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HABITAT FRAGMENTATION EFFECTS ON BIRDS IN SOUTHERN CALIFORNIA: CONTRAST TO THE "TOP-DOWN" PARADIGM

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Abstract. I review the existing literature on habitat fragmentation and its effects on avian populations in coastal sage scrub and chaparral habitat in coastal southern California. Included in this review is a consideration of the effect of fragmentation on nest predators, brood parasites, food availability, and habitat structure and quality. Fragmentation and the creation of edge are extensive in this region. The primary contemporary fragmenting land-use is residential development. In comparison to forested landscapes in the East and Midwest, fragmentation in this region seems to cause more isolation in bird populations. Local extinctions in isolated habitat fragments are common among some species of the shrub habitat avifauna and colonizations are relatively rare. This difference may be due to more limited dispersal ability in the year-round residents that are characteristic of this region as compared to the long-distance migrants in the East and Midwest. Perhaps due to the semi-arid nature of the region, fragmentation may be accompanied by more habitat degradation than in mesic regions, which could contribute to the lack of successful colonization. In contrast to studies in the East and Midwest, the only demographic study of avian edge effects in this system indicates that nest predation and brood parasitism do not increase near anthropogenically-induced edges. In isolated habitat fragments mammalian mesopredators appear to undergo "mesopredator release" in the absence of coyotes (*Canis latrans*). In habitat fragments the availability of potential arthropod prey is positively related to fragment size and negatively related to fragment age, but does not appear to be a function of distance to edge. In large habitat blocks, however, the abundance of a number of arthropod taxa is lower near edges. A particularly striking edge effect is the invasion of non-native Argentine ants along urban edges. The effect of Argentine ants on native ants is severe but their effect on arthropods that are more important as avian prey is less clear.

Key Words: *Aimophila ruficeps*; Argentine ants; bottom-up; edge effects; habitat fragmentation; *Linepithema humile*; mesopredator release; nest predation; Rufous-crowned Sparrow; southern California; top-down.

Birds display varying degrees of edge and fragment area sensitivity, with abundance of some species declining sharply with fragment area or proximity to fragment edge (Blake and Karr 1987, Soulé et al. 1988, Robbins et al. 1989a, Herkert 1994). The mechanisms generating these sensitivities are often obscure. Since the principal determinant of avian reproductive success is the rate of nest predation (Ricklefs 1969), most mechanistic studies of the effect of fragmentation and edge on birds have focused on the "top-down" effects of nest predation and brood parasitism. In fragmented forests in the East and Midwest of North America nest predation and brood parasitism on neotropical migrant forest birds has been shown to increase with proximity to forest edge and with the degree of fragmentation in the landscape (Paton 1994, Robinson et al. 1995a, Donovan et al. 1997, Hartley and Hunter 1998). Avian and mammalian predators may increase along ecotones in response to increased density of nesting birds attracted to changes in habitat structure (Gates and Gysel 1978), or to resource subsidies provided by human land-use (Wilcove 1985, Andrén 1992). Because of this, highly fragmented landscapes in the Midwest are apparently population sinks (Pulliam 1988) for some neotropical migrant bird species. Their persistence in those landscapes appears dependent upon immigration from large, unfragmented source areas (Robinson et al. 1995a).

These striking findings have led to the current "top-down" paradigm in temperate zone fragmentation studies. However, generalizations derived from these studies may not apply to other species, ecosystems, and land-use types (Wiens 1997, Tewksbury et al. 1998). One land-use that has become increasingly common is urban development (Berry 1990, Roodman 1996). As the world becomes increasingly urban, edge between urban development and natural habitat increases as does the importance of understanding the ecological changes that occur at these interfaces (Babbitt 1999). Urban/natural edges may be especially ecologically active due to high inputs of materials, water, energy, nutrients, human commensal species, and high human population density (McDonnell et al. 1993). Only recently have "bottom-up" effects of habitat fragmentation on avian food availability received attention (Burke and Nol 1998, Zanette et al. 2000).

In coastal southern California, urban residential development is currently the principal land-use that fragments the native shrub habitats, coastal sage scrub and chaparral. Historically, agriculture and grazing also contributed to the pattern of fragmentation. There is a conservation planning effort ongoing for this region (Atwood and Noss 1994) and the reserve system that results from this effort will by necessity be set within an urban matrix. So understanding urban edge and fragmentation effects will be vital to the success of this conservation effort.

In this paper I summarize research on the patterns of distribution and abundance of breeding bird species in these fragmented landscapes and the ecological mechanisms that shape these distributions. I first suggest a conceptual framework describing fragmentation effects and the ecological mechanisms that generate these effects. Original data on bird abundance in the edge and interior of large habitat blocks in San Diego County are also presented. Finally, I review the available literature on fragmentation effects in this region and assess the evidence for a number of ecological mechanisms that might generate the effects. This review is limited to a consideration of species, predominantly passerines, that have coastal sage scrub and/or chaparral as one of their principal breeding habitats or occur in mosaic landscapes with these shrub habitats and non-native grassland.

METHODS

EDGE AND INTERIOR BIRD SURVEYS

To examine the edge sensitivity of the coastal sage scrub avifauna, variable distance point counts (Ralph et al. 1993) were conducted in the spring of 1997, 1998, and 1999 in edge and interior locations of three large coastal sage scrub habitat blocks in San Diego County, CA. Details of the sites are available in Morrison and Bolger (2002). For the analyses below, only detections within 70m of the point count station were used. Most detections of Common Ravens (see Appendix for scientific names of vertebrate species) were beyond 70m so detections up to 150m were allowed for this species. For most species fly-overs were not included in the analyses. However, for species for which most detections were by fly-over, fly-over data were included if the path of flight intercepted a 70-m circle around the point count station. These included Common Raven, Anna's Hummingbird, Costa's Hummingbird, and Western Scrub-Jay.

Point count locations were a minimum of 150m apart and edge locations were at least 70m from the urban edge. A total of 24 locations were surveyed in 1997, 15 in 1998, and 31 in 1999. Three eight-minute counts were conducted per point per year between March 29 and June 13. To achieve statistical independence, locations that were sampled in more than one year were only used in one year in the analyses, producing the final number of locations in Table 1. The choice of locations included in each year's dataset was made to maximize sample sizes.

For common species, the mean number of detections/station/visit was analyzed with two-way ANOVA with year and treatment (edge vs. interior) as the factors. For uncommon species, parametric methods were not appropriate. Instead, the frequency of presence/absence was analyzed with three-way contingency tables: present/absent × year × treatment. If a species was detected at least once at a location in a given year it was designated present and absent otherwise. The significance of the treatment effect (edge vs. interior) was tested by comparing the chi-square value from the log-linear model that contained all pair-wise interactions to a model that did not contain the treatment × present/absent term. The significance of the treatment × present/absent term was tested by the difference in chi-square value between the models using one degree of freedom.

RESULTS AND DISCUSSION

SOUTHERN CALIFORNIA LANDSCAPES AND AVIFAUNA

There are five primary terrestrial habitats within the coastal zone of southern California: coastal sage scrub, chaparral (mixed and chamise), riparian woodland/scrub, oak woodland, and non-native grassland (Beauchamp 1986). The two shrub habitat types, coastal sage scrub (henceforth CSS) and chaparral, predominate and most research on habitat fragmentation in this region has been conducted in those habitats. The fragmentation studies reviewed below have been conducted in coastal San Diego County (predominantly in CSS habitat), the Palos Verdes Peninsula in Orange County (CSS), and the Santa Monica Mountains in Los Angeles County (chaparral). Most studies cited here were conducted within 20km of the coast, so for the purpose of this review I will define that 20 km band within these three counties as the coastal southern California region.

Coastal sage scrub is a small-statured community of subshrubs and shrubs with average shrub height of 1 m (Mooney 1977) that occurs below 600m elevation in parts of seven southern California counties: San Diego, Riverside, Orange, San Bernardino, Los Angeles, Ventura and Santa Barbara counties (Davis et al. 1995). CSS shrubs are thin-leaved and drought-deciduous. In contrast, chaparral is composed of large, woody sclerophyllous, evergreen shrubs and is geographically more widespread than CSS. It occurs from the coast to the interior Peninsular and Transverse Ranges up to 1500 m elevation.

Coastal sage scrub stands show considerable local (DeSimone and Burk 1992) and regional (Axelrod 1978, Westman 1981) variation in structure and floristics. The most characteristic elements are *Artemisia californica, Eriogonum fasiculatum,* and several *Salvia* species. Regionally, there are at least three recognized subassociations, the southern coastal variety predominantly in San Diego County, the northern coastal variety, and the inland variety primarily in

Riverside County (Axelrod 1978). Local structural variation is due to slope, aspect, substrate, disturbance history, and the influence of non-native grasses.

Undeveloped landscapes in this region are mosaics of patches of the native woody communities and non-native grasslands (Mooney 1977, DeSimone and Burk 1992). Near the coast CSS tends to occur on slopes and generally drier sites, mixed chaparral on steep north-facing slopes, and chamise chaparral on mesa-tops. Disturbance (fire, grazing, and mechanical) contributes to the mosaic because coastal sage scrub is often a successional community following disturbance to chaparral stands. The arrival of widespread non-native grasses and herbs may have exacerbated this patchiness, although there is disagreement over the pre-European extent of native grass and herbaceous stands (Minnich and Dezzani 1998). Frequent or intense fires can type convert CSS and chaparral to non-native grassland (Zedler et al. 1983). CSS in particular is vulnerable to conversion to non-native grassland (Minnich and Dezzani 1998).

There are two gradients of note in this region. First, development, and thus fragmentation, has been most extensive nearest the coast. Consequently, there is an east-west gradient in habitat availability and fragment size in the region (see Figure 2 for an example). There also is a habitat gradient; coastal sage scrub predominates near the coast, and chaparral becomes more common inland and with increasing elevation.

Of the two shrub habitat types, CSS is of greater conservation concern and has been more extensively studied for fragmentation effects. CSS is notable for its restricted range within the U.S. and high diversity of endemic plants and animals (Atwood 1993, Atwood and Noss 1994). CSS is widely reported to have declined to 10–15% of its former range; however, this percentage is based on a disputed assumption of the pre-European cover of coastal sage scrub (Minnich and Dezzani 1998).

There is considerable overlap in the chaparral and coastal sage scrub avifauna (Miller 1951). A number of bird species occur in relatively equal numbers in CSS and chaparral, including Wrentit, Spotted Towhee, California Towhee, Sage Sparrow, Bewick's Wren, California Thrasher, Western Scrub-Jay, Common Bushtit, Lazuli Bunting, and Anna's and Costa's hummingbirds. Several species usually associated with chaparral do breed in CSS, particularly when it is occurs in a mosaic with chaparral, especially Blue-gray Gnatcatcher and Black-chinned Sparrow. Only a few species are restricted to coastal sage scrub. The California Gnatcatcher and Rufous-crowned Sparrow predominantly breed in CSS, occurring only in chaparral that is relatively open or disturbed. Several grassland species occur in open CSS: Western Meadowlark, Grasshopper Sparrow, and Lark Sparrow.

The landscape of coastal southern California consists of four general elements. (1) *The urban matrix.* This land-use is the predominant land-cover in the region and is characterized by high density single-family residential development. Ornamental vegetation ranges from sparse in the higher density neighborhoods to lush in some of the older or more affluent neighborhoods. (2) *Isolated habitat fragments* (ranging from 1 to 1000ha). Fragments occur throughout most of the highly developed portion of the landscape. (3) *The edge of large habitat blocks*; habitat within 250m of the urban edge. (4) *The interior of large habitat blocks*; habitat greater than 250m from the urban edge. These large habitat blocks are either embedded in the urban matrix or are contiguous with the mountainous areas to the east.

CONSERVATION PLANNING IN THE REGION

Partly in response to petitions at the state and federal levels to list the California Gnatcatcher as an endangered species, the state of California initiated the Natural Communities Conservation Planning Program (NCCP; Atwood and Noss 1994). The state coordinates subregional planning processes that prioritize lands based on conservation value. Private landowners voluntarily participate in the planning process. Putative reserves are identified and funding sought for acquisition of lands not currently publicly owned. The eventual listing of the gnatcatcher as a federally threatened species in 1993 gave further impetus to the program as participation in the program gave landowners an avenue to pursue incidental take permits. Planning occurs in 11 subregions with the purpose of designating an interconnected system of reserves, which should result in no reduction in the ability of the region to maintain viable populations of target species (Atwood and Noss 1994). A Central-Coastal Orange County subregional plan has been approved, including 37,000 acres of reserve, and an MSCP subregional plan in San Diego has been approved that includes 170,000 acres of reserves (see http://ceres.ca.gov/CRA/NCCP/updates.htm).

CONCEPTUAL FRAMEWORK

Landscape patterns that suggest fragmentation effects

Conservation biologists often use phrases such as "the effect of habitat fragmentation on birds"; however, exactly what these effects of fragmentation are has been hard to define. Some of the confusion results from confounding the patterns of abundance that result from fragmentation with the ecological processes that generate these patterns. Patterns of abundance or demographic rates in the landscape are often presented as evidence of the effects of fragmentation. These patterns fall into the following categories. (1) *Area sensitivity*—density, probability of occurrence, survival, or reproductive success change with fragment size, or there is a significant difference between those rates in isolated fragments and in large, unfragmented habitat areas. (2) *Age sensitivity*—density, probability of occurrence, survival, or reproductive success changes with fragment age (time elapsed since insularization). (3) *Edge sensitivity*—density, probability of occurrence, survival, or reproductive success changes with proximity to the fragment edge. (4) *Distance sensitivity*—density or probability of occurrence changes in habitat fragments with proximity to other fragments or large habitat blocks.

No directionality of change is implied in these definitions to acknowledge that fragmentation can have positive or negative effects on bird species. These are patterns of abundance or demographic rates in space and time that suggest these parameters change as a consequence of fragmentation. Demonstrating a causal relationship between fragmentation and these patterns requires a consideration of the ecological mechanisms that proximally affect rates of birth, death, immigration, and emigration.

Ecological mechanisms that cause fragmentation effects

How are the patterns of fragmentation sensitivity, as defined above, produced in the landscape? The ecological consequences of habitat fragmentation are complex, diverse, and pervasive because fragmentation affects animal and plant populations via a number of interacting pathways (Wilcove et al. 1986, Robinson et al. 1992, Didham 1997). For example, *area effects* are manifest through the initial sampling effect that determines the initial avian community (Bolger et al. 1991), and through the effect of area on population sizes and rates of extinction. *Isolation effects* occur when the intervening human-modified matrix is relatively impermeable to successful dispersal to isolated patches. This may result in faunal relaxation in fragments, or faunal collapse in the extreme of zero recolonization (Brown 1971, Soulé et al. 1979). *Edge effects* are biotic and abiotic effects derived from the adjacent human-modified matrix that cause gradients in light, moisture, and wind velocity, increased exposure to invasive human commensal species, and increased density of "edge species" (Murcia 1995). Island biogeographic treatments of habitat fragmentation focus on the relationship between stochastic extinction and recolonization (MacArthur and Wilson 1967, Brown 1971). However, when fragmentation is due to the intervention of intense human land uses, such as urbanization, habitat degradation due to edge effects and other anthropogenic disturbance are likely to be significant influences on abundance and extinction rates. The intensity of edge effects may also depend on the relative amount of the developed matrix present in the landscape (Donovan et al. 1997). The direct effects of area reduction, isolation, and edge can lead to *secondary effects* (also called cascading, community, or trophic effects), whereby the direct effects of fragmentation on predators, parasites, competitors, resource species, or mutualists in turn affect species with which these interact. Changes in the abundance of the resource, predator, and parasite species that birds interact with can change bird abundance through their effect on birth and death rates. *Local habitat selection* by birds can affect abundance through changes in immigration and emigration rates. Birds may avoid habitat in small fragments or adjacent to edges due to structural and floristic changes in the vegetation and altered food availability and predator and parasite abundance (Kristan et al. in press). *Landscape-scale habitat selection* occurs when birds choose habitat not only on the basis of local habitat conditions but also on the basis of landscape-scale factors such as patch area, isolation, and edge proximity. As with local habitat selection this mechanism would affect abundance through its effect on relative immigration and emigration rates.

Understanding the consequences of fragmentation has been hampered by our inability to isolate the effects of these different phenomena on the biota. These different effects can act in opposition or in concert. For instance, area and edge effects can be difficult to separate because the percentage of edge-affected habitat increases as fragment area decreases.

FRAGMENTATION PATTERNS IN SOUTHERN CALIFORNIA

Area and age sensitivity

The resident breeding birds of coastal southern California display varying degrees of sensitivity to fragment size and age. Soulé et al. (1988) found that the species richness of a group of eight shrub habitat bird species (Bewick's Wren, Spotted Towhee, California Thrasher, Wrentit, California Quail, Greater Roadrunner, Cactus Wren, and California Gnatcatcher) showed both area and age effects; richness increased with fragment area (range 0.4–103 ha) and declined with fragment age (range 2–86 years). Quite small fragments (1–5 ha), if they were relatively young (<10 years), supported many species from this group. Species not as restricted to shrub habitat did not show similar sensitivity. These fragments range from 1 km to 15 km from the coast and most were predominated by coastal sage scrub. Some of the fragments also contained stands of mixed or chamise chaparral. Although the fragments are predominantly CSS, Soulé et al. (1988) referred to these generically as "chaparral" habitat fragments following the then popular terms of "soft chaparral" for coastal sage scrub and "hard chaparral" for mixed and chamise chaparral.

The observed decline in species richness with fragment age observed by Soulé et al. (1988) implies relaxation or faunal collapse: non-equilibrium dynamics with local extinctions in excess of infrequent recolonizations across the urban matrix (Brown 1971, Soulé et al. 1979). The existence of this extinction-recolonization imbalance is supported by the observation that species richness in the fragments was significantly lower than that in similar-sized plots in continuous blocks of habitat (Bolger et al. 1991). The species richness in unfragmented plots is an estimate of the species richness initially present in fragments of a similar size. In a recent resurvey of the same fragments ten years later, Crooks et al. (2001) tested the inferences drawn from the static patterns. Consistent with the relaxation conclusion, there were approximately twice as many extinctions (30) as colonizations (12) between 1987 and 1997 among the original group of species considered by Soulé et al. (1988).

Bolger et al. (1991) demonstrated that the distribution patterns in these fragments of the five most common of these species (Bewick's Wren, Spotted Towhee, California Thrasher, Wrentit, California Quail) were nested; species in species-poor fragments were a non-random subset of those in species-rich fragments. They concluded that this pattern was generated by a gradient in extinction vulnerability among the species. Nested occurrence patterns are common in real and virtual islands and can be produced by among-species differences in extinction vulnerability (Patterson and Atmar 1986). This pattern suggested that Wrentit was the most resistant of the five to extinction, Bewick's Wren and Spotted Towhee were intermediate, and California Thrasher and California Quail went extinct most quickly. Consistent with this, Crooks et al. (2001) found that populations of the Wrentit were only now going extinct in the smallest/oldest fragments (5 extinctions, no colonizations). California Quail, the most sensitive species (9 extinctions, no colonizations), underwent additional extinctions in several larger fragments (15–64 ha) as well as a number of small/young fragments (having apparently already gone extinct in the smaller/older fragments). California Thrasher exhibited a similar pattern, going extinct in four small/young fragments and colonizing one. The distribution of the Spotted Towhee changed very little in the intervening years (2 colonizations, no extinctions) and appeared to be in quasi-equilibrium. Soulé et al. (1988) had apparently reached the wrong conclusions about Bewick's Wren, which appears able to recolonize across the urban matrix, experiencing 6 colonizations and only 1 extinction between 1987 and 1997. In this group of five easily surveyed species, extinctions outnumbered colonizations 19 to 9. The results of Crooks et al. (2001) also point out that in this system area-sensitivity cannot be defined independently of fragment age; both variables are important predictors of species distributions in this fragmented landscape (Fig. 1).

Lovio (1996) studied fragments in another part of San Diego and found generally higher diversity in the same species group considered by Soulé et al. (1988) in similar-sized fragments. The differing results are probably the result of differing levels of isolation in the two study areas. The Soulé et al. (1988) and Crooks et al. (2001) study area was in the western part of the county and the fragments were generally isolated canyon fragments embedded in highly developed coastal mesas. Lovio's study area was slightly east and south in the Rancho San Diego area and many of the fragments were portions of slopes and ridgetops that formed a fairly dense network of patches (Lovio 1996). The mean interpatch distances were smaller in Lovio's study area (476 vs. 674 m), and the intervening urban matrix was characterized by a higher cover of mature ornamental vegetation (Weser 1996; D. Bolger, pers. obs.). A number of the fragments were connected to other fragments by narrow habitat strips or areas of disturbed and non-native vegetation (Lovio 1996) and the set of fragments was immediately adjacent to a large unfragmented habitat block. So the difference between Lovio's results and those of Soulé et al. (1988) may be indicative of the importance of the degree of fragment isolation and the permeability of the urban matrix. However, Lovio did not ascertain the age of fragments, so differing fragment ages could also be responsible for the differences between the studies.

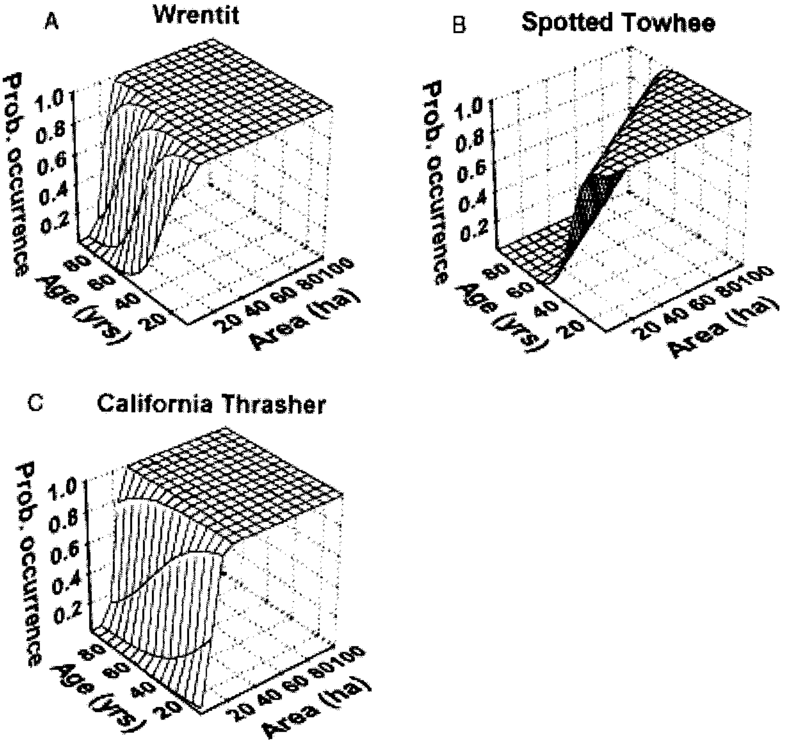

FIGURE 1. Graphical results of multiple logistic regression of the presence/absence of (A) Wrentit, (B) Spotted Towhee, and (C) California Thrasher on fragment area and age. Area sensitivity is a function of fragment age. Larger fragment area is required for persistence in older fragments. From Crooks et al. (2001).

Edge sensitivity

Bolger et al. (1997) analyzed the patterns of abundance of the 20 most common breeding bird species in a 260 sq. km landscape in coastal San Diego County (Fig. 2). This landscape encompassed a land-use gradient that included the interior of a large unfragmented habitat block, its edge, and isolated fragments in the adjacent urban matrix. For 14 of the 20 species, the fit of logistic regression models to bird abundance was improved by the addition of landscape metrics to models containing variables describing local habitat conditions. These landscape metrics described the percentage of CSS and chaparral habitat versus developed land and the amount of urban area and the amount of urban edge in the larger landscape (250 m to 3 km) around each sample point. Based on these analyses and a canonical correspondence analysis, the 20 species were characterized as edge/fragmentation-insensitive (10 species), edge/fragmentation-reduced (6 species) or edge/fragmentation-enhanced (4 species). The finding that half of the common species appear to respond to larger-scale patterns of edge and fragmentation suggests that landscape structure is a significant determinant of bird abundance in this region.

One surprising result of this study was the elevated abundance of urban-exploiting birds some distance into the non-fragmented habitat block. The abundances of House Finch, Anna's Hummingbird (Fig. 2b), Northern Mockingbird, and Lesser Goldfinch, species common in the urban matrix, were higher in habitat adjacent to the urban edge than further into the patch interior. The region of higher density extended as far as a kilometer in Anna's Hummingbird and House Finch. These results suggest that the urban matrix could be a net source of these species, elevating densities in natural habitat adjacent to the matrix.

In chaparral habitat in the Santa Monica Mountains, Sauvajot et al. (1998) found no correlation between bird abundance and proximity to the urban edge. They also found that bird abundance did not respond to disturbance-induced changes in vegetation structure. In contrast, in inland CSS Kristan et al. (in press) observed strong correlations between bird abundance and edge-proximity that was specifically

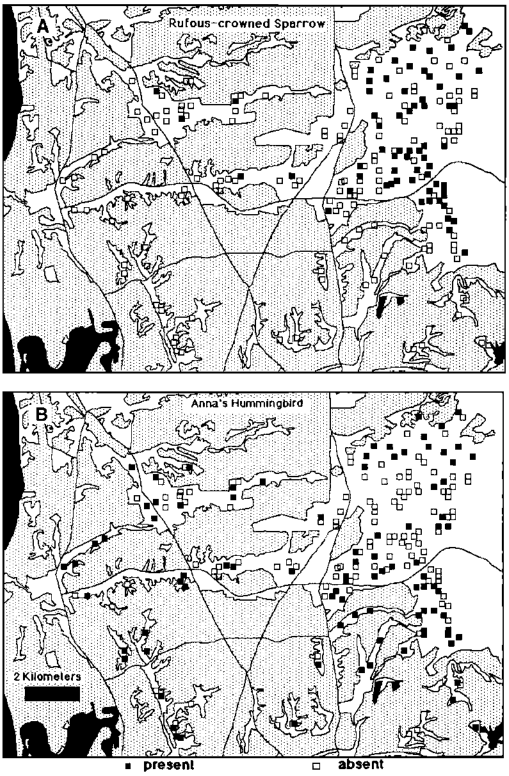

FIGURE 2. The landscape distribution patterns of (A) Rufous-crowned Sparrow and (B) Anna's Hummingbird within a 260 km^2 study area in coastal San Diego County. Presence/absence denotes either detection or non-detection in a single 8-min point count at each of 202 random locations during the spring of 1993. White areas are the undeveloped habitat mosaic of coastal sage scrub and chaparral. Stippling represents residential and commercial development. From Bolger et al. 1997.

associated with edge-related changes in habitat quality based on known, independent relationships to vegetation composition and structure. The lack of a correlation of disturbance to edge proximity in chaparral may have to do with the differing physical structure of chaparral and CSS vegetation. Dense and robust, chaparral probably rebuffs direct human disturbance along edges better than the smaller statured coastal sage scrub.

In the only demographic study of edge sensitivity in this region I am aware of (Morrison and Bolger 2002), no difference was found in breeding success of Rufous-crowned Sparrows, a ground-nesting year-round resident species, between edge and interior plots. Total reproductive output and daily nest predation rate did not differ between pairs in habitat adjacent to urban development (<200 m from the urban edge) as compared to those a minimum of 500 m from urban edge during the 1997–1999 breeding seasons. P. Mock (pers. comm.) reported similar results with California Gnatcatchers at one site in San Diego.

EDGE SENSITIVITY

Of 21 species common enough for analysis, 11 differed significantly in abundance between edge and interior plots in CSS in 1997–1999 (Table 1). Anna's Hummingbird, House Finch, Northern Mockingbird, and Western Scrub-Jay were significantly more abundant in edge locations. Common Raven showed a trend of higher abundance in edges, but its abundance was highly variable and the treatment effect was non-significant. Black-chinned Sparrow, California Towhee, Common Bushtit, Lazuli Bunting, Rufous-crowned Sparrow, Spotted Towhee, and Wrentit were significantly less abundant along edges. California Thrasher showed a consistent, but non-significant, trend of lower abundance along edges. In a similar study, Kristan et al. (in press) noted significant negative edge relationships for California Towhee, California Thrasher, and Sage Sparrow, and significant positive effects for Northern Mockingbird and European Starling.

PATTERNS OF LANDSCAPE SENSITIVITY IN THE COASTAL SOUTHERN CALIFORNIA AVIFAUNA

I categorized patterns of landscape sensitivity in the CSS avifauna through a consideration of three factors: (1) area sensitivity, (2) edge sensitivity, and (3) ability to exploit the urban matrix (Table 2). The area sensitivity designations are approximate and not quantitative estimates. Area sensitivity in this system certainly depends on fragment age (Crooks et al. 2001) and possibly on isolation (Lovio 1996), so a simple categorization is not possible. The two categories (10–20 ha and 100–200 ha) represent a qualitative contrast of area sensitivity for patches of CSS between 20 and 60 years old and isolated by at least 500 m of residential development. Species categorized as sensitive to fragmentation at the scale of 10–20 ha are often found in fragments of this size but have been shown to experience local extinction (Soulé et al. 1988, Bolger et al. 1991, Crooks et al. 2001). Species categorized as having 100–200 ha area sensitivity are generally absent or rare in fragments smaller than that size range (Lovio 1996, Bolger et al. 1997; D. Bolger et al., unpubl. data; K. Crooks et al., unpubl. data). Edge sensitivity was derived from a consideration of the relative abundance of species in the interior and near the edge (<250m from urban edge) of large habitat blocks (Fig. 2, Table 1; Bolger et al. 1997). The

TABLE 1. MEAN NUMBER OF DETECTIONS (STANDARD ERROR) WITHIN 70 M OF POINT COUNT STATIONS IN EDGE AND INTERIOR LOCATIONS IN 1997–1999

	1997		1998		1999		F or Chi-square	P
	Edge	Interior	Edge	Interior	Edge	Interior		
N	10	9	7	7	11	7		
California Quail	0.20	0.11	0.29	0.30	0.48	0.43	0.57	0.45
	(0.11)	(0.11)	(0.17)	(0.14)	(0.15)	(0.25)		
Mourning Dove	0.00	0.00	0.10	0.22	0.15	0.12	2.22	0.15
	(0.00)	(0.00)	(0.10)	(0.08)	(0.09)	(0.08)		
Costa's Hummingbird	0.42	0.17	0.05	0.36	0.61	0.57	0.06	0.82
	(0.13)	(0.09)	(0.03)	(0.11)	(0.18)	(0.26)		
Anna's Hummingbird[a]	1.48	1.00	0.97	0.72	1.52	1.01	5.69	0.021
	(0.17)	(0.17)	(0.28)	(0.24)	(0.17)	(0.15)		
Western Scrub-Jay	0.10	0.09	0.24	0.00	1.00	0.05	4.79	0.03
	(0.07)	(0.06)	(0.17)	(0.00)	(0.32)	(0.05)		
Common Raven	0.48	0.20	0.72	0.25	1.00	0.13	0.93	0.37
	(0.14)	(0.17)	(0.29)	(0.14)	(1.00)	(0.10)		
Common Bushtit[a]	1.20	1.28	0.74	1.34	0.88	0.86	0.99	0.033
	(0.28)	(0.29)	(0.34)	(0.36)	(0.22)	(0.28)		
Bewick's Wren	0.28	0.33	0.07	0.04	0.75	0.42	1.83	0.16
	(0.09)	(0.15)	(0.05)	(0.04)	(0.15)	(0.14)		
Northern Mockingbird	1.00	0.19	0.61	0.03	0.26	0.05	6.82	0.009
	(0.29)	(0.08)	(0.22)	(0.03)	(0.10)	(0.05)		
California Thrasher	0.15	0.24	0.22	0.45	0.08	0.27	1.23	0.30
	(0.06)	(0.11)	(0.09)	(0.14)	(0.04)	(0.17)		
Wrentit[a]	0.55	1.28	0.65	1.40	0.51	0.85	13.23	<0.001
	(0.18)	(0.17)	(0.18)	(0.24)	(0.18)	(0.31)		
California Gnatcatcher	0.08	0.17	0.11	0.08	0.03	0.05	0.36	0.60
	(0.06)	(0.07)	(0.07)	(0.08)	(0.03)	(0.05)		
Lesser Goldfinch	0.30	0.52	1.42	0.77	0.76	1.13	0.84	0.37
	(0.16)	(0.20)	(0.59)	(0.25)	(0.26)	(0.28)		
House Finch	1.90	0.22	1.36	0.14	1.64	0.10	20.91	<0.001
	(0.50)	(0.15)	(0.66)	(0.14)	(0.29)	(0.06)		
Lazuli Bunting	0.00	0.15	0.06	0.92	0.00	0.29	14.36	<0.001
	(0.00)	(0.11)	(0.04)	(0.36)	(0.00)	(0.11)		
Spotted Towhee[a]	0.80	0.74	0.42	0.98	0.36	1.01	6.25	0.016
	(0.20)	(0.20)	(0.13)	(0.24)	(0.12)	(0.21)		
California Towhee[a]	2.32	2.81	2.11	2.32	1.64	1.64	0.65	0.042
	(0.37)	(0.41)	(0.36)	(0.24)	(0.32)	(0.38)		
Rufous-crowned Sparrow[a]	0.78	1.17	1.80	3.08	0.23	1.14	15.86	<0.001
	(0.14)	(0.17)	(0.23)	(0.49)	(0.08)	(0.38)		
Black-chinned Sparrow	0.03	0.15	0.00	0.12	0.00	0.17	7.36	0.008
	(0.03)	(0.08)	(0.00)	(0.07)	(0.00)	(0.11)		
Lark Sparrow	0.00	0.17	0.00	0.08	0.00	0.00		
	(0.00)	(0.09)	(0.00)	(0.06)	(0.00)	(0.00)		
Grasshopper Sparrow	0.10	0.06	0.11	0.03	0.00	0.05	0.46	0.50
	(0.10)	(0.06)	(0.11)	(0.03)	(0.00)	(0.05)		

[a] Data from these species were analyzed with 2-way ANOVA; all others were analyzed with three-way contingency tables (see METHODS).

urban-exploiter category includes species that occur in the urban matrix during the breeding season as determined by Lovio (1996) and K. Crooks et al. (unpubl. data). This list includes the species likely to be found in areas of relatively dense, single-family dwellings that support moderate densities of ornamental vegetation. The list of urban-exploiters would probably differ if higher- or lower-density development were considered (Blair 1996). Based on a consideration of these three factors I placed species into three categories: (1) species that appear strongly negatively affected by fragmentation in the landscape, (2) species that appear moderately negatively affected by fragmentation, and (3) species that appear positively affected or neutral (Table 2).

Species in the first category, strongly negatively affected, are generally found only in the largest habitat blocks remaining in the region. These species do not occur in the urban matrix, generally have reduced abundance near urban edges (Table 1; Bolger et al. 1997), and are extremely rare in smaller fragments (K. Crooks et

TABLE 2. PATTERNS OF LANDSCAPE SENSITIVITY IN THE AVIFAUNA OF COASTAL SOUTHERN CALIFORNIA

Species	Area sensitivity (ha)	Exploits urban matrix	Edge response	Habitat	Migratory status	Nest location
Strongly negative						
Lesser Nighthawk	100–200	No	?	CSS/Chap.	migrant	ground
Blue-gray Gnatcatcher	100–200	No	?	Chap/Woodland	migrant	shrub/tree
Sage Sparrow	100–200	No	negative	CSS/Chap.	resident	shrub
Rufous-crowned Sparrow	100–200	No	negative	CSS	resident	ground
Black-chinned Sparrow	100–200	No	negative	CSS/Chap.	migrant	shrub
Lark Sparrow	100–200	No	negative	Grassland	migrant	ground/shrub
Grasshopper Sparrow	100–200	No	neutral	Grassland	?	ground
Western Meadowlark	100–200	No	negative	Grassland	resident	ground
Moderately negative						
California Quail	10–20	No	neutral	CSS/Chap.	resident	ground
Costa's Hummingbird	10–20	Yes	?	CSS/Chap.	migrant	shrub/tree
Bewick's Wren	10–20	Yes	neutral	CSS/Chap./Rip.	resident	cavity
California Thrasher	10–20	No	negative	CSS/Chap.	resident	shrub
Wrentit	10–20	No	negative	CSS/Chap.	resident	shrub
California Gnatcatcher	10–20	No	neutral	CSS	resident	shrub
Lazuli Bunting	10–20	No	negative	CSS/Chap.	migrant	shrub
Spotted Towhee	10–20	No	negative	CSS/Chap.	resident	ground
Positive or neutral						
Mourning Dove	None	Yes	neutral	Grass/CSS/Chap./Rip.	resident	ground/shrub/tree
Anna's Hummingbird	None	Yes	positive	CSS/Chap.	resident	shrub/tree
Western Scrub-Jay	None	Yes	positive	CSS/Chap.	resident	shrub/tree
American Crow	None	Yes	positive	CSS/Chap./Rip.	resident	tree/cliff
Common Raven	None	Yes	positive	CSS/Chap./Rip.	resident	tree/cliff
Common Bushtit	None	Yes	neutral	CSS/Chap./Rip.	resident	shrub
Northern Mockingbird	None	Yes	positive	CSS/Chap./Rip.	resident	shrub/tree
Lesser Goldfinch	None	Yes	neutral	CSS/Chap.	short dist.	shrub/tree
House Finch	None	Yes	positive	CSS/Chap.	resident	shrub/tree/structure
California Towhee	None	Yes	neutral	CSS/Chap.	resident	shrub

Notes: Classifications of area sensitivity derive from Soulé et al. (1988), Lovio (1996), Bolger et al. (1997), Crooks et al. (2001), and D. Bolger, unpubl. data. Presence in the urban matrix is from Lovio (1996) and Crooks et al. (2001). Edge responses are derived from Bolger et al. (1997) and Table 1. Habitat use is from Bolger et al. (1997) and Unitt (1984). Residency status is from Unitt (1984). Nest locations are from accounts in the *Birds of North America*, Harrison (1979), and D. Bolger, pers. obs.

al., unpubl. data). They are a mixture of resident and migrant species. This is the most problematic category because the fewest data are available and alternative explanations for the landscape patterns of these species need further investigation. Many of these species are primarily grassland or chaparral species that often occur within the coastal habitat mosaic in open CSS habitat and grassland/CSS ecotones or CSS/chaparral ecotones. Their patterns of abundance could reflect the distribution of these less common habitat elements that may be distributed non-randomly with respect to fragment size or edge proximity.

Lark Sparrows, Grasshopper Sparrows, and Western Meadowlarks are primarily associated with grassland but reliably occur in open coastal sage scrub habitat in large habitat blocks. CSS in habitat fragments is generally open, often with a continuous understory of non-native grasses. But these species are rarely present in fragments. Lesser Nighthawks occur in both chaparral and CSS, but require bare ground on mesa tops for breeding and are rare in fragments (Lovio 1996).

Interpretation of the distribution of some of these species, particularly those primarily associated with chaparral, is complicated by historical distribution patterns. The Blue-gray Gnatcatcher and the Black-chinned Sparrow were historically rare in the immediate vicinity of the coast (Unitt 1984), possibly due to an east-west gradient in the cover of chaparral habitat. So their rarity in fragments closest to the coast may not be due to fragmentation sensitivity. Of course, it is possible that those historical patterns already reflected the effects of earlier, agriculturally-induced habitat fragmentation. Lovio (1996) found the Blue-gray Gnatcatcher in his unfragmented control area, but it was absent from all but the largest fragments in the immediately adjacent landscape. The Black-chinned Sparrow does show edge- (Table 2; Bolger et al. 1997) and area-sensitivity (Lovio 1996) within its historical range.

Bolger et al. (1997) found that as a group the Rufous-crowned Sparrow, Lark Sparrow, Black-chinned Sparrow, Sage Sparrow, Western Meadowlark and Costa's Hummingbird displayed an edge-sensitive abundance pattern even when the three habitat types they examined (chamise chaparral, CSS, and mixed chaparral) were considered separately. However, when analyzed individually with regard to habitat, the distribution of Sage Sparrows and Western Meadowlarks suggested their pattern may be driven by the spatial distribution of habitat types. The other four species did display reduced abundance in appropriate habitat near edges. Bolger et al. (1997) found Sage Sparrows to be associated with chamise chaparral in their study area, but they also occur in CSS (Unitt 1984, Lovio 1996). Lovio (1996) found Sage Sparrows only in the two largest CSS fragments (>150 ha) in his study area.

The species in this group whose pattern most compellingly suggests fragmentation-sensitivity is the Rufous-crowned Sparrow. It is abundant and ubiquitous in unfragmented habitat, but less abundant near edges (Table 1) and rare in isolated habitat fragments (Fig. 2; Bolger et al. 1997; K. Crooks et al., unpubl. data).

I suspect that the distribution of most of the species in this category are determined at least in part by patterns of fragmentation and edge. Yet because of their idiosyncratic distributions and habitat affinities it will be difficult to demonstrate this conclusively. Kristan et al. (in press) constructed interior-based habitat association models for a suite of CSS species using data collected from >200 points throughout southern California. They then applied each model to a new set of points surveyed along an explicit edge-to-interior gradient. Habitat quality (as indexed by predicted probability of a species occurrence at a point) varied significantly for the eight species analyzed (Cactus Wren, California Towhee, California Gnatcatcher, California Thrasher, Sage Sparrow, Western Scrub-Jay, Northern Mockingbird, European Starling). Interestingly, Sage Sparrows and California Thrashers were significantly reduced at edges despite the presence of suitable habitat. Clearly the distribution of these species requires closer examination for evidence of processes producing fragmentation sensitivity. Despite the uncertainties, it is prudent at this time to consider these species very sensitive to fragmentation.

The second category is comprised of species that show area sensitivity in the range of 10–20 ha. A number of these species have been shown to undergo local extinction in habitat fragments (Soulé et al. 1988, Bolger et al. 1991, Crooks et al. 2001). They generally occur at lower abundance in habitat fragments than in unfragmented habitat (K. Crooks et al., unpubl. data). Some of the species show edge sensitivity, others are neutral with regard to edge (Table 1; Bolger et al. 1997). These are generally resident species and are among the common and distinctive species of these habitats. They appear to be shrub habitat generalists occurring abundantly in both CSS and chaparral (Bolger et al. 1997). Most of these species are rarely observed in the urban matrix; however, K. Crooks et al. (unpubl. data) found Costa's Hummingbird to be reasonably abundant in the urban matrix and detected Spotted Towhee and Bewick's Wren there at very low abundance.

The species categorized as neutrally or positively affected by fragmentation are all urban exploiters. They reside and breed within developed habitats in San Diego as well as other disturbed habitats (Unitt 1984; D. Bolger, pers. obs.). All display positive or neutral edge responses (Table 1; Bolger et al. 1997). They vary in abundance in unfragmented habitat and none display obvious area sensitivity; in fact most are more abundant in fragments than in unfragmented habitat (K. Crooks et al., unpubl. data).

MECHANISMS CAUSING FRAGMENTATION EFFECTS IN SOUTHERN CALIFORNIA

Isolation and dispersal limitation

There is currently no direct measure of the ability of most of the species listed in Table 2 to disperse through the urban matrix. However, there is a good deal of correlative evidence for some of the fragmentation-sensitive species that suggests their ability to disperse across the urban matrix is constrained relative to fragmentation-tolerant species.

The relative inability of these species to colonize across the urban landscape is supported by the lack of a relationship between degree of fragment isolation and the distribution of these species. Soulé et al. (1988) found no relationship between fragment isolation and species richness. Crooks et al. (2001) analyzed single species distributions and found only Bewick's Wren's occurrence to be significantly positively correlated with proximity to other fragments. This is consistent with its ability to recolonize fragments, and its occasional detection in the urban matrix (Crooks et al. 2001). Lovio (1996) did find an effect of isolation on species richness; this difference is likely due to the factors mentioned earlier, smaller interpatch distances and a more permeable matrix in his study area. Taken together the results of Lovio (1996) and Soulé et al. (1988) suggest a threshold of isolation and matrix permeability below which dispersal is an important influence on distributions. Bolger et al. (2001) demonstrated that a group of fragmