

Alternative causes of edge-abundance relationships in birds and small mammals of California coastal sage scrub

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Changes in the distribution and abundance of bird and small mammal species at urban-wildland edges can be caused by different factors. Edges can affect populations directly if animals respond behaviorally to the edge itself or if proximity to edge directly affects demographic vital rates (an “ecotonal” effect). Alternatively, urban edges can indirectly affect populations if edges alter the characteristics of the adjacent wildland vegetation, which in turn prompts a response to the altered habitat (a “matrix” or “habitat” effect). We studied edge effects of birds and small mammals in southern Californian coastal sage scrub, and assessed whether edge effects were attributable to direct behavioral responses to edges or to animal responses to changes in habitat at edges. Vegetation species composition and structure varied with distance from edge, but the differences varied among study sites. Because vegetation characteristics were correlated with distance from edge, responses to habitat were explored by using independently-derived models of habitat associations to calibrate vegetation measurements to the habitat affinities of each animal species. Of sixteen species examined, five bird and one small mammal species responded to edge independently of habitat features, and thus habitat restoration at edges is expected to be an ineffective conservation measure for these species. Two additional species of birds and one small mammal responded to habitat gradients that coincided with distance from edge, such that the effect of edge on these species was expressed via potentially reversible habitat degradation.

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Urban and agricultural development fragments wildland habitats, and creates sharp boundaries, or edges, between the natural and human-altered habitats. Edges can alter abiotic processes such as microclimate, light intensity, and hydrology (e.g., Janzen 1983, Murcia 1995, Camargo and Kapos 1995, Sisk et al. 1997), and biotic factors such as predator communities, habitat structure, and food availability (e.g., Yahner 1988, Soulé et al. 1988, Matlack 1994, Murcia 1995). Animals may avoid the increased human activity at developed edges, an effect that has been observed at reservoir edges (Franci and Schnell 2002) and roads (Forman and Alexander 1998). These changes in conditions at

edges can be associated with changes in abundance of birds and small mammals due to changes in their demographic rates (Paton 1994, Donovan et al. 1997), or through behavioral avoidance of or attraction to the edge (Sisk et al. 1997, Lidicker and Peterson 1999). Fragmentation generally increases the amount of edge per unit land area, and species that are adversely affected by edges can experience reduced effective area of suitable habitat (Temple and Cary 1988), which can lead to increased probability of extinction in fragmented landscapes (Woodroffe and Ginsberg 1998).

Rapid urbanization in southern California over the last 50–100 yr has resulted in loss of large areas of

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native habitats, particularly in cis-montane coastal regions. One of the characteristic vegetation types in this region, coastal sage scrub (CSS), has been reduced to 10–30% of its former extent by conversion to human use, and now supports ca 100 animal and plant species considered by California or federal wildlife agencies to be rare, sensitive, threatened, or endangered (Atwood 1993, McCaull 1994, Dobson et al. 1997). Although the direct effects of habitat loss to urbanization are fairly obvious and irreversible, the indirect effects of urbanization on adjacent remaining patches of habitat can be more subtle, and are potentially subject to intervention and mitigation by land managers. Understanding how these remaining habitat patches are affected by surrounding lands through their shared edges is an important step towards protecting the populations of plants and animals that depend on remnant habitat in urbanizing landscapes.

Although many studies of various types of edge effects have been conducted (avian studies recently reviewed by Sisk and Battin 2002; small mammal studies reviewed in Lidicker 1999), there is substantial disagreement among studies about the existence and intensity of edge effects and no clear, general patterns have emerged (Murcia 1995). In part this variety of results may be due to the variety of effects that edges can have on populations, only a subset of which may be expressed at a particular site (Donovan et al. 1997). For example, edge-abundance relationships are frequently interpreted as a behavioral response to the sharp transition found at edges between habitats with different structures (Sisk et al. 1997; called the “ecotonal effect” by Lidicker and Peterson 1999). A direct, behavioral response to the edge itself is an emergent property of edges that cannot be explained by the responses of animals to the same habitats in isolation from the edge (Lidicker and Peterson 1999). In contrast, species may instead respond to changes induced in the vegetation at edges, and may be indifferent to the edge itself (called the “matrix effect” by Lidicker and Peterson 1999, and the “habitat effect” by Kingston and Morris 2000).

Changes in vegetation at edges will depend on a variety of factors that will differ in site-specific ways. Inconsistent effects of edge on adjacent habitat would produce inconsistent patterns of change in abundance of animals relative to edge, even if the animals consistently respond to the changes in habitat when they occur (i.e. a “matrix effect”). Conversely, similar patterns of change in abundance among species at a particular edge can be caused by different mechanisms, in that an “ecotonal effect” in one species may produce the same change in abundance at an edge as a “matrix effect” in another (Lidicker 1999). In spite of these observations, few studies have been designed to distinguish between these alternative mechanistic explanations for edge effects (Murcia 1995, Lidicker 1999, Sisk and Battin 2002). In this study we concentrate on

distinguishing direct effects of edge from effects of the changes produced by urban edges in the structure or floristic composition of the adjacent coastal sage-scrub vegetation, on the occurrence of birds and small mammals. Although changes in abundance at edges can affect populations regardless of the cause, these alternative mechanisms suggest different remediation strategies, and our findings are important considerations for the potential success of edge habitat restoration in urbanizing landscapes.

Methods

CSS vegetation

CSS is a drought-deciduous shrubland found in cis-montane southern California and Baja California that is dominated by shrubs of 0.5–2.0 m in height (Westman 1981). CSS is distinguished from other vegetation types in southern California by its distinct plant species composition and structure. The dominant shrubs include California sagebrush *Artemisia californica*, black sage *Salvia mellifera*, white sage *Salvia apiana*, California encelia *Encelia californica*, brittlebush *Encelia farinosa*, and California buckwheat *Eriogonum fasciculatum* (Westman 1981, 1983, O’Leary et al. 1992). However, there is substantial geographic variation in plant species composition within this broadly defined vegetation type (Westman 1983, White and Padley 1997).

Analytical strategy

Our analytical strategy combined information from two independent studies. The first study was designed to characterize associations of birds and small mammals with vegetation throughout CSS, in the absence of edge effects. The second study was designed to estimate the relative importance of the habitat associations of species and distance to edge in determining animal distribution and abundance around urban edges within CSS. Our measures of habitat association were based on a regional assessment of bird and small mammal distributions in CSS throughout San Diego, Orange, and Riverside counties (the “regional study”; Rotenberry et al. 1999). Assessments of edge-abundance relationships were based on a smaller set of sites that contained developed edges (the “edge study”). We used this approach because, in the absence of an independent measure of habitat association, the anticipated correlation between distance from edge and the structure and species composition of the vegetation would make it difficult to determine whether species were responding to a vegetation gradient or to the edge itself. Statistically, this problem is expressed as strong multicollinearity among the independent variables (Zar 1984). Once

independent models of habitat associations were obtained, they were used to calibrate vegetation measurements from the edge study to the habitat associations of each species. These could then be compared to the observed distributions of each species in relation to edges. Although the correlation between habitat and distance to edge remained after this calibration step, it became possible to distinguish between response to habitat and response to edge by comparing the observed distribution of animals to the distribution expected based on a species' habitat associations. Plant and animal sampling methods were the same for these two studies, except for the geographic extent and duration of sampling and the methods used to select sampling points, as noted below.

Study areas

Regional study

We sampled birds, small mammals and vegetation at 22 sites located throughout Orange, Riverside, and San Diego counties (Fig. 1). Sites were selected to maximize geographic coverage of CSS; thus, all of the sites contained CSS vegetation (especially California sagebrush), but varied geographically in other elements of floristic composition (Rotenberry et al. 1999). Sites in Riverside County contained greater amounts of brittlebush and buckwheat, whereas Orange County sites contained

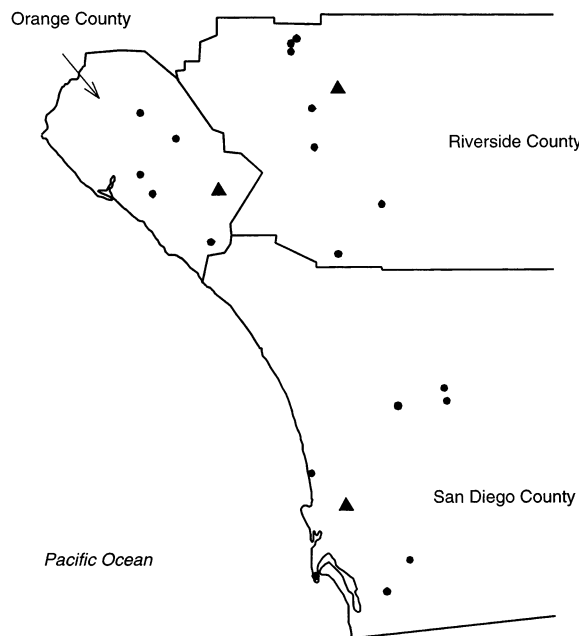


Fig. 1. Regional and edge study sites in southern California. Three edge sites were surveyed in 1997 (triangles: LAPE = Lake Perris; STRA = Starr Ranch; MIRA = Miramar). Twenty-two regional sites (circles, plus STRA and LAPE) were surveyed between 1995 and 1997.

greater amounts of laurel sumac *Malosma laurina* and chamise *Adenostoma fasciculatum*, the latter a dominant shrub in chaparral vegetation. San Diego sites had higher coverages of California encelia and lemonade-berry *Rhus* spp. All sites had been invaded to varying degrees by exotic grasses of the genera *Avena*, *Bromus*, and *Schismus*. The invasion consisted of infusion of the CSS with exotic grasses in some areas and replacement of shrubs by grasslands in other areas. These are steps in a process of change from shrubland to grassland occurring throughout the region, driven by changes in fire frequency and intensity as exotic grasses invade (Minnich and Dezzani 1998).

Edge study

We studied edge effects at three areas that contained extensive, continuous areas of CSS, and which collectively encompassed the range of variation in CSS floristic composition found throughout the region. These sites were Lake Perris State Recreation Area in Riverside County (LAPE), Starr Ranch Audubon Sanctuary in Orange County (STRA), and Marine Corps Air Station Miramar in San Diego County (MIRA) (Fig. 1). In addition to the typical CSS plants, MIRA contained a fairly large amount of chamise. Each site was adjacent to suburban housing developments consisting of single-family homes. The edge at LAPE was actively developing, with houses completed and occupied at one end but under construction at the other. A golf course was situated between the houses and the CSS edge for part of its length at LAPE, separating the CSS from the houses by a maximum of 75 m. At STRA a narrow belt of irrigated landscaping (< 50 m wide) separated the CSS edge from the houses. Houses were immediately adjacent to CSS at MIRA.

Although land uses of the CSS at each edge study site were nominally similar, there was some variation in the amount of recreational use. LAPE was open to the public and the LAPE edge received the greatest degree of recreational use, primarily hiking. MIRA and STRA were not open to the public, but the edges were not patrolled and trespassing appeared to be fairly common, resulting in similar recreation-related impacts at the edges at all three sites (e.g. trails, trampling of vegetation). LAPE had been most extensively invaded by exotic grasses, and contained large patches of shrubless, exotic grasslands. Exotic grasses were common at both STRA and MIRA, but these sites also contained larger, more continuous patches of shrubs than LAPE.

Sampling design

Regional study

Sampling points were selected to fall within CSS habitat and were at least 250 m apart. Distances from edge varied, but most were in the "intermediate" to "inter-

rior" distance range of the edge study (250–1000 m). Between five and 25 points were located within each of the 22 sites, depending on the area of CSS habitat, for a total of 233 points. At each point we sampled birds and vegetation. Differences in the logistical constraints of sampling birds and small mammals prevented us from sampling small mammals at all 233 points, but we were able to sample small mammals at 172 of them. Data were collected between 1995 and 1997, with sites surveyed one, two, or three years for birds, one or two years for small mammals, and once for vegetation.

Edge study

We established sampling points at three distances from the urban edge. "Edge" points were placed within undeveloped habitat as close as possible to the edge (typically < 10 m). "Interior" points were placed a minimum of 1000 m from the edge, and "intermediate" points were placed 250 m from the edge. Sampling points were spaced at least 250 m apart, with the total number of points constrained by the length of the developed edge (five were used at each distance class at Lake Perris, ten at Miramar, and twelve at Starr Ranch). At each point we surveyed birds and small mammals, and measured vegetation composition and structure. Birds were sampled in the spring of 1997, and small mammals were sampled in the winter of 1996 and spring of 1997, and combined to represent one year of sampling. Vegetation was sampled once at each point in the spring of 1997.

Survey methods

Survey methods within a sampling interval were identical between regional and edge studies, except where noted below.

Birds

Each spring, birds were sampled using two 5-min unlimited-radius counts conducted at each point (Ralph et al. 1995). All birds detected from the point center were included, except for those not using the scrub or urban habitat types (such as birds flying over the point) or those species that are not well-sampled by point counts (such as raptors). Individuals of the species included in this analysis could usually only be detected from one sampling point, but if individuals were detected at more than one point they were assigned to the closest sampling point. First counts began in mid-March and were concluded by late-April. Second counts began shortly after conclusion of the first counts (late April–early May) and were completed by early June. Sites were visited in the same order for first and second samples so that samples at a point were conducted 4–5 weeks

apart, ensuring an opportunity to detect both early breeders and late arriving species (as suggested by Ralph et al. 1995). To avoid observer bias, each point was sampled by different observers on the first and second visit. Point counts took place between sunrise and 5 h after sunrise on mornings with no rain or strong wind, and the order in which points were sampled within each site was reversed between the first and second visits to avoid potential bias due to changes in detectability of species.

Small mammals

Small mammals were sampled with three consecutive days of trapping at each point in the regional study, and over five consecutive days in the edge study, using Sherman live-traps. Three-day trapping periods were chosen in the regional study because longer-term trapping at a subset of points showed that 90% of all species detected with a 7-d trap period were detected at each trapping point by the third day (Price et al. unpubl.). A 4 × 4 array of 16 traps spaced 8 m apart and centered on the sampling point was used in the regional study. Either a 1 × 5 or 2 × 5 array was used in the edge study. Small mammals were trapped on two occasions several months apart for the edge study, with autumn samples conducted between October and December and spring samples conducted between May and June. Because small mammal activity can be affected by moonlight (Price et al. 1984), trapping was not done for two days before and after a full moon.

Traps were situated under the shelter of a shrub canopy and baited with a mixture of rolled oats, peanut butter, and corn syrup. Traps were opened at dusk, then cleared and closed between 05:30 and 11:00 the following day. If a legally protected species was detected at any census point, the protocol was immediately changed so that traps were opened at dusk, and then cleared immediately after dawn for the duration of sampling at all census points at the particular site. When nights were cold, traps were checked and closed at midnight. Mammals were identified to species using customized keys derived from Ingles (1965) and Jameson and Peeters (1988), and were aged, sexed, weighed, marked, and then released at the point of capture.

Vegetation

Vegetation structure and species composition were measured at sampling points using a modified version of the technique described by Wiens and Rotenberry (1981). All edge study vegetation measurements were taken in the spring of 1997. Regional study measurements were also taken in the spring, in 1996 for most sites, but in 1997 for sites that were not added until after spring 1996. Vegetation was sampled along two perpendicular 50-m transects connected at the end in an "L" shape. The vertex of the L was placed at the center of the

sampling point, and at edge points the legs were constrained to fall within CSS.

We used line intercepts to estimate coverage values for different classes of emergent vegetation (as opposed to substrate or ground cover). These structural classes were 1) percent cover of exotic forbs, the most common of which was a species of *Brassica*, 2) percent cover of native forbs, 3) percent cover of exotic grasses, 4) percent cover of shrubs, and 5) percent cover of standing dead shrubs. To estimate coverage values for substrate types and individual species we passed a 4-mm diameter rod vertically through the vegetation at a random point within each 2-m interval along each of the two 50-m legs (50 points total). At each point we recorded the nature of the ground cover or substrate, and the species identity of each plant that touched the pin. Substrate classes included 1) bare ground, 2) fine litter, usually from grass or small forbs, 3) coarse litter, usually from woody shrubs, and 4) rock. We recorded the total number of plant species contacted at each point, and we also recorded the number of vegetation contacts ("hits") occurring in three height classes: 1–3 dm, 3–5 dm, and > 5 dm above the substrate surface. Litter depth was measured to the nearest 1 cm at the point. As an index of local heterogeneity, along each 50-m section of the line we recorded the number of times the vegetation changed between grass, shrub, or rock/bare categories. Vegetation was sampled once at each point for both the regional and edge studies.

Analyses

Habitat variable reduction

Our sampling resulted in 15 structural habitat variables and 24 plant species variables (Appendices 1 and 2). Because of large scale patterns in the distribution of habitat attributes (e.g., patterns of co-occurrence of plant species throughout the region) many were highly intercorrelated. Thus, it was appropriate to reduce the number of habitat variables using standard, correlation-based multivariate techniques. These techniques produce new, synthetic variables that account for major patterns of covariation in the original habitat variables and that are logical combinations of them.

We used principal components analysis (PCA; Tabachnick and Fidell 1983, Pielou 1984) to identify independent patterns of covariation among the habitat structure variables. PCA constructs new, synthetic variables that are linear combinations of the raw variables. Each sampling point can be scored on each PCA axis based upon the values of its raw variables, and these scores can be used as proxies for entire sets of intercorrelated raw variables in other analyses.

We use detrended correspondence analysis (DCA) to quantify the relationship among the set of points based on the similarity of their species composition (Gauch

1982, Pielou 1984). DCA assumes that species change in abundance across a gradient, many going from absent to abundant to absent again; thus DCA models the nonlinear pattern of turnover in communities better than would a linear method, such as PCA. In DCA, species are scored on axes based on their patterns of occurrence among points, and species with similar patterns of distribution will have similar scores. The score of a sampling point on a DCA axis is a weighted average of the abundance of the species that occur there, so that sampling points with similar species composition will have similar axis scores. To a considerable degree, then, DCA condenses information about the relative abundances of all species at a point down to a single number for that point, which can be used as a measure of the species composition at those points in other analyses.

Vegetative differences among distances to edge

Once the coefficients relating DCA and PCA axes to raw vegetation data were obtained from the regional study, we scored each point from the edge study into these ordinations, a process similar to predicting values for new observations from a fitted linear regression model based on the regression coefficients. The scores obtained represent the position of each edge study point relative to the major vegetative gradients in plant species composition and vegetation structure of CSS throughout southern California. Once edge study points were scored, we confirmed that sites and distances from edge differed in vegetation structure and species composition by comparing scores on PCA1, PCA2, DCA1, and DCA2 using factorial MANOVA, with study site and distance to edge as the main effects. This analysis was followed by univariate ANOVA's for each of the dependent variables to determine which had the greatest effect upon the multivariate result.

Bird and small mammal regional habitat relationships

Habitat associations were derived from the regional data set using logistic regression, relating the presence of species to the vegetation sampled at a point (Hosmer and Lemeshow 1989). The vegetation variables used consisted of the scores of each point on two DCA axes and two PCA axes (see Results), plus additional raw variables that were poorly represented by the PCA or DCA axes (i.e., those with low correlations with PCA or DCA axes). Because points were sampled for different numbers of years at different sites in the regional study, we used the number of years a point was sampled as a covariate in all models. Overall significance of the relationship between animals and habitat was assessed with likelihood ratio tests comparing the model with all variables (vegetation variables and numbers of years sampled) to the model with only the number of years sampled.

Calibrating edge vegetation data to animal habitat affinity

We used the regional habitat relationship models to calibrate the edge study vegetation measurements to the habitat associations of each species. Once a logistic regression model was derived for each species based on the regional survey, predicted values were calculated for each edge point based on the vegetation. The regional regressions used the number of years a point was sampled as a covariate; for the edge points this was equal to one. Assuming that species' responses to habitat were consistent between the regional and edge studies, these predicted values were interpretable as the probability that a species would be detected at a point given the vegetation there. Hereafter we will refer to these predicted values simply as "habitat suitability", and use them in assessing the relative effects of habitat and distance to edge on a species' distribution.

The relative effects of habitat suitability and distance to edge

We analyzed differences in habitat suitabilities (i.e., the predicted occurrence of a species at an edge study point based on the regional regression models) among distances to edge using univariate ANOVA's. The final analysis of the effects of habitat suitability and distance to edge on species occurrence was a logistic regression of the presence/absence of a species on habitat suitability, distance to edge, and site (included to account for differences in vegetation characteristics and overall population sizes among study sites). Species whose edge effects were due to response to habitat changes had significant differences in habitat suitability scores among distances that paralleled their observed distribution patterns. This approach had the further advantage that it could detect inverse relationships between habitat suitability and abundance, such that species that were less abundant at edges in spite of the presence of preferred habitat could be accurately identified.

Results

The regional vegetation context

Twenty-four plant taxa (mainly species, but some taxa were lumped to genus) occurred on at least 10% of the 233 regional points and thus were retained for additional analyses (Appendix 2). Detrended correspondence analysis yielded two axes that we retained (Fig. 2). The first had an eigenvalue of 0.80, indicating a robust ordination. Its length was 4.46, which implied that turnover from one extreme point to the other was virtually complete, and that those points shared few, if any, plant species in common. Although the second axis had a smaller eigenvalue of 0.42, it, too, was relatively long, with a length of gradient = 3.66. The

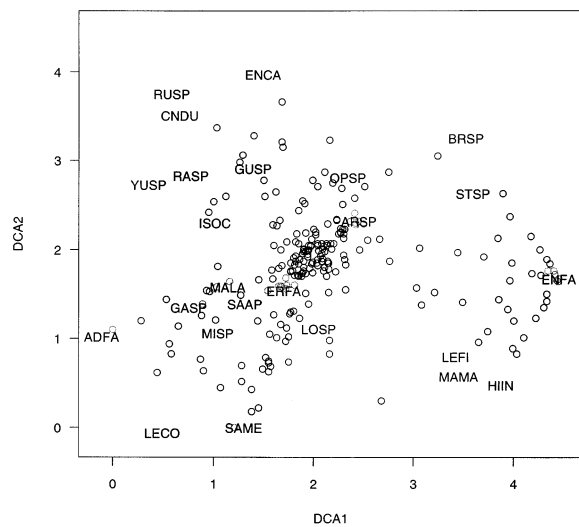


Fig. 2. Plant species scores on Detrended Correspondence Analysis axes based on plant species composition throughout the region. Open circles represent the positions of sampling points, and text codes represent positions of plant species in the ordination. Some circles were colored gray to improve legibility of species codes, but are otherwise identical to black circles. See Appendix 2 for species codes.

first axis represented a gradient from points dominated by species characteristic of inland Riversidian coastal sage scrub (e.g., *Encelia farinosa* [ENFA]; Fig. 2), to those that included a substantial amount of chaparral vegetation (e.g., *Adenostoma fasciculatum* [ADFA]). The second axis contrasted points with *Encelia californica* (ENCA), *Rhus* spp. (RUSP), and *Cneoridium dumosum* (CNDU), characteristic of southern coastal sites, with northern inland points dominated by *Elymus condensatus* (LECO), and *Salvia mellifera* (SAME).

Principal component analysis of the structural variables yielded two components with eigenvalues greater than one that we retained for additional analyses (Table 1). The first structural principal component ("shrub vs grass") represented a gradient between shrub-dominated vs exotic grass-dominated points. Points that had high scores on this component had greater shrub cover, more vegetation hits in all three height categories, had greater coverage of litter with greater litter depth, and had more shrub species. This component captured over a third of the total structural variation among all points throughout the region. The second component ("litter vs bare") contrasted points with relatively high coverage of bare ground vs those with more woody debris on the surface and greater litter depth. Points with high scores had more litter.

Vegetation found at the edge sites fell well within the range of compositional and structural variation found at the regional level (Fig. 3). The sites were floristically distinct from one another (Fig. 3A). LAPE was typical of Riverside County sites, containing greater amounts of brittlebush than the other two sites. STRA vegeta-

Table 1. Principal components analysis of habitat structural variables. Entries are factor loadings. Bold denotes factor loadings > 0.5. See Appendix 1 for codes.

Variable	Loadings	
	PCA1	PCA2
PC_GRASS	-0.85	0.16
PC_SHRUB	0.84	0.01
HITS_1_3	0.74	0.25
HITS_3_5	0.82	0.20
HITS_>5	0.82	0.04
NO_SP	0.83	-0.02
GC_LITTER	0.81	0.24
LITTER DEPTH	0.50	0.70
GC_BARE	0.26	-0.74
GC_WOOD	0.22	0.64
NUM CHANGES	-0.33	0.18
GC_ROCK	-0.21	-0.21
PC_FORB	-0.11	0.10
PC_BRAS	-0.22	-0.35
PC_SN	-0.05	0.18
Eigenvalue	5.79	1.88
Percent variance explained	38.61	12.54
Cumulative variance explained	38.61	51.15

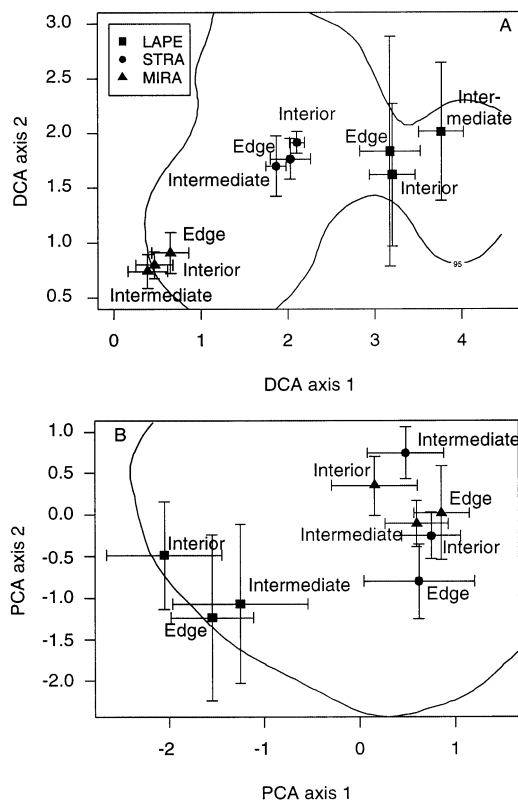


Fig. 3. Variation in vegetation among edge sites (symbols are means, error bars are ± 1 SE), superimposed on regional patterns of variation in vegetation (95% contour). Vegetative species composition (A) and structure (B) varied among edge study sites and among distance to edge within sites (Table 2), but fell within the regional range of variation. LAPE = Lake Perris; STRA = Starr Ranch; MIRA = Miramar.

tion was dominated by California sagebrush and buckwheat, whereas MIRA fell toward the edge of the regional gradients, with relatively higher amounts of chamise. Structurally, LAPE had sparser, shorter shrubs, and a greater amount of exotic grasses than either of the other edge sites, but STRA and MIRA had similar vegetative structures (Fig. 3B). All three sites lay within the range of regional variation in vegetation structure. Overall, then, our use of regional habitat models to assess suitability of habitat at edge sites was not compromised by extrapolation beyond the boundaries of the habitat data used to construct the models.

Overall, all four vegetation variables differed among the three edge study sites and among distances (Table 2). Distances differed from one another, primarily due to higher PCA2 scores at the edge (i.e., relatively more litter and woody debris, less bare ground). The differences among distances in PCA1 and DCA1 were only evident in the interaction term, indicating that these variables differed among distances, but the differences were not consistent among sites (Fig. 3). DCA2 did not differ among distances and had no interaction with site, indicating that although the study sites differed in the amount of shrubs and exotic grasses, the relative amounts did not differ among distances at any of the sites.

Regional habitat associations of animal species

At a regional scale, 14 of the 16 birds and small mammals analyzed were significantly associated with local vegetation characteristics (Table 3), with only California towhee and cactus mouse exhibiting no association with local vegetation characteristics. Structural variables (STFAC1, STFAC2, GC_CRYPT, PC_BG, PC_TREE) and floristic variables (DCA1 and DCA2) were significantly associated with occurrence in several species. Some species were also influenced by the presence of cactus, but the presence of rock outcrops and trails were not associated with any species.

Species responses to site, distance to edge, and habitat suitability

Five species of birds exhibited changes in occurrence among distances to edge (Table 4). A significant proportion of the variation in the observed presence of 12 of 16 species was accounted for by an overall model that included site, distance to edge, and habitat suitability (Table 5). Model R^2 for significant models ranged from 0.12 for western harvest mouse to 0.64 for cactus wren. California gnatcatcher, California towhee, San Diego pocket mouse, and cactus mouse did not have significant overall models (Table 5), although the models for California towhee and cactus mouse had $p < 0.1$.

Table 2. Univariate (ANOVA) and multivariate (MANOVA) analysis of differences in vegetation structure (PC1 and PC2) and floristics (DCA1 and DCA2) among edge sites (Lake Perris, Starr Ranch, Miramar) and among distance classes (edge, intermediate, interior). Bold denotes $p < 0.05$.

Effect	Variables	Test	F	DF	Statistical significance
Whole Model	All	Multivariate	19.46 ^a	24, 201	< 0.001
	PC1	Univariate	17.02	8, 71	< 0.001
	PC2		7.08	8, 71	< 0.001
	DCA1		117.30	8, 71	< 0.001
	DCA2		12.93	8, 71	< 0.001
Site	All	Multivariate	88.42 ^a	6, 138	< 0.001
	PC1	Univariate	59.16	2, 71	< 0.001
	PC2		10.88	2, 71	< 0.001
	DCA1		453.60	2, 71	< 0.001
	DCA2		49.42	2, 71	< 0.001
Distance	All	Multivariate	1.78 ^a	6, 138	0.107
	PC1	Univariate	1.94	2, 71	0.152
	PC2		4.51	2, 71	0.014
	DCA1		1.12	2, 71	0.332
	DCA2		0.25	2, 71	0.777
Site × Distance	All	Multivariate	3.37 ^a	12, 183	< 0.001
	PC1	Univariate	1.79	4, 71	0.139
	PC2		5.42	4, 71	< 0.001
	DCA1		4.58	4, 71	0.002
	DCA2		1.10	4, 71	0.361

^a Approximate F-statistic from Wilks' lambda.

For every species, habitat suitabilities differed among sites (Table 6). Habitat suitability also differed among distances to edge for several species (Table 6). As expected, species that had no unique contributions of vegetation or edge in Table 5 (e.g., cactus wren) but differed in occurrence among distances to edge (Table 4) differed in habitat suitability among distances, indicating that these species responded to vegetation gradients that coincided with distance to edge. In contrast, independent contributions of distance to edge were detected for California towhee (Table 5), even though habitat suitability differed among distances to edge (Table 6). This was due to a large number of towhees at interior points (Table 4), where the habitat suitability predicted smaller numbers, and an intermediate number of towhees at intermediate points where the habitat suitability predicted larger numbers (Fig. 4). Edges provided equivalent habitat to interiors (Table 6) for several species that exhibited edge abundance relationships (e.g., sage sparrow, California thrasher, deer mouse, which were less abundant at edges, and northern mockingbird, European starling, which were more abundant at edges; Figs 4 and 5). California gnatcatcher and San Diego pocket mouse did not respond to distance or habitat (Table 5), in spite of significant differences in habitat among distances (Table 6).

Discussion

Urban edges are heterogeneous

Recent attempts to reconcile the inconsistent results

among edge studies have noted that not all edges are alike (Sisk and Battin 2002). Our results exemplify this point, since PCA1 (diverse patches of large shrubs to exotic grass) and DCA1 (Riversidian CSS species, such as ENCA, to coastal CSS and chaparral species, such as ADFA) displayed site-specific patterns of change with increasing distance from edge, even though our sites were all nominally urban-wildland edges within the same habitat type. Only one variable, the gradient in structure from bare ground to coarse deep litter (PCA2), differed in a consistent, linear manner with increasing distance from edge. Differences in PCA2 scores showed that edge points contained less bare ground and more coarse litter than intermediate or interior points, presumably due to the consistently increased human activity at edges, and associated physical damage to the vegetation. These differences among sites illustrate the problems with interpreting results from edge studies conducted at single study sites, as well as the need to account for habitat heterogeneity when studying edge effects.

Edges are expected to be entry points for materials from outside of a habitat patch, including invasive exotic plants (Wiens et al. 1985, Cadenasso and Pickett 2001). However, we did not find a consistent, exotic edge flora. For example, exotic grasses have become common throughout each of these sites, but are patchily distributed across our three distance classes; exotic grass cover was unrelated to distance from edge, as indicated by the significant difference among sites in PCA1 scores but no distance effect, or site by distance interaction. The vegetation was relatively undifferentiated among distances at MIRA compared with LAPE and STRA (Fig. 3). If exotic grasses originally entered

Table 3. Effects of local vegetation variables on the occurrence of birds and small mammals in the regional CSS data set. Entries denote the sign of significant ($p < 0.05$) regression coefficients.

	Variable										Model		
	GC_CRYP	PC_BG	PC_TREE	STFAC1	STFAC2	DCA1	DCA2	CACTUS	ROCK	TRAIL	Deviance	DF	p
Cactus wren		-						+			82.36	10	<0.001
California gnatcatcher								+			22.54	10	0.013
California towhee											10.68	10	0.383
California thrasher						+					34.62	10	<0.001
European starling							-	-			22.80	10	0.011
Northern mockingbird			-		+	-	-	+			60.27	10	<0.001
Sage sparrow				+	+	-					132.31	10	<0.001
Western scrub-jay				-		+		-			59.20	10	<0.001
San Diego pocket mouse				+							48.82	10	<0.001
Pacific kangaroo rat					+						43.28	10	<0.001
Dusky-footed woodrat	-			-		+					55.71	10	<0.001
San Diego woodrat	-			-		-					31.24	10	0.001
California mouse	-			-		+		+			66.84	10	<0.001
Cactus mouse											10.42	10	0.405
Deermouse				+							47.39	10	<0.001
Western harvest mouse					-		-				19.29	10	0.037

the study areas via edges, they have spread sufficiently to erase the spatial signature of the event.

We intentionally chose study sites that were positioned along a gradient in vegetation structure and species composition so that we could better distinguish between consistent responses to edge (“ecotonal effects”) and responses to vegetation (“matrix effects”). The differences we found in vegetation among sites were therefore expected. All of our sites were adjacent to the same type of urban edge (i.e., single-family houses), yet some of the heterogeneity among urban edges was due to differences between sites on the urban side of the edge. At STRA, for example, a narrow strip of irrigated landscaping separated the houses from the developed edge, and by a narrow strip of golf course at LAPE, whereas houses abutted the edge at MIRA. This heterogeneity could lead to differences among sites in the magnitude of an ecotonal edge response, and this sort of heterogeneity may have contributed to the inconsistency among studies of the edge responses of species (Sisk and Battin 2002).

Heterogeneity in the urban sides of edges can produce different effects on the CSS side of the edge as well. For example, the irrigation system at the STRA edge contributed water to the plants on the CSS side of the edge, but at LAPE we did not observe any water subsidy. Given the substantial variability in the characteristics of urban/wildland edge found in a single, geographically variable vegetation type and a single edge type, it is possible for consistent responses by animals to characteristics of edges to result in very different edge effects among studies.

Similar patterns of occurrence are consistent with different mechanistic explanations

Several species were less common at edges than at intermediate or interior distances (Table 4). However, species with similar patterns of occurrence did not all respond to the same characteristics of the edge. For example, both cactus wren and sage sparrow were less common at edges than at other distances. Cactus wren habitat suitability was lower at edges (Table 6), and edge made no unique contribution to cactus wren occurrence (Table 5). In contrast, sage sparrow habitat suitability did not differ among distances (Table 6), and edge made a unique contribution to sage sparrow occurrence (Table 5). We interpret these results as evidence that cactus wren responded to a habitat gradient that was correlated with distance from edge, but did not respond directly to the edge, whereas sage sparrow avoided the edge in spite of the presence of suitable habitat (Fig. 4). Both species were responsive to local vegetation conditions in the regional analysis (Table 3), and sage sparrow selected suitable habitat when it occurred at interior or intermediate distances, as indi-

Table 4. Numbers of the 27 edge study points at which species were detected at each distance from edge, and logistic regression results relating occurrence to distance from edge. Degrees of freedom for all tests was 2. Bold denotes $p < 0.05$.

Species	Edge	Intermed.	Inter.	Deviance	p
Cactus wren	7	9	11	1.3	0.510
California gnatcatcher	1	2	3	1.1	0.570
California towhee	17	22	26	10.5	0.010
California thrasher	7	18	15	9.9	0.010
European starling	17	3	2	26.1	< 0.001
Northern mockingbird	23	8	6	27.6	< 0.001
Sage sparrow	1	9	6	9.0	0.010
Western scrub-jay	16	15	13	0.7	0.710
San Diego pocket mouse	4	9	6	2.6	0.270
Pacific kangaroo rat	3	6	5	1.3	0.530
Dusky-footed woodrat	18	14	13	2.1	0.350
San Diego woodrat	9	11	11	0.4	0.810
California mouse	20	20	20	0.0	1.000
Cactus mouse	17	20	21	1.6	0.460
Deermouse	9	11	17	5.2	0.070
Western harvest mouse	14	15	13	0.3	0.860

Table 5. Effects of site, distance from edge, and habitat suitability on the distribution of birds and small mammals. Species with a unique effect of edge in this analysis exhibit an “ecotonal” edge effect. Bold denotes likelihood ratio tests with $p < 0.05$.

Species	Overall			Site		Habitat		Edge		Edge response
	R ²	χ ²	p	χ ²	p	χ ²	p	χ ²	p	
Birds										
Cactus wren	0.64	65.62	<0.001	36.16	<0.001	0.01	0.92	3.62	0.160	
California gnatcatcher	0.14	6.03	0.300	4.88	0.090	0.00	1.00	1.18	0.550	
California towhee	0.13	10.08	0.070	0.63	0.730	0.54	0.46	9.44	0.010	—
Western scrub-jay	0.17	18.71	<0.001	5.42	0.070	0.18	0.67	0.99	0.610	
Sage sparrow	0.50	39.75	<0.001	22.50	<0.001	4.22	0.04	9.96	0.010	—
Northern mockingbird	0.30	32.75	<0.001	2.92	0.230	2.43	0.12	27.64	<0.001	+
European starling	0.33	30.65	<0.001	0.04	0.980	5.29	0.02	29.56	<0.001	+
California thrasher	0.16	17.30	<0.001	6.78	0.030	0.07	0.79	10.57	0.010	—
Small mammals										
San Diego pocket mouse	0.10	8.51	0.130	1.67	0.430	1.35	0.25	2.26	0.32	
Pacific kangaroo rat	0.32	24.01	<0.001	0.54	0.760	7.31	0.01	0.52	0.77	
Dusky-footed woodrat	0.30	32.94	<0.001	20.73	<0.001	2.14	0.14	3.33	0.19	
San Diego woodrat	0.57	60.91	<0.001	35.61	<0.001	0.10	0.75	0.98	0.61	
California mouse	0.57	51.14	<0.001	22.84	<0.001	0.18	0.67	0.02	0.99	
Cactus mouse	0.11	10.29	0.070	8.35	0.020	1.95	0.16	2.15	0.34	
Deermouse	0.36	40.01	<0.001	1.10	0.580	6.22	0.01	6.19	0.05	—
Western harvest mouse	0.12	13.29	0.020	11.82	<0.001	0.37	0.54	0.39	0.82	

cated by the significant effect of habitat on sage sparrow occurrence (Table 5).

Habitat suitability differed among distances to edge for three bird and two small mammal species (Table 6). For these species, our intermediate points were intermediate in habitat suitability for three species (cactus wren, California gnatcatcher, and San Diego pocket mouse), and California gnatcatcher habitat was more similar between edge and intermediate points than between intermediate and interior points. The effects of edge should extend for different distances for different vegetation variables, which should be reflected in differences in the distances of edge effects on species habitat. In contrast, the habitat suitability for two species (California towhee and California mouse) was greatest at intermediate distances. If these patterns of habitat suitability are produced by the edge, they may represent a

form of intermediate disturbance effect for some vegetation variables. Alternatively, given the heterogeneity in the vegetation we observed, these patterns may be chance similarities between edge and interior points in those vegetation variables with which the species is most strongly associated. Detailed study of the mechanisms of edge associated vegetation change would be required to distinguish these possibilities.

Responses that can be explained by the habitat associations away from edges have been called “matrix effects” (Lidicker 1999) or “habitat effects” (Kingston and Morris 2000). Although the clearest case of this type of response in our study was the cactus wren, California gnatcatcher and San Diego pocket mouse habitat also differed among distances, and they occurred less often at edges than at intermediate or interior distances (Figs 4 and 5). However, the differences

Table 6. Differences in the habitat suitability (i.e. ANOVA of the predicted probability of occurrence for each species based on its NCCP habitat model) among sites and distances to edge. Bold denotes $p < 0.05$.

Species	Site and Distance			Site		Distance	
	R ²	F	p	F	p	F	p
Birds							
Cactus wren	0.54	22.35	<0.001	41.11	<0.001	3.99	0.022
California gnatcatcher	0.36	10.53	<0.001	17.54	<0.001	3.26	0.044
California towhee	0.28	7.20	<0.001	9.65	<0.001	4.66	0.012
Western scrub-jay	0.67	37.80	<0.001	75.50	<0.001	0.44	0.647
Sage sparrow	0.71	46.62	<0.001	93.23	<0.001	0.09	0.910
Northern mockingbird	0.82	87.46	<0.001	174.85	<0.001	0.14	0.867
European starling	0.20	4.73	0.002	7.02	0.002	2.41	0.100
California thrasher	0.71	45.49	<0.001	90.39	<0.001	1.14	0.324
Small mammals							
San Diego pocket mouse	0.65	34.33	<0.001	64.32	<0.001	3.35	0.041
Pacific kangaroo rat	0.55	45.79	<0.001	45.79	<0.001	0.54	0.585
Dusky-footed woodrat	0.56	24.11	<0.001	47.41	<0.001	0.87	0.420
San Diego woodrat	0.45	15.61	<0.001	30.58	<0.001	0.60	0.552
California mouse	0.66	36.70	<0.001	67.5	<0.001	7.11	0.001
Cactus mouse	0.70	43.47	<0.001	85.56	<0.001	2.09	0.130
Deermouse	0.90	180.38	<0.001	360.61	<0.001	1.02	0.366
Western harvest mouse	0.36	10.83	<0.001	21.54	<0.001	0.08	0.923

in occurrence among distances for California gnatcatcher and San Diego pocket mouse were not statistically significant (Table 4). Both species were relatively uncommon, and the effects may have been too subtle to detect statistically with our data.

Patterns of response to edge that exceed the expected response to change in habitat have been called “ecotonal effects” (Lidicker and Peterson 1999), which are direct responses to the edge. This analysis clearly demonstrated that the decreased occurrence of sage sparrow, California thrasher, California towhee, and deermouse at edges could not be explained by habitat degradation since their habitat suitabilities did not parallel changes in occurrence with distance to edge (Figs 4 and 5), in spite of the significant association with local habitat variables for all but the California towhee in the regional study (Table 3). Similarly, northern mockingbird and European starling were more common at edges in spite of similar habitat suitability among distances from edge, and both were responsive to local vegetation in the regional study. Consequently, the positive or negative edge-abundance relationships for these species appear to be direct responses to properties of the edge. The apparent cases of edge responses in opposition to habitat suitability (a form of ecotonal response that would be difficult to detect without independent measures of habitat associations) in western scrub-jay and cactus mouse (Figs 4 and 5, respectively) are weakened by the lack of significant difference in habitat suitability among distances to edge in the western scrub-jay (Table 6), and non-significant models of occurrence for the cactus mouse (Tables 3 and 5). In contrast, California mice were found in equal numbers at each distance to edge in spite of significantly poorer habitat at the edge, which we interpret as weak evidence of a positive edge response.

We note that whereas a change in occurrence is positive evidence of an edge effect, lack of such a change does not imply that edges are benign. Edges can affect animal performance in a variety of ways, some of which may not produce changes in distribution (Lidicker 1999). For example, demographic changes at the edge due to increased predation may be offset by immigration from the interior, and mask the increased loss of individuals at the edge. In this case, abundance would reflect habitat quality poorly (Van Horne 1983), and would fail to reveal an edge effect.

Birds and small mammals were affected differently by edge

The occurrences of five birds were affected by edge, but the occurrence of only one small mammal species, the deermouse, was significantly affected by edge. Data for the Pacific kangaroo rat exhibits a pattern consistent with a habitat effect, and dusky-footed woodrat, San Diego woodrat, cactus mouse, and San Diego pocket mouse exhibited patterns that were consistent with ecotonal effects, but the results for these species were not significant. Consequently, it appears that in general the effects of edge on small mammal occurrence were smaller than on bird occurrence. Lack of edge effects have been found in small mammals at forest-farm edges (Heske 1995), but we found a lack of edge response even in cases where species responses to habitat would be expected to produce one. Experimental studies of the ability of small mammals to navigate toward forest edges indicate that small mammals may have little capacity to detect landscape-level features at a distance (Zollner and Lima 1997, 1999). Birds are more mobile, and may be better able to respond behaviorally to edges

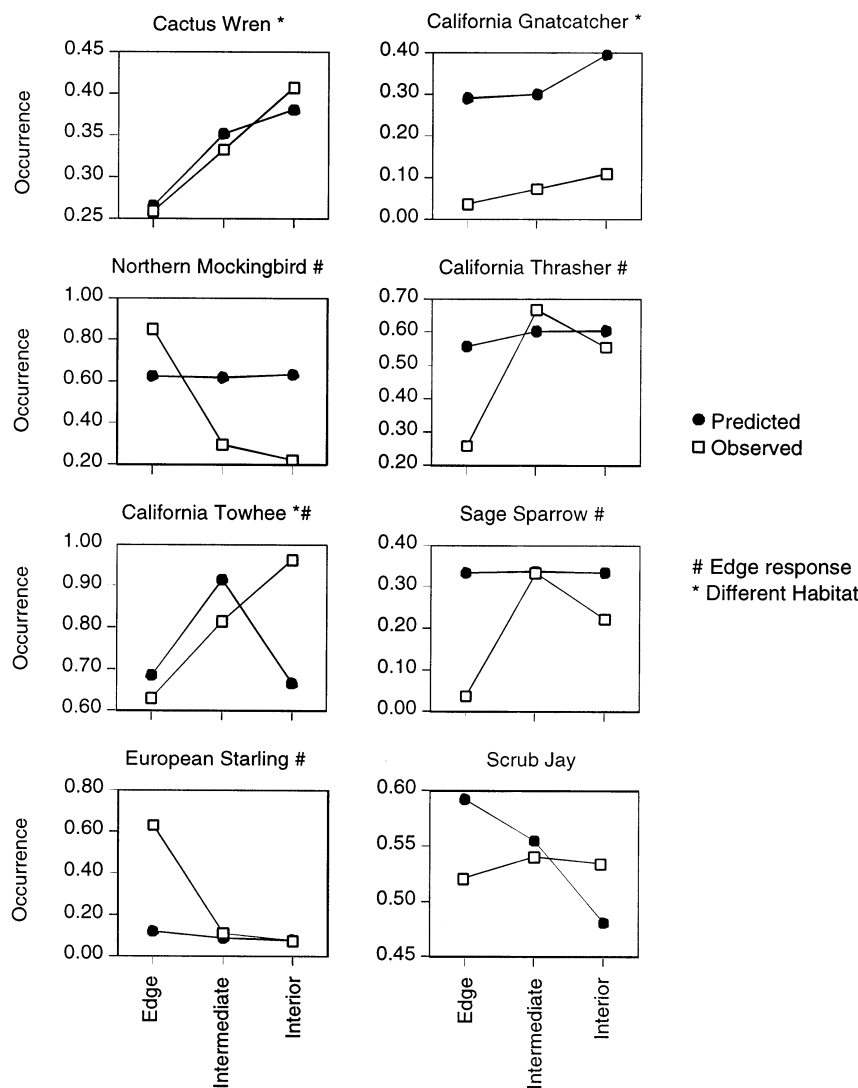


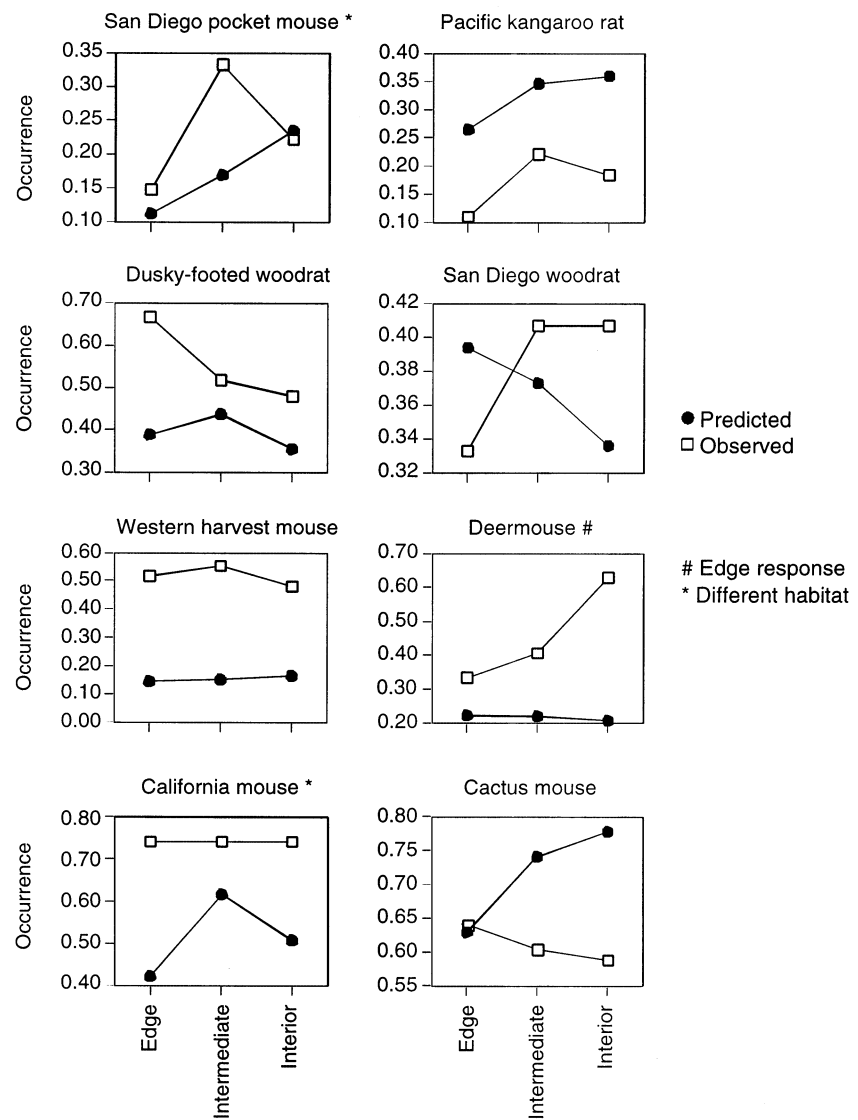
Fig. 4. Observed (open squares) and predicted (black circles) occurrence of birds among distances from edge. Significant differences in preferred habitat among distances to edge (Table 6) are denoted with *, and significant effects of edge on occurrence (Table 5) are denoted with #.

than small mammals (Lidicker and Koenig 1996). Small mammals may have suffered greater mortality at edges due to the increased mammalian predator activity we observed there (Kristan 2001), but the apparent increase in predation risk at edges was not associated with decreased small mammal occurrence in most species. Increases in predator activity at edges has been observed for wild predators (Dijak and Thompson 2000), and suburban development is known to be a source of subsidized domestic predators, such as house cats (Churcher and Lawton 1987). This could mean that mortality at edges was not sufficient to reduce small mammal populations, that increased mortality was offset by immigration from areas farther from the edge, or that depredation of the deer mouse was greater than other species.

Use of independent measures of habitat associations

Our analyses relied heavily on habitat suitability scores obtained from independently-derived habitat models. Lacking independent knowledge of the habitat associations of each species, we would have needed to fit models that included distance from edge and vegetation variables to patterns of animal occurrence in the edge study data, and allow the association between occurrence and vegetation to indicate the habitat affinities of the species. Because vegetation differed among distances from edge, the results of such an analysis would be equally consistent with a direct response to edge (an ecotonal effect) or an edge-associated change in habitat (a matrix or habitat effect). By calibrating our vegetation data to the habitat associations of each species we were better able to evaluate how species responded to

Fig. 5. Observed (open squares) and predicted (black circles) occurrence of small mammals among distances from edge. Significant differences in preferred habitat among distances to edge (Table 6) are denoted with *, and significant effects of edge on occurrence (Table 5) are denoted with #.



the habitat gradient that was associated with distance to edge, and reduced the ambiguity of the analysis. Our method would reduce the ambiguity of this type of analysis in several circumstances:

1) Animals had a significant association with a vegetation gradient that did not differ with distance to edge. In this case using predicted habitat suitability scores would reduce the statistical confounding between vegetation and distance to edge, making direct responses to edge easier to detect.

2) Animals had significant association with the vegetation gradient that differed with distance to edge. For these species, using habitat suitability scores did not eliminate the confounding between vegetation and distance from edge, but calibrated the vegetation gradient to the habitat affinities of the species. Once the vegetation variables were calibrated, it was possible to detect

cases in which edge-abundance relationships were due to positive response to habitat suitability gradients by observing a parallel between the observed occurrence of the species and the habitat suitability scores. In these cases the effect of edge was expressed through a change in the species' habitat. It would also be possible to detect cases in which the species responded to the edge in opposition to its habitat associations instead of in parallel with its habitat associations, conditions that would be indistinguishable if raw vegetation variables were used.

3) Animals had non-significant associations with vegetation. For species that had no significant association with vegetation, the variation in vegetation that we observed would be expected to have no effect on the species' distribution. This reduced uncertainty by flattening (through regression coefficients near zero) the

vegetation relative to distance to edge and across sites, and better represented our knowledge of the responsiveness of the species to local vegetation than would inclusion of raw vegetation variables.

In all of the cases described above, we preferred to use the independently-derived habitat models instead of deriving habitat associations from the edge study data directly. Compared with the edge study, the habitat models were based on more extensive and intensive sampling, conducted in the absence of urban edge effects, and thus we expected them to be more reliable estimates of the responses of species to variation in vegetation. We also expected the usual difficulties in using habitat models to predict distribution and abundance to be reduced in our case because we sampled both the regional and edge studies at the same time and within the same geographical area (at the same study sites for LAPE and STRA). This meant that our predicted habitat suitabilities were spatially and temporally interpolated rather than extrapolated. As our edge study points fell largely within the 90% contour of the regional study points (Fig. 3), we were interpolating in variable space as well.

Conservation implications

Our results suggest different strategies for reducing the effects of edges on different species. Both sage sparrows and California thrashers showed strong evidence of direct, negative responses to edges. These species are also known to be fragmentation sensitive (Bolger et al. 1997), and our results suggest that this may be due in part to their edge sensitivity. Other species, particularly cactus wren and possibly the California gnatcatcher and San Diego pocket mouse, may also be fragmentation sensitive due to their relationships with edge, but for these species the mechanism is likely to be habitat degradation rather than aversion to the edge per se. This distinction is important, because the reduced effective area of habitat caused by the developed edge would not be reversed by restoring the habitat at edges for sage sparrows or California thrashers, but may be reversed for cactus wrens, California gnatcatchers, or the San Diego pocket mouse.

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References

- Atwood, J. L. 1993. California gnatcatchers and coastal sage scrub: the biological basis for endangered species listing. – In: Keeley, J. E. (ed.), *Interface between ecology and land development in California*. Southern California Acad. Sci., pp. 149–166.
- Bolger, D. T., Scott, T. A. and Rotenberry, J. T. 1997. Breeding bird abundance in an urbanizing landscape in coastal southern California. – *Conserv. Biol.* 11: 406–421.
- Cadenasso, M. L. and Pickett, S. T. A. 2001. Effect of edge structure on the flux of species into forest interiors. – *Conserv. Biol.* 15: 91–97.
- Camargo, J. L. C. and Kapos, V. 1995. Complex edge effects on soil moisture and microclimate in central Amazonian forest. – *J. Trop. Ecol.* 11: 205–221.
- Churcher, J. B. and Lawton, J. H. 1987. Predation by domestic cats in an English village. – *J. Zool. Lond.* 212: 439–456.
- Dijk, W. D. and Thompson, F. R. 2000. Landscape and edge effects on the distribution of mammalian predators in Missouri. – *J. Wildl. Manage.* 64: 209–216.
- Dobson, A. P. et al. 1997. Geographic distribution of endangered species in the United States. – *Science* 275: 550–553.
- Donovan, T. M. et al. 1997. Variation in local-scale edge effects: mechanisms and landscape context. – *Ecology* 78: 2064–2075.
- Forman, R. T. T. and Alexander, L. E. 1998. Roads and their major ecological effects. – *Annu. Rev. Ecol. Syst.* 29: 207–231.
- Francel, K. E. and Schnell, G. D. 2002. Relationships of human disturbance, bird communities and plant communities along the land-water interface of a large reservoir. – *Environ. Monitor. Assess.* 73: 67–93.
- Gauch, H. G. 1982. *Multivariate analysis in community ecology*. – Cambridge Univ. Press.
- Heske, E. J. 1995. Mammalian abundances on forest-farm edges versus forest interiors in southern Illinois: is there an edge effect? – *J. Mammal.* 76: 562–568.
- Hosmer, D. W. Jr and Lemeshow, S. 1989. *Applied logistic regression*. – Wiley.
- Inglis, L. G. 1965. *Mammals of the Pacific States*. – Stanford Univ. Press.
- Jameson, E. W. Jr and Peeters, H. J. 1988. *California mammals*. – Univ. of California Press.
- Janzen, D. H. 1983. No park is an island: increase in interference from outside as park size decreases. – *Oikos* 41: 402–410.
- Kingston, S. R. and Morris, D. W. 2000. Voles looking for an edge: habitat selection across forest ecotones. – *Can. J. Zool.* 78: 2174–2183.
- Kristan, W. B. III 2001. *Effects of habitat selection on avian population ecology in urbanizing landscapes*. – Unpubl. Ph.D. thesis, Univ. of California, Riverside, CA.
- Lidicker, W. Z. Jr 1999. Responses of mammals to habitat edges: an overview. – *Landscape Ecol.* 14: 333–343.
- Lidicker, W. Z. Jr and Koenig, W. D. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. – In: McCullough, D. R. (ed.), *Metapopulations and wildlife conservation*. Island Press, pp. 85–109.
- Lidicker, W. Z. Jr and Peterson, J. A. 1999. Responses of small mammals to habitat edges. – In: Barrett, G. W. and Peles, J. D. (eds), *Landscape ecology of small mammals*. Springer, pp. 211–227.
- Matlack, G. R. 1994. Vegetation dynamics of the forest edge-trends in space and successional time. – *J. Ecol.* 82: 113–123.

- McCaull, J. 1994. The Natural Community Conservation Planning Program and the coastal sage scrub ecosystem of southern California. – In: Grumbine, R. E. (ed.), Environmental policy and biodiversity. Island Press, pp. 281–292.
- Minnich, R. A. and Dezzani, R. J. 1998. Historical decline of coastal sage scrub in the Riverside-Perris Plain, California. – *Western Birds* 29: 366–391.
- Murcia, C. 1995. Edge effects in fragmented forests: Implications for conservation. – *Trends Ecol. Evol.* 10: 58–62.
- O'Leary, J., Murphy, D. and Brussard, P. 1992. The coastal sage scrub community conservation planning region. – NCCP Spec. Rep. No. 2. California Environmental Trust, San Francisco.
- Paton, P. W. C. 1994. The effect of edge on avian nest success: how strong is the evidence? – *Conserv. Biol.* 8: 17–26.
- Pielou, E. C. 1984. The interpretation of ecological data: a primer on classification and ordination. – Wiley.
- Price, M. V., Waser, N. M. and Bass, T. A. 1984. Effects of moonlight on microhabitat use by desert rodents. – *J. Mammal.* 65: 353–356.
- Ralph, C. J., Sauer, J. R. and Droege, S. 1995. Monitoring bird populations by point counts. – Gen. Tech. Rep. PSW-GTR-149. Albany, CA: Pacific Research Station, Forest Service, U.S. Dept of Agriculture.
- Rotenberry, J. T., Price, M. V. and Kristan, W. B. III 1999. Local and landscape vegetation context: the habitat template for animal species' distributions. – Unpubl. USGS-BRD Rep.
- Sisk, T. D. and Battin, J. 2002. Habitat edges and avian ecology: geographic patterns and insights for western landscapes. – *Stud. Avian Biol.* 25: 30–48.
- Sisk, T. D., Haddad, N. M. and Ehrlich, P. R. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. – *Ecol. Appl.* 7: 1170–1180.
- Soulé, M. E. et al. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. – *Conserv. Biol.* 2: 75–92.
- Tabachnick, B. G. and Fidell, S. 1983. Using multivariate statistics. – Harper and Row.
- Temple, S. and Cary, J. 1988. Modeling dynamics of habitat-interior bird populations in fragmented landscapes. – *Conserv. Biol.* 2: 340–347.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. – *J. Wildl. Manage.* 47: 893–901.
- Westman, W. E. 1981. Factors influencing the distribution of species of Californian coastal sage scrub. – *Ecology* 62: 439–455.
- Westman, W. E. 1983. Xeric Mediterranean-type shrubland associations of Alta and Baja California and the community/continuum debate. – *Vegetatio* 52: 3–19.
- White, S. D. and Padley, W. D. 1997. Coastal sage scrub series of Western Riverside County, California. – *Madroño* 44: 95–105.
- Wiens, J. A. and Rotenberry, J. T. 1981. Habitat associations and community structure of birds in shrubsteppe environments. – *Ecol. Monogr.* 51: 21–41.
- Wiens, J. A., Crawford, C. S. and Grosz, J. R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. – *Oikos* 45: 421–427.
- Woodroffe, R. and Ginsberg, J. R. 1998. Edge effects and the extinction of populations inside protected areas. – *Science* 280: 2126–2128.
- Yahner, R. H. 1988. Changes in wildlife communities near edges. – *Conserv. Biol.* 2: 333–339.
- Zar, J. H. 1984. Biostatistical analysis. – Prentice-Hall.
- Zollner, P. A. and Lima, S. L. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. – *Oikos* 80: 51–60.
- Zollner, P. A. and Lima, S. L. 1999. Illumination and the perception of remote habitat patches by white-footed mice. – *Anim. Behav.* 58: 489–500.

Appendix 1. Vegetation variable codes and descriptions.

Variable	Description
GC_Bare	Percent of ground cover that is bare ground.
GC_BG	Percent of ground cover that is bunch grass.
GC_Cac	Percent of ground cover that is cactus.
GC_Crypt	Percent of ground cover that is cryptogammic soil.
GC_Forb	Percent of ground cover that is forb.
GC_Grass	Percent of ground cover that is exotic grass.
GC_Litter	Percent of ground cover that is litter (small, disaggregated debris).
GC_Rock	Percent of ground cover that is rock.
GC_Wood	Percent of ground cover that is woody debris.
Hits_1_3	Number of times plants touched the pin between 1 and 3 dm.
Hits_3_5	Number of times plants touched the pin between 3 and 5 dm.
Hits_>5	Number of times plants touched the pin over 5 dm.
Litter_Depth	Average depth of litter.
Max_ht	Average height of the tallest plant at each pin drop.
Mean size	Mean horizontal patch size.
Num_sp	Mean number of species that touched each pin drop.

Code	Common name	Scientific name
Plants		
ADFA	Chamise	<i>Adenostoma fasciculatum</i>
AMME	Fiddlenecks	<i>Amsinckia menziesii</i>
ARCA	California sagebrush	<i>Artemisia californica</i>
BG	Bunch grasses	
BRAS	Mustard	<i>Brassica</i> spp.
BRSP	Thistle	<i>Brickellia</i> spp.
CAC	Prickly pear and cholla	<i>Opuntia</i> spp.
CETO	California-lilac	<i>Ceanothus tomentosus</i>
CNDU	Bushrue	<i>Cneoridium dumosum</i>
ENFA	Brittle bush	<i>Encelia farinosa</i>
ERCR	Yerba santa	<i>Eriodictyon crassifolium</i>
ERFA	California buckwheat	<i>Eriogonum fasciculatum</i>
FORB	Herbaceous dicots	
GASP	Bedstraw	<i>Galium</i> spp.
GRASS	Exotic grasses	
HEAR	Toyon	<i>Heteromeles arbutifolia</i>
LEFI	Cham	<i>Lessingia filaginifolia</i>
LOSP	Deerweed	<i>Lotus scoparius</i>
MALA	Laurel sumac	<i>Malosma laurina</i>
MAMA	Wild cucumber	<i>Marah macrocarpus</i>
MISP	Monkey flower	<i>Mimulus</i> spp.
QUSP	Oak	<i>Quercus</i> spp.
RUSP	Lemonadeberry	<i>Rhus</i> spp.
SAAP	White sage	<i>Salvia apiana</i>
SAME	Black sage	<i>Salvia mellifera</i>
SN	Standing dead woody	
XYBI		<i>Xylococcus bicolor</i>
Birds		
CACW	Cactus wren	<i>Campylorhynchus brunneicapillus</i>
CAGN	California gnatcatcher	<i>Poliophtila californica</i>
CALT	California towhee	<i>Pipilo crissalis</i>
CATH	California thrasher	<i>Toxostoma redivivum</i>
CORA	Common raven	<i>Corvus corax</i>
EUST	European starling	<i>Sturnus vulgaris</i>
NOMO	Northern mockingbird	<i>Mimus polyglottos</i>
SAGS	Sage sparrow	<i>Amphispiza belli</i>
SCJA	Western scrub-jay	<i>Aphelocoma coerulescens</i>
Small mammals		
CHCA	Dulzura pocket mouse	<i>Chaetodipus californicus femoralis</i>
CHFA	San Diego pocket mouse	<i>Chaetodipus fallax fallax</i>
DIAG	Pacific kangaroo rat	<i>Dipodomys agilis</i>
NEFU	Dusky-footed woodrat	<i>Neotoma fuscipes</i>
NELE	San Diego woodrat	<i>Neotoma lepida intermedia</i>
PECA	California mouse	<i>Peromyscus californicus</i>
PEER	Cactus mouse	<i>Peromyscus eremicus</i>
PEMA	Deermouse	<i>Peromyscus maniculatus</i>
REME	Western harvest mouse	<i>Reithrodontomys megalotis</i>