural habitat and urban development. Our second objective was to qualitatively categorize species as edge/fragmentation reduced, edge/fragmentation enhanced, and edge/fragmentation insensitive. Such a categorization is valuable for prioritizing conservation research and planning efforts. Ultimately, we hope to understand the mechanisms that generate landscape patterns of bird abundance. This knowledge would allow species to be more effectively conserved in the region.

Methods

Study Area

The study area occupies approximately 260 km² in the City and County of San Diego, California, and encompasses a pronounced gradient in landscape pattern (Fig. 1). The eastern portion of the gradient is composed of large patches of native habitat, the boundaries of which are determined by residential and commercial development. Proceeding west this development occupies a higher percentage of the landscape, and though there are still large patches of undeveloped land, the patch boundaries are more convoluted and patches are internally fragmented by development. The western portion of the gradient is characterized by a residential landscape matrix surrounding discrete, island-like patches of habitat ranging in size from 50 to 400 ha. The large patches of natural habitat in the east and central portion of the study area include the U.S. Navy facilities Miramar Naval Air Station and Camp Elliott, and Mission Trails City Park. The largest island-like patch in southwestern portion of the study area is Tecolote Canyon Natural Park.

The vegetation of this area is a mosaic composed predominantly of three shrub habitat types (coastal sage scrub, chamise chaparral, and mixed chaparral) and smaller amounts of riparian vegetation and exotic grassland (Beauchamp 1986). The spatial distribution of these habitats depends on local topography and disturbance history. In undisturbed conditions, mixed chaparral occurs on steep north, east, and west facing slopes. Chamise chaparral occurs on mesa tops, and coastal sage scrub occurs on south facing slopes and in flatter areas. Disturbance history in this area affects the relative abundance of the shrub habitats (Zedler et al. 1983). Fire and mechanical disturbance of shrub habitats initiates a change from all three shrub types to exotic grasslands and coastal sage scrub. These factors combine to produce a landscape that is vegetatively patchy at a small (hectare) scale.

GIS Database

The database was constructed by photointerpretation of 1:36,000 aerial photographs flown in October, 1990. Land cover was classified into two categories, developed land and undeveloped natural habitat, and polygon boundaries were mapped onto U.S.G.S. 1:24,000 scale quad sheets with the aid of a zoom transfer scope. The minimum mapping unit was 4 ha, so polygons of any landuse type less than that size were not mapped. Polygon boundaries were hand digitized into an ARCINFO GIS database. Polygon boundaries were defined by an edge between developed land and natural habitat, and by multilane highways. Surface roads were not mapped in our GIS and thus were not used to define polygon boundaries. Because it was not possible to reliably differentiate among the shrub habitat types in this region with 1:36,000 aerial photos, all habitats were lumped into the natural habitat category. Consequently, landscape-scale patterns of the interspersions of vegetation types will not be explicitly considered here.

Point Counts of Bird Abundance

Single 8-minute point counts (Ralph et al. 1992) were conducted at 202 locations. The counts occurred between 11 April and 1 June, 1993. All counts were performed between sunrise and 1030 hours. Detections of all birds were recorded and the distance to the detection estimated with the aid of a rangefinder. In the subsequent analyses the data used are those detections within 100 m of the observation point.

The point locations were randomly chosen with the help of the GIS database. Points were all within the undeveloped portion of the landscape, at least 200 m apart and at least 100 m from a developed edge. To choose the point locations a 200-m grid was generated and superimposed on the GIS habitat coverage. A random subset of 202 of these points was chosen using a random

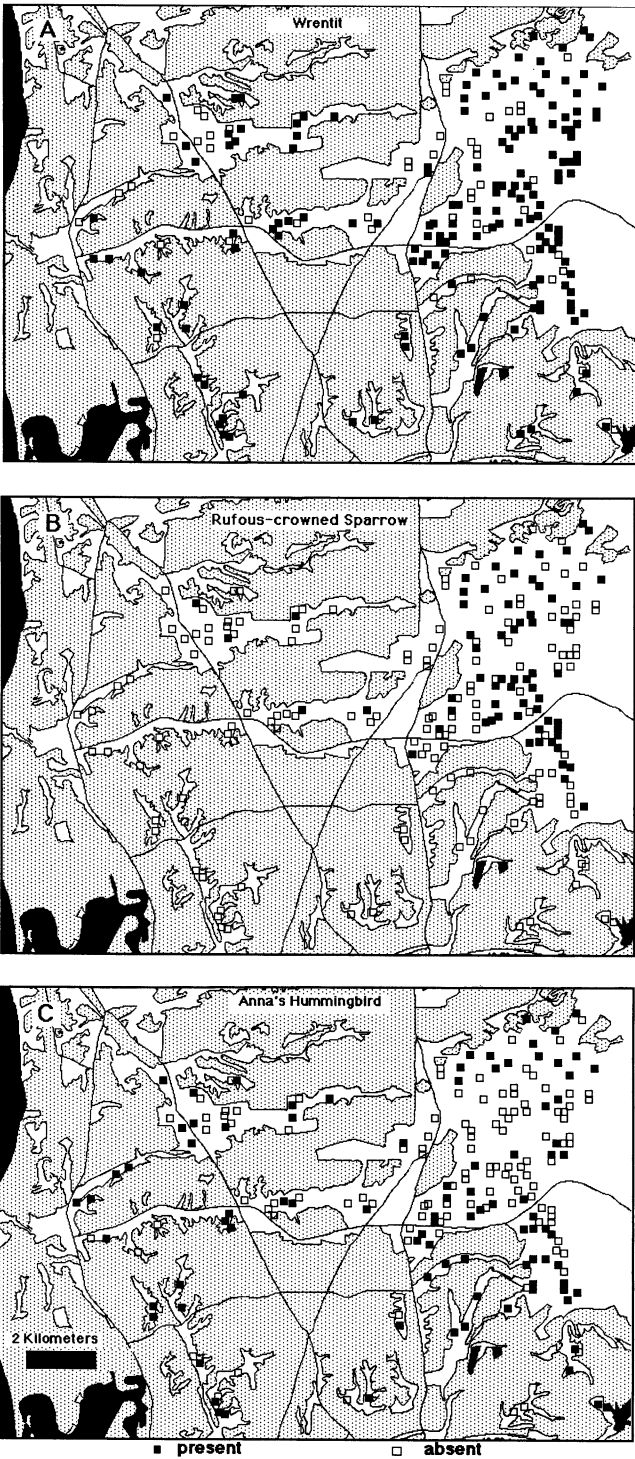


Figure 1. Landscape distribution of Wrentit, Rufous-crowned Sparrow, and Anna's Hummingbird in south-coastal San Diego County, California. Stippled area represents the developed portions of the landscape. The white area is a habitat mosaic of coastal sage scrub and chaparral. Black areas are water. Lines are multilane state and interstate highways. Filled boxes mark point count locations at which the species was detected. Open boxes are points at which the species was not detected. The body of water in the lower left corner of the map is Mission Bay.

number algorithm. If ground-truthing revealed that the random point fell within a patch of riparian or grassland vegetation, the point was discarded or moved slightly so that the vegetation surveyed was primarily shrub habitat.

Our objective was to maximize our power to make statistical inferences about the association of bird abundance with landscape and habitat variation. To accomplish this we increased our replication in space rather than censusing fewer points and performing multiple point counts at each point. This methodology leads to less certainty about a particular species absence at any individual point, but more certainty of the relationship of species abundance to variation in landscape and habitat variables.

Because it was not our intention to generate estimates of absolute density or to compare density between species, an analysis of relative detectability was not necessary. Detections within a fixed, 100-m radius give a relative index of abundance which could be compared within a species between sites that differ in landscape and habitat variables.

Landscape and Local Habitat Variables

Several variables measured from the GIS database were used to describe the landscape context of each point, including the size of the patch of undeveloped habitat in which the point is located (POLYAREA), the distance from the point to the nearest developed edge (EDGEDIST), and several buffer variables measured at radii of 250, 500, 1000, 2000, and 3000 m. These buffer measurements were the proportion of undeveloped habitat within the buffer circle (NAT250, NAT500, NAT1000, NAT2000, NAT3000) and the amount of linear edge between developed land and undeveloped habitat within the buffer (EDGE250, EDGE500, EDGE1000, EDGE2000, EDGE3000). An urban exposure index was constructed from the proportions of developed land in concentric rings around the point extending out to 250, 500, 1000, and 2000 m. The proportion in the 250-m circle was given a weight of 1.0; the proportion in the 500-m buffer a weight of 0.5; 1000-m a weight of 0.25, and 2000-m a weight of 0.125. These weighted proportions were then summed to form the exposure index (URB_EXP). An index of the amount of edge between developed land and habitat was constructed in an analogous fashion (EDGE_EXP).

A variety of variables were measured to describe the local habitat and physical conditions in a 100-m circle surrounding each point count location. A Braun-Blanquet scale (six categories of percent cover: <1%, 1–5%, 6–15%, 16–30%, 31–50%, 51–75%, 76–100%) was used to estimate the total shrub cover (SHRUB), tree cover (TREES), grass/herbaceous cover (HERB), and bare ground (BARE). Similarly, the percent cover of any shrub or tree species that occupied more than 1% of the 100-m radius circle was also estimated. The percent cover of five habitat types: coastal sage scrub (CSS), mixed chaparral (MIXED), chamise chaparral (CHAM), riparian woodland and scru-

bland (RIPARIAN), and grassland (GRASS) was estimated to the nearest 10%. The presence or absence of a recent burn within the circle was noted (BURN). The average height of each shrub species in the plot was estimated to the nearest meter, and slope and aspect were measured. Several indices were derived from these variables including shrub species diversity (SP_DIV), height diversity (HI_DIV), and habitat diversity (HAB_DIV) using the Shannon-Wiener formula (Krebs 1989).

Logistic Regression

Stepwise logistic regression (SAS Statistical Institute 1990) was used to assess the relative strength of association between the presence and absence of individual species and landscape and local habitat variables. First the presence/absence of each species at each point was regressed on the local habitat variables. Then the landscape descriptors were added to the list of independent variables and the analysis was rerun. The predictive ability of each model was assessed by its concordance score (SAS Statistical Institute 1990). Concordance is calculated as a percentage of all possible combinations of sites where at one site of the pair the species being analyzed is present, and at the other site, absent. A pair is concordant if the logistic model predicts a higher probability of species presence for the “presence” site than the “absence” site (SAS Institute Inc. 1990). Concordance is thus a measure of rank correlation between the predicted probability of “presence” and the actual presence/absence of the site. Rank correlation measures give an approximate measure of predictive power and are useful for comparing the relative fit of different models to the same data set (Agresti 1996). A model with a higher concordance score has a greater ability to correctly classify sites as present or absent. Deviance (D) has sometimes been used to compare the fit of different logistic models to biological data (Trexler & Travis 1993). However, logistic models are most appropriately fit with maximum likelihood methods, and D is calculated as the logarithm of the maximum likelihood ratio for the model. Consequently, D does not provide an intuitive, linear interpretation of model fit and predictive ability such as that provided by the r^2 of a least squares regression. We have used concordance as our model diagnostic because it does allow a linear interpretation and thus provides a more intuitive interpretation of the relative predictive abilities of different models (see Hosmer & Lemeshow [1989] for caveats on the use of this type of diagnostic for interpreting model fit).

Canonical Correspondence Analysis

To examine the associations among local and landscape-scale variation and breeding bird community composition at our sites we used the program CANOCO to per-

form a canonical correspondence analysis (CCA) (Ter Braak 1986). The CCA is a multivariate direct ordination technique that is useful for qualitatively summarizing the divergent associations of members of a community to relevant ecological gradients. Species are ordered on axes constrained to be linear combinations of the independent variables. The CCA assumes a unimodal relationship between species abundance and the relevant environmental variables. It creates synthetic variables (axes) that maximally separate (ordinate) the unimodal distributions of the species. If species abundance is affected by the environmental variables measured and species differ in their response to these variables, then CCA can order their distributions along the axes created from these variables. The eigen-values associated with each axis give a relative indication of the ability of the axis to separate or order species distributions. We ordinated species abundance (number of unique detections within 100 m) at each point using the local and landscape variables described above. The significance of the ordinations was determined with Monte Carlo permutation tests performed by the CANOCO program.

Results

Distribution Maps

Inspection of distribution maps for each species suggested three general types of patterns (Fig. 1). Pattern

one is relatively high abundance in all parts of the landscape and was exhibited by the Wrentit (Fig. 1), Rufous-sided Towhee, California Towhee, Bewick’s Wren, Scrub Jay, Common Bushtit, California Thrasher, California Quail, and Mourning Dove. The California Gnatcatcher also displayed a similar distribution but was much less abundant than the other species in this category (Table 1). Pattern two was exemplified by the Rufous-crowned Sparrow (Fig. 1), which had a pattern of relatively high abundance in the larger patches in the landscape and rarity in the more fragmented areas. The Sage Sparrow, Western Meadowlark, and Costa’s Hummingbird also displayed this pattern, as did the Black-chinned Sparrow and Lark Sparrow, but these latter two species are much less abundant than the others (Table 1). The third pattern appears to be one of edge enhancement; for instance, Anna’s Hummingbird abundance was much higher in highly fragmented areas, and adjacent to developed edges (Fig. 1). Northern Mockingbird, Lesser Goldfinch, and House Finch shared this pattern.

Canonical Correspondence Analysis

Canonical correspondence analysis was used to examine the relative strengths of association of the bird community with habitat and landscape descriptors (Fig. 2). The ordination was significant ($p < 0.01$) and the first canonical axis (eigen-value = 0.178) was essentially a landscape axis, contrasting sites with large values of the

Table 1. Detection frequency and edge/fragmentation sensitivity category for the 20 most common breeding birds recorded at 202 point count stations.^a

Abbreviation ^b	Common name	Scientific name	Number of sites detected	Number of detections per all sites	Number of detections per sites detected	Category of edge/fragmentation sensitivity
BCSP	Black-chinned Sparrow	<i>Spizella atrogularis</i>	21	0.13	1.29	reduced
SAGS	Sage Sparrow	<i>Amphispiza belli</i>	30	0.24	1.60	reduced
LASP	Lark Sparrow	<i>Chondestes grammacus</i>	15	0.12	1.67	reduced
RCSP	Rufous-crowned Sparrow	<i>Atmophila ruficeps</i>	65	0.49	1.51	reduced
COHU	Costa’s Hummingbird	<i>Calypte costae</i>	22	0.11	1.00	reduced
WEME	Western Meadowlark	<i>Sturnella neglecta</i>	44	0.32	1.48	reduced
CAQU	California Quail	<i>Callipepla californica</i>	85	0.81	1.92	insensitive
CATH	California Thrasher	<i>Toxostoma redivivum</i>	66	0.42	1.27	insensitive
RSTO	Rufous-sided Towhee	<i>Pipilo erythrophthalmus</i>	141	1.17	1.68	insensitive
WREN	Wrentit	<i>Chamaea fasciata</i>	143	1.20	1.70	insensitive
BEWR	Bewick’s Wren	<i>Thyomanes bewickii</i>	115	0.93	1.63	insensitive
CATO	California Towhee	<i>Pipilo crissalis</i>	160	1.57	1.98	insensitive
CAGN	California Gnatcatcher	<i>Polioptila californica</i>	14	0.09	1.36	insensitive
SCJA	Scrub Jay	<i>Aphelocoma coerulescens</i>	76	0.50	1.34	insensitive
COBU	Common Bushtit	<i>Psaltiriparus minimus</i>	85	1.32	3.14	insensitive
MODO	Mourning Dove	<i>Zenaidura macroura</i>	85	0.73	1.73	insensitive
NOMO	Northern Mockingbird	<i>Mimus polyglottos</i>	41	0.24	1.20	enhanced
ANHU	Anna’s Hummingbird	<i>Calypte anna</i>	96	0.62	1.31	enhanced
LEGO	Lesser Goldfinch	<i>Spinus psaltria</i>	37	0.35	1.89	enhanced
HOFI	House Finch	<i>Carpodacus mexicana</i>	78	1.42	3.67	enhanced

^aBased on the analysis presented in the text, species were assigned to categories representing their associations with landscape scale variables. Order of species is the same as their ranking on CCA axis 1 (Fig. 2).
^bAmerican Ornithological Union species abbreviations used in subsequent tables and figures.

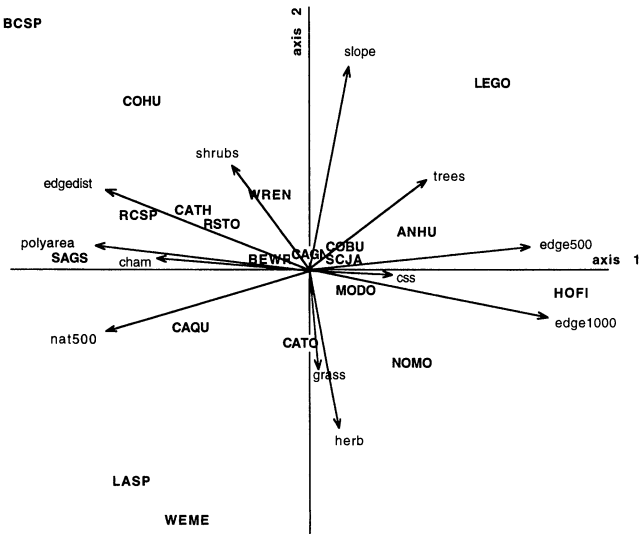


Figure 2. Canonical correspondence analysis ordination diagrams of 20 bird species ordered on axes that are linear combinations of local and landscape variables. Bird species abbreviations are defined in Table 1. Axis one is most strongly correlated with the landscape variables and axis two with the local habitat variables. Locations of the center of each species distribution on the axes is given by the projection from the species abbreviation to the axis. Variables are marked with arrows with variable name abbreviations at their ends. The angle of the arrows with the axes is indicative of their correlation with the axes. Arrows that are parallel with an axis are highly correlated, those that are perpendicular are uncorrelated. The length of the arrows are representative of the extent to which species distributions differ along the range of that environmental variable (Ter Braak 1986). Some of the independent variables with lower correlations were not included in the diagram to simplify the figure.

polygon area variables, the natural area buffer variables, and the EDGEDIST variable with sites with large values for the edge buffer measures (Fig. 2, Table 2). Thus bird species at the positive end of axis one were associated with smaller patches and points near developed edges, whereas those at the negative end of the axis were associated with interior areas.

The percent cover of coastal sage scrub and chamise chaparral were also correlated with the first axis (Fig. 2, Table 2). This suggests that vegetation types are not uniformly distributed with regard to fragmentation and edge. The far left of the axis is dominated by chamise sites because the center of our largest patch (Camp Elliott) is dominated by chamise. So at distances greater than 1 km from a developed edge, many sites are chamise, creating this correlation. At distances less than 1 km sites are well mixed among the three habitat types.

Table 2. Correlation coefficients between the independent variables and the first and second canonical correspondence axes.

Variable	Axis 1 ^a	Axis 2 ^a
SLOPE	0.09	0.46***
HIDIV ^b	0.32***	0.16*
SP_DIV ^b	0.23**	0.19**
HABT_DIV ^b	0.07	-0.09
CSS ^c	0.20**	-0.01
CHAM ^c	-0.38***	0.00
MIXED ^c	0.07	0.05
GRASS ^c	0.01	-0.22**
RIPARIAN ^c	0.24***	0.10
SHRUBS ^d	-0.18*	0.23**
TREES ^d	0.29***	0.22**
HERB ^d	0.07	-0.38***
BARE ^d	-0.09	0.09
BURN ^e	-0.21**	0.08
POLYAREA ^f	-0.55***	0.05
NEAREEDGE ^g	-0.52***	0.16*
EDGE250 ^h	0.45***	0.09
EDGE500 ^h	0.56***	0.06
EDGE1000 ^h	0.60***	-0.10
EDGE2000 ^h	0.48***	-0.12
EDGE3000 ^h	0.50***	-0.17*
NAT250 ⁱ	-0.46***	-0.15*
NAT500 ⁱ	-0.53***	-0.14*
NAT1000 ⁱ	-0.64***	0.04
NAT2000 ⁱ	-0.59***	0.01
NAT3000 ⁱ	-0.58***	0.03

^a*p* < 0.05, ^{**} *p* < 0.01, ^{***} *p* < 0.001.
^b Height diversity, species diversity, and habitat diversity calculated with the Shannon-Wiener formula.
^c The percent cover of coastal sage scrub, chamise chaparral, mixed chaparral, grassland, and riparian habitats within a 100-m radius of the point count station.
^d The percent cover of the structural types: shrubs, trees, grass/herbaceous cover, and bare ground within a 100-m radius of the point count station.
^e The presence or absence of a recent burn within a 100-m radius of the point count station.
^f The size of the patch of undeveloped habitat in which the point is located.
^g The distance from the point to the nearest developed edge.
^h The amount of linear edge between developed land and undeveloped habitat within buffer radii of 250, 500, 1000, 2000, and 3000 m around the point.
ⁱ The proportion of undeveloped habitat within buffer radii of 250, 500, 1000, 2000 and 3000 m around the point.

The smallest fragments are usually coastal sage scrub, explaining the correlation of CSS with axis one.

The second axis (eigen-value = 0.090) is a local habitat axis and primarily represents the variation in shrub and grass/herbaceous cover (Fig. 2, Table 2). Axis 2 also correlates highly with slope because grasslands, and most human-caused disturbances which decrease shrub cover, occur on flat ground. Species at the negative end of this axis are associated with sites of low shrub cover and high grass/herbaceous cover. Species at the positive end are associated with relatively high shrub cover.

To examine the relative influence of landscape variables independent of local habitat variation we performed a partial canonical correspondence analysis. In

Table 3. Results of stepwise logistic regression analyses of species presence/absence at 202 points on local habitat and landscape variables.

Species ^a	Model cbl-square ^e	df	1st variable entered	Standardized coefficient ^{b,c}	2nd variable entered	Standardized coefficient ^b	3rd variable entered	Standardized coefficient ^b	4th variable entered	Standardized coefficient ^b	Concordance (%)	Relative improvement (%) ^d
Local habitat variables only ^e												
BCSP	9.32**	1	HERB	-0.39**							62.5	
SAGS	20.70**	1	CHAM	0.49***							59.8	
LASP				INTERCEPT ONLY								
RCSF	8.27**	1	TREES	-0.32**							26.6	
COHU	14.80**	2	SHRUBS	0.78*	HABT_DIV	0.38**					65.5	
WEME	41.33**	4	HIDIV	-0.26***	HERB	0.46**			TREES	-0.55*	79.1	
CAQU	17.12**	2	SHRUBS	0.35**	HERB	0.28**					63.8	
CATH	12.87**	1	SHRUBS	0.36***							43.9	
RSTO	22.10**	1	SHRUBS	0.41***							51.4	
WREN	20.55**	2	GRASS	-0.21***	SHRUBS	0.23*					54.5	
BEWR	21.47**	2	SHRUBS	0.32***	RIPARIAN	-0.19*					53.2	
CATO	15.57**	1	HERB	0.38***							61.6	
CAGN	14.54**	2	CSS	0.65**	HABT_DIV	0.47**					73.9	
SCJA	8.38**	1	SHRUBS	0.26**							39.8	
COBU	8.96**	1	RIPARIAN	0.25**							20.5	
MODO	9.58**	1	CHAM	-0.25**							40.0	
NOMO				INTERCEPT ONLY								
ANHU	18.39**	2	CHAM	-0.35***	GRASS	-0.20*					55.6	
LEGO	19.28**	2	TREES	0.20***	SP_DIV	0.44**					69.9	
HOFI	9.99**	1	CHAM	-0.27***							41.3	
Local and landscape variables ^f												
BCSP	27.29**	2	EDGE1000	-0.69***	HERB	-0.33*					81.2	29.9
SAGS	27.45**	2	CHAM	0.42***	EDGE1000	-0.35*					78.0	30.4
LASP	13.35**	2	POLYAREA	0.53**	HERB	0.38*					72.1	
RCSF	62.30**	2	NAT1000	0.99***	CSS	0.35***					79.9	200.4
COHU	37.67**	4	EDGE1000	-1.15***	RIPARIAN	0.32**	SHRUBS	0.63*	EDGE2000	0.39*	83.8	27.9
WEME	45.53**	4	NAT500	0.57***	HERB	0.49***	HIDIV	-0.32**	CSS	-0.31*	81.2	2.7
CAQU	21.93**	3	SHRUBS	0.35**	HERB	0.31**	NAT2000	0.19*			67.9	6.4
CATH	26.35**	2	GRASS	-0.41**	EDGEDIST	0.33*					68.7	56.5
RSTO	34.18**	2	SHRUBS	0.39***	EDGE1000	-0.32***					72.4	40.9
WREN			UNCHANGED									0.0
BEWR			UNCHANGED									0.0
CATO	21.11**	2	HERB	0.32***	EDGE3000	0.24*					71.9	16.7
CAGN			UNCHANGED									0.0
SCJA			UNCHANGED									0.0
COBU			UNCHANGED									0.0
MODO			UNCHANGED									0.0
NOMO	17.46**	2	NAT1000	-0.43***	HIDIV	-0.22*					70.9	
ANHU	31.06**	2	URB_EXP	0.31***	EDGEDIST	-0.24*					72.0	29.5
LEGO	38.11**	3	NAT500	-0.32***	SP_DIV	0.45**	EDGEDIST	-0.44*			79.8	14.2
HOFI	54.08**	3	NAT1000	-0.49***	NAT3000	-0.33**	TREES	-0.22*			78.9	91.0

Table 3. Continued.

Species ^a	Model chi-square ^c	df	1st variable entered	Standardized coefficient ^{b,c}	2nd variable entered	Standardized coefficient ^f	3rd variable entered	Standardized coefficient ^f	4th variable entered	Standardized coefficient ^f	Concordance (%)	Relative improvement (%) ^d
Landscape variables only ^g												
BCSP	21.00**	1	EDGE1000	-0.77***							73.8	18.1
SAGS	13.77**	1	EDGE_EXP	-0.43***							70.1	17.2
LASP	8.12**	1	POLYAREA	0.47*							51.1	
RCSP	51.02**	1	NAT1000	0.86***							73.0	174.4
COHU	29.54**	3	EDGE1000	-0.64**	NAT500	-1.86*	URB_EXP	-1.81*			81.3	24.1
WEME	30.92**	3	NAT500	0.51*	EDGE3000	0.48***	EDGE500	-0.46*			74.7	-5.6
CAQU	6.54*	1	NAT1000	0.21*							54.7	-14.3
CATH	14.86**	1	POLYAREA	0.33***							50.4	14.8
RSTO	15.94**	1	EDGE1000	-0.35***							67.0	30.4
WREN	5.28*	1	EDGE3000	-0.20*							58.8	7.9
BEWR				INTERCEPT ONLY								
CATO	15.70**	2	EDGE3000	0.45***	NAT250	0.23*					68.4	11.0
CAGN				INTERCEPT ONLY								
SCJA				INTERCEPT ONLY								
COBU	5.42*	1	NAT3000	-0.18*							58.6	185.9
MODO	5.85*	1	NAT250	-0.19*							35.8	-10.5
NOMO	13.20**	1	NAT100	-0.34***							68.4	
ANHU	31.06**	2	URB_EXP	0.31**	EDGEDIST	-0.24*					72.0	29.5
LEGO	29.31**	2	NAT500	-0.35***	EDGEDIST	-0.44*					76.0	8.7
HOFI	48.92**	2	NAT1000	-0.37***	NAT3000	-0.32**					78.0	88.9

^aSpecies abbreviations as in Table 1.
^bStandardized coefficients can be directly compared to assess the predictive value of each variable in the model.
^c* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
^dThe improvement in concordance of the landscape-habitat and landscape-only models relative to the habitat-only models.
^eResults from models fit to local habitat variables only.
^fResults from models fit to local habitat variables and landscape variables.
^gResults from models fit to landscape variables only.

this analysis the local habitat variables were used as covariates and thus the variation in species abundance correlated with these variables is removed from the data set before performing an ordination on the landscape variables. After the variation associated with local habitat variation was removed there were still significant amounts of variation distributed along the landscape axes. The eigenvalues of the first two axes of this analysis are one-third to two-thirds lower than those of the combined habitat and landscape analysis (0.100 and 0.027). If the order is reversed and the landscape variables are used as covariates, the eigenvalues on the first two habitat axes are smaller (0.066 and 0.048) than those of the preceding analysis. These partial canonical correspondence results suggest that important variation in the landscape variables is independent of local habitat variation and is useful in ordering the bird species.

We have used the location of species along the first CCA axis (Fig. 2) as a rank index of landscape sensitivity. Rankings along the axis were used to assign species to three groups. We classified species at the negative end of the axis as edge/fragmentation reduced, species at the positive end edge/fragmentation enhanced, and species in the middle of the gradient as edge/fragmentation insensitive (Table 1). Cutpoints between groups are subjective and were chosen by inspection of the CCA results and distribution maps. We have used this categorization heuristically to structure the remainder of the results and discussion.

Canonical correspondence analysis was designed to maximally separate species along relevant environmental gradients created by linear combinations of the independent variables. The relatively low eigenvalues in this analysis result in part from the central group of species, the group we classified as edge/fragmentation insensitive, which does not respond strongly to either a landscape or a habitat gradient (their distributions span both gradients). When these edge/fragmentation insensitive species are removed from the canonical analysis, the eigenvalues for the first two axes increase to 0.273 and 0.100, and the edge/fragmentation enhanced and reduced species are well separated by the first axis.

Logistic Regression

The predictive value of stepwise logistic models that incorporate only local habitat variables was compared to that of models that include landscape and habitat variables and those that contain only landscape variables (Table 3). A significant habitat-only model was fit for all species except the Lark Sparrow and Northern Mockingbird. Landscape descriptors significantly improved the predictive ability of these models. When the landscape descriptors were added to the mix of variables available for incorporation into the final model, the new model included at least one landscape descriptor in 14 of 20 spe-

cies and mean model concordance in these 14 models increased from 56% to 73%. The resulting models are generally consistent with the patterns evident in Figures 1 and 2. In general, the landscape variables were not significant in models for the species classified as edge/fragmentation insensitive. Significant models with only landscape variables could be fit for all species but Bewick's Wren, California Gnatcatcher, and Scrub Jay. All but two of those models provided a higher concordance than did the corresponding local habitat model (Table 3).

In general, the best habitat predictors of abundance were the gross structural variables that represent the relative cover of shrubs, trees, and herbaceous/grass vegetation (SHRUBS, HERB, TREES, GRASS). This was particularly true for the edge/fragmentation insensitive species that are associated with sites of moderate to high shrub cover and low cover of grass and herbaceous vegetation. The abundance of several of the edge/fragmentation enhanced species was inversely related to the cover of chamise chaparral. A variety of the landscape variables were significant predictors of bird abundance. No single landscape variable or buffer distance stands out as being generally predictive across species.

Presence/absence as a Function of Distance to a Developed Edge

The results suggest that landscape descriptors are associated with bird abundance independently of any association between local habitat variation and landscape descriptors. All of our landscape variables describe aspects of the patterns of interspersed natural habitat and developed land in the vicinity of the point count site. They are also highly inter-correlated (Table 2). A clearer understanding of the relationship of bird abundance to the landscape might result from a univariate analysis of the relationship of abundance with one of the simplest landscape descriptors, distance to a developed edge (EDGE-DIST). There are two components of the effect of habitat fragmentation on animal populations: isolation effects (limited habitat area and dispersal) and edge effects (juxtaposition of natural habitat and human modified habitat). With our data it is difficult to separate the two because point counts performed in small, isolated fragments are sure to be relatively close to a developed edge and therefore subject to both edge effects and isolation. So the EDGEDIST variable is a proxy for both effects and thus is an excellent choice for univariate analysis.

To examine the association of bird abundance with the EDGEDIST variable we performed logistic regressions of species presence/absence on the EDGEDIST variable (Table 4). With the exception of the Lark Sparrow significant regressions were obtained for all the edge/fragmentation enhanced and reduced species with the expected signs for the coefficients. Of the species classified as insensitive, Rufous-sided Towhee increased

Table 4. Standardized logistic regression coefficients relating species presence/absence to the distance of each point count site from a developed edge (EDGEDIST variable).

Species ^a	EDGEDIST only ^{b,c}	Local habitat plus EDGEDIST ^{b,d}
BCSP	0.40***	0.34**
SAGS	0.30**	
LASP		
RCSP	0.36***	0.33***
COHU	0.30**	0.35**
WEME	0.30***	
CAQU		
CATH		0.26**
RSTO	0.44***	0.38**
WREN		
BEWR		
CATO	−0.25**	−0.18*
CAGN		
SCJA		
COBU		
MODO		
NOMO	−0.46**	−0.46**
ANHU	−0.40***	−0.33**
LEGO	−0.65**	−0.56**
HOFI	−0.65***	−0.61***

^aSpecies abbreviations as in Table 1.
^b* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
^cCoefficients from regressions of presence/absence on EDGEDIST only.
^dPartial regression coefficients from regressions in which EDGEDIST was added to the best-fit local habitat model presented in Table 3.

significantly with distance from an edge while California Towhee decreased.

To determine whether the significance of the edge variable was due to correlations with local habitat we performed a partial logistic regression wherein the EDGEDIST variable was added to the habitat-only model fitted previously (Table 3). The EDGEDIST was no longer significant for Sage Sparrow and Western Meadowlark, but became significant for the California Thrasher (Table 4).

To examine these relationships graphically we created incidence functions (Diamond 1975) to examine how the probability of a species being present at a point changes with the distance of the point from an urban edge (Fig. 3). In general the species we have termed edge/fragmentation reduced show low incidence between 100 and 500 m of an edge (Fig. 3a and b). The reduction in incidence is most pronounced in the Rufous-crowned Sparrow and Western Meadowlark. Incidence functions for the edge/fragmentation enhanced species decline sharply with EDGEDIST (Fig. 3e), whereas incidence of the insensitive species is much more uniform with distance (Fig. 3c and d). Consistent with the logistic regressions (Table 4), incidence of California Thrasher, Rufous-sided Towhee, and California Towhee show trends with EDGEDIST. In general these are not as pronounced as the trends in the enhanced and reduced species.

To qualitatively evaluate the possibility that the edge-oriented patterns we saw were due to the distribution of

habitats that vary with EDGEDIST, we graphed the sites within each habitat type separately. To condense the presentation we aggregated the single species data into the three groups of species. The group patterns suggested in Fig. 3 are also apparent in each of the three shrub habitat types (Fig. 4).

The EDGEDIST variable may be a proxy for both the edge and isolation effects of habitat fragmentation. The patterns shown in Figs. 3 and 4 might be mostly a function of differences in abundance between large and small patches rather than having any real relationship with distance to an edge. To evaluate this possibility we repeated the graphical analysis including only the point counts located within the two largest patches in the study area (91.7 and 27.1 km²). The patterns with EDGEDIST for the three species groups remained qualitatively unchanged (Fig. 5).

Discussion

Landscape descriptors appear to be significant predictors of the abundance of some bird species in an urbanizing landscape in coastal southern California. For approximately half the 20 species analyzed, abundance in natural habitat was correlated with position in the landscape relative to urban development. For these species landscape descriptors significantly improved the fit of logistic models containing only local habitat variables and models containing only landscape variables were often more predictive of presence/absence than were models with only local habitat variables (Table 3). Our analyses suggest that correlations between landscape position and local habitat variables are not responsible for this effect (Tables 3 and 4).

We categorized the 20 most common breeding bird species of shrub habitats into three groups: edge/fragmentation enhanced, edge/fragmentation reduced, and edge/fragmentation insensitive. Although we recognize these species probably occupy a semi-continuous gradient of sensitivity to landscape variation, we feel the categorization is a useful heuristic tool for organizing the discussion of our results and, with proper consideration of its limitations, can be used to prioritize species for research and planning efforts or in reserve design and management.

The edge/fragmentation enhanced species, House Finch, Northern Mockingbird, Lesser Goldfinch, and Anna's Hummingbird, are species whose association with humans and ability to use resources provided in human-modified areas are well known. They occur within the developed matrix, apparently without regard to proximity to natural habitat (Unitt 1984). However, the elevated abundance of these species in natural habitat near edges and for a substantial distance into the interior of habitat patches has to our knowledge not been docu-

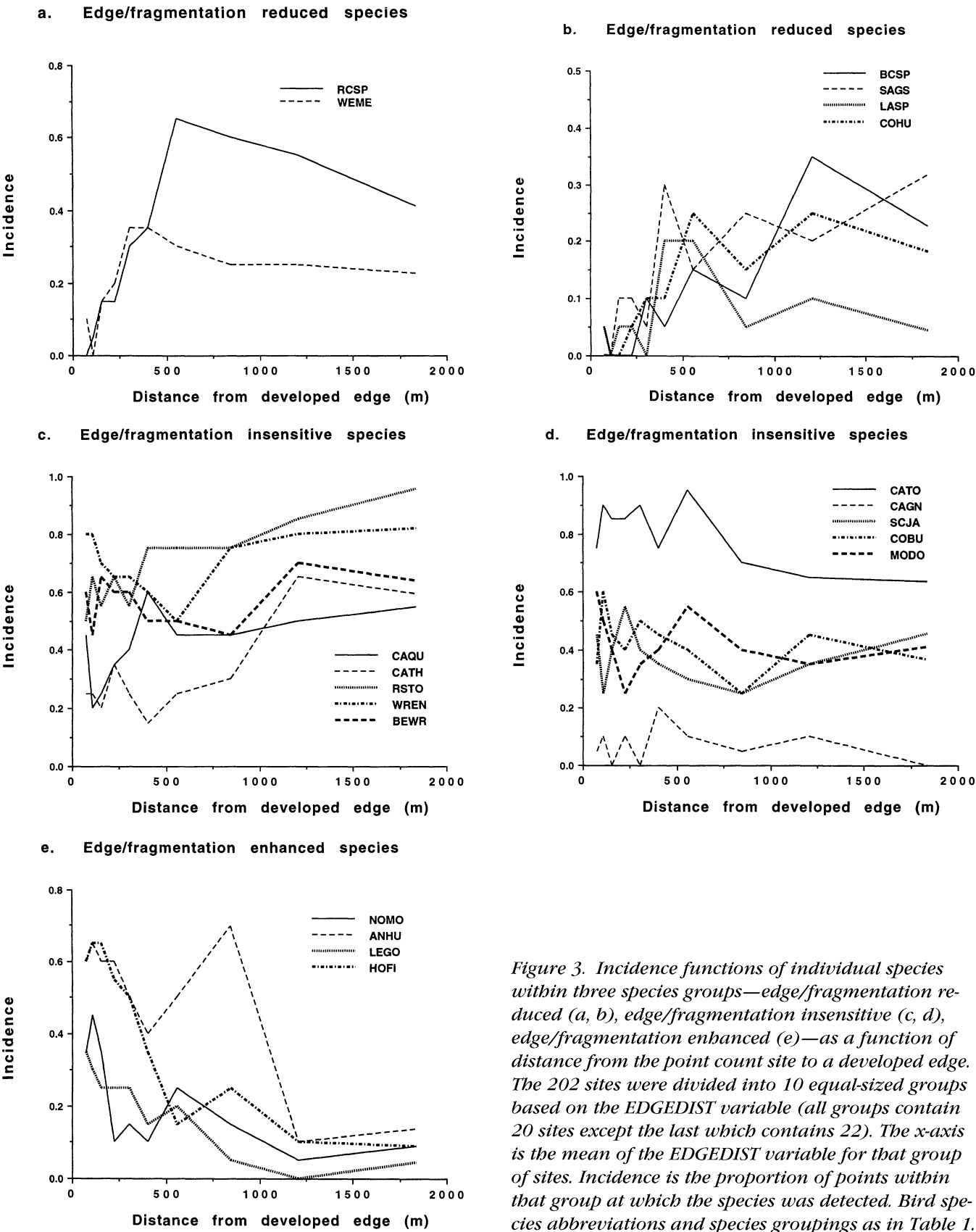


Figure 3. Incidence functions of individual species within three species groups—edge/fragmentation reduced (a, b), edge/fragmentation insensitive (c, d), edge/fragmentation enhanced (e)—as a function of distance from the point count site to a developed edge. The 202 sites were divided into 10 equal-sized groups based on the EDGEDIST variable (all groups contain 20 sites except the last which contains 22). The x-axis is the mean of the EDGEDIST variable for that group of sites. Incidence is the proportion of points within that group at which the species was detected. Bird species abbreviations and species groupings as in Table 1.

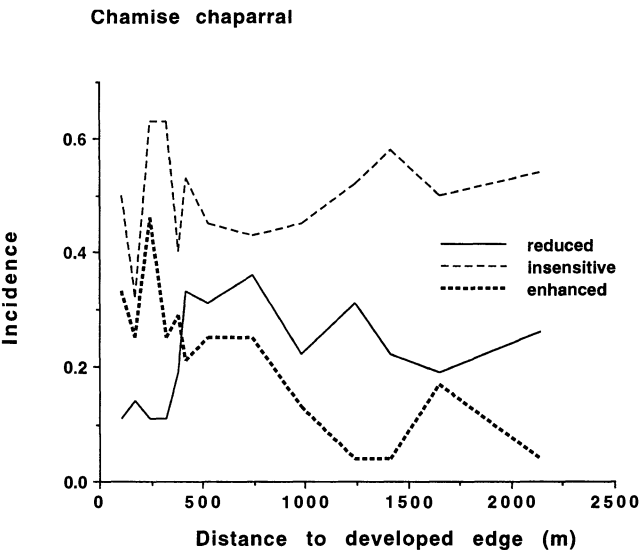
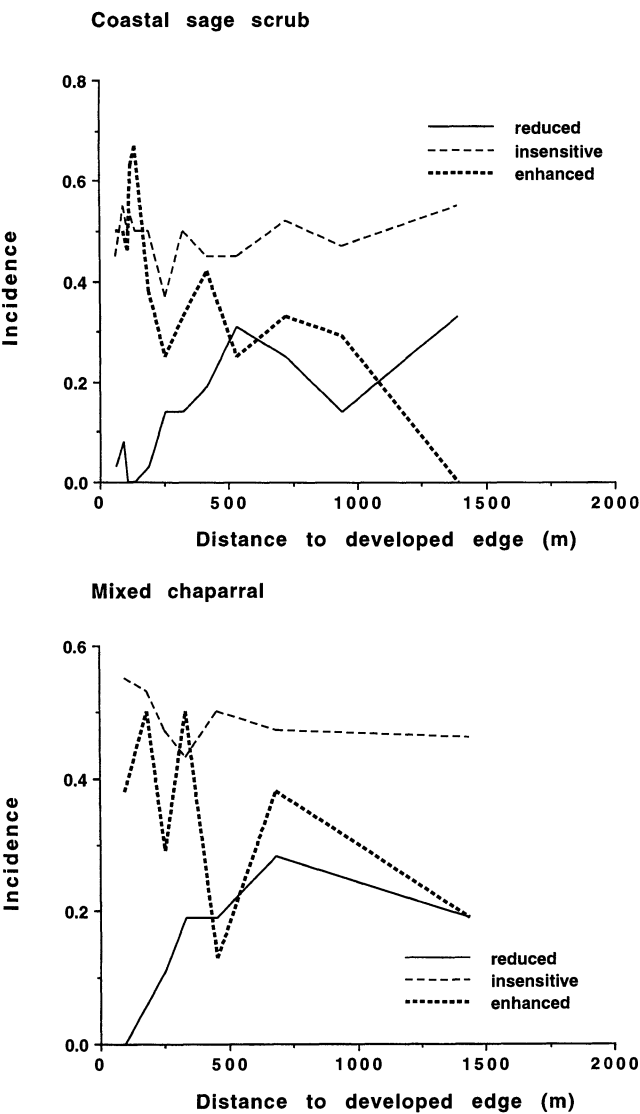


Figure 4. Incidence functions for the three species groups (edge/fragmentation reduced, edge/fragmentation enhanced, edge/fragmentation insensitive) at point count sites containing at least 40% cover of one of the three shrub habitat types: coastal sage scrub (13 groups of six sites), chamise chaparral (13 groups of six sites), and mixed chaparral (six groups of six sites). Groups of sites were formed as in Fig. 3. Incidence in this case is the mean proportion of the species group present at each point within the site group.

mented before. The density of Anna's Hummingbird, for example, is higher in the area within a kilometer of an urban edge than further into the interior of a habitat patch (Fig. 3, 4 and 5).

The first four species at the landscape-reduced end of the CCA gradient are sparrows. The pattern of landscape sensitivity is most pronounced for the Rufous-crowned Sparrow, which is abundant and appears to be a habitat generalist in the larger patches in the landscape, but is rare near edges and in smaller fragments. Sage Sparrow is rarer in the large patches and is strongly associated with chamise chaparral in this landscape (Table 3). However, it is much less abundant in similar habitat in the edgy, fragmented areas (Fig. 3). Sage Sparrow in shrub communities in the Great Basin also exhibits a pattern suggesting landscape sensitivity (Knick & Rotenberry 1996). Lark Sparrow and Black-chinned Sparrow were also detected predominantly in the largest patches in the landscape, but are much less abundant than Sage

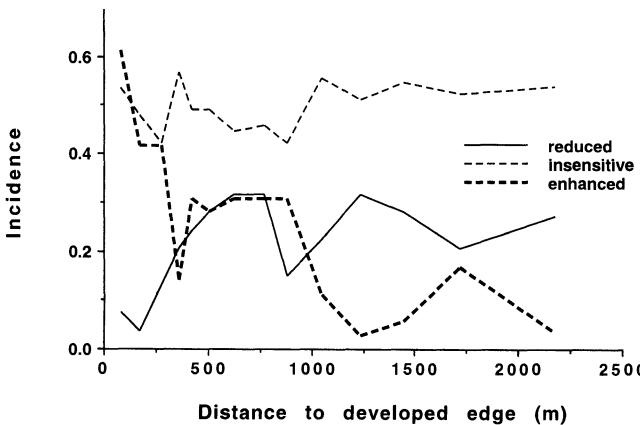


Figure 5. Incidence functions for the three species groups at point count sites in the two largest patches within the study area (91.7 and 27.1 km²). Fourteen groups of nine sites each were formed as in Fig. 3. Incidence is defined as in Fig. 4.

and Rufous-crowned sparrows. The concordance of logistic regression models for these four species improved considerably with the inclusion of landscape variables. Costa's Hummingbird, another species in this category, has lower density within 500 m of an urban edge (Fig. 3) and landscape variables are significant predictors of its abundance in logistic models (Tables 3 and 4).

Inspection of distribution maps and CCA results led us to classify the Western Meadowlark as edge/fragmentation reduced; however, logistic models were only marginally improved by the addition of landscape variables (Table 3). The relative rarity of this species near edges is clear (Fig. 3a), yet after local habitat variables are entered into a logistic model there is not a significant partial effect of the EDGEDIST variable (Table 4). These results suggest that the apparent edge/fragmentation sensitivity of this species was due to a correlation of local habitat variation and landscape position. Knick and Rotenberry (1996) found the distribution of the Western Meadowlark to be independent of landscape features.

The edge/fragmentation insensitive species are the characteristic species of shrub habitats in this region. They are abundant and widely distributed across the landscape and habitat gradients. For these species the addition of the landscape variables to the logistic regression analyses does not produce better models than the regression on local habitat variables alone (Table 3). Rufous-sided Towhee, Wrentit, California Quail, and Bewick's Wren are mainly restricted to shrub habitats in this landscape. Scrub Jay, Mourning Dove, California Towhee, and Common Bushtit, however, like the edge-enhanced species, are known to commonly reside and breed in residential areas (Unitt 1984), but differ in that they do not have elevated abundances in habitat near edges (Fig. 3). The California Gnatcatcher also falls into this category; however, its abundance is much lower than the other species in the group (Fig. 3).

Despite falling in the center of the landscape axis in the canonical correspondence analysis, three species in this category, California Thrasher, Rufous-sided Towhee, and California Towhee, had a significant partial association with the edge distance variable (Table 4). Higher abundance of the California Towhee is associated with sites closer to developed edges, whereas the other two species are less common nearer to edges. The patterns these species display differ from the species in the enhanced and reduced categories in that the density enhancement or reduction is not as pronounced. California Towhee, for instance, is still relatively abundant in the interior of large patches, and thrasher and Rufous-sided Towhee densities are not as low in edge areas as are those of the species in the reduced category (Fig 3).

At the relatively large scale considered here this shrub generalist group of species apparently does not respond strongly to landscape variation. However, in an earlier study (Soulé et al. 1988; Bolger et al. 1991), at a smaller

spatial scale, several of these species (Rufous-sided Towhee, California Thrasher, California Quail, Bewick's Wren and Wrentit) showed a strong response to patch size and age (time since isolation) in patches ranging in size from 1–100 ha. This suggests that species are affected by habitat fragmentation at different spatial scales and highlights the fact that species-habitat relationships determined at one scale may not apply at other scales.

The predictive ability of landscape variables is perhaps more surprising because we have ignored a potentially important component of landscape variation. We have only examined landscape patterns of natural habitat and urban development. We have not considered landscape-scale patterns of habitat-type variation including patch sizes of different habitat types and interspersions of habitat types. These might be important determinants of abundance for some of these species. It seems likely that incorporation of this variation into future statistical models will strengthen the association of landscape pattern and bird abundance for these species.

What inferences can be drawn from these data about the demographic mechanisms that generate these spatial patterns? As with all studies of the association of bird abundance with habitat features we must recognize the limitation that bird abundance at a location is not necessarily a reliable indicator of demographic productivity in that habitat or landscape location (Van Horne 1983; Vickery et al. 1992; but see Holmes et al. 1996). We suggest two hypotheses for the mechanism generating these distribution patterns: the landscape-demographic and the landscape-selection hypotheses. Under the latter hypothesis it is assumed that different bird species have preferences as to where in the landscape they establish breeding territories. In effect, distance from a developed edge becomes one of the criteria that birds use when assessing breeding habitat suitability. So the spatial patterns are generated by dispersal and settlement biases due to habitat selection. This preference can be unrelated to the reproductive and survival success those individuals will enjoy in their preferred sites. If some species have difficulty dispersing to isolated fragments, this would also contribute to producing the edge/fragmentation reduced pattern.

The landscape-demographic hypothesis presumes that spatial patterns of abundance are generated by differences in survival and reproduction associated with different areas of the landscape. For instance for the edge/fragmentation enhanced species the urban matrix and habitat patch edges may be source areas (Pulliam 1988; Pulliam & Danielson 1991) providing a surplus of new recruits that can disperse into the interior of habitat patches and that this process maintains elevated abundance some distance into the interior of the patch. The edge/fragmentation reduced species may have reduced demographic success in areas near development. This may result from reduced survival, reduced fecundity, or

increased emigration from those areas. These demographic differences could result from changes in predator (Paton 1994), parasite (Brittingham & Temple 1983), competitor, and resource abundance and dynamics in those areas. For the insensitive species, survival and reproductive rates must be relatively uniform across the landscape or dispersal obliterates any differences in density due to differing demographic success.

The existence of strong associations of some members of the bird community with landscape setting raises questions that have important implications for the design and management of nature reserves in this region. If these patterns are generated by landscape demographic differences, will the edge/fragmentation reduced species be able to persist in anything but very large reserves? And what are the implications for bird community dynamics of the elevated abundance of the edge/fragmentation enhanced species? Although the depression of species densities near edges has been widely discussed and investigated, the spatial extent of the enhancement of edge species, other than predators and parasites, and the implications for community dynamics, has received little attention. The increase in edge/fragmentation enhanced species could intensify interspecific competition or other inter-specifically density-dependent processes, such as nest predation (Martin 1988). If the proximity to urban edges causes significant changes in community dynamics, can "natural" communities be conserved anywhere but in the interior of very large reserves?

The statistical models we have presented are not sufficiently refined and validated to serve as prescriptive conservation planning tools (Noon 1986). This will require data collection and model building and testing in other years and other landscapes in this region. However, the qualitative results of these analyses support the view that landscape patterns of habitat fragmentation and urban/habitat edge are important determinants of the abundance of birds in coastal southern California. Our results also underscore the need for landscape-scale variation to be explicitly incorporated in wildlife-habitat relationship models, particularly if they are to be applied to heterogeneous landscapes. The species in the edge/fragmentation reduced category may be at significantly higher risk than a simple assessment of the amount of potential habitat in this landscape might suggest. And, their conservation in this landscape may require management measures beyond the preservation of the appropriate vegetative habitat.

At this time we know little about possible ecological mechanisms generating edge and fragmentation effects in this system, but we suspect that they are pervasive, sometimes subtle, and as these data suggest, spatially extensive. These are important influences which need to be addressed through further research and planning efforts. A more thorough understanding of these effects

will be necessary to effectively conserve bird communities in these landscapes.

Acknowledgments

We wish to thank J. Konecny and S. Zimmerman for help in the field. P. Lee, N. Pratini and S. Key constructed the GIS database. P. Lee, R. Stemberger, M. Blake, R. Dezzani, and J. Dykes helped with data analysis. I. Kay and the U.C. Kendall-Frost Reserve provided logistical support. We are grateful to the U.S. Navy and N.A.S. Miramar for allowing us to work on the base, and M. Scott and T. Wright for facilitating our work there. Comments by D. Doak, D. Holmes, S. Morrison, J. Ruben, and three anonymous reviewers greatly improved the manuscript. This work was supported by a contract from the California Department of Transportation (CALTRANS) to T. S. and J. R. J. Rieger of CALTRANS greatly helped to facilitate our work. D. T. B. would like to express his gratitude to M. Soulé for introducing him to the study of urbanizing landscapes in southern California.

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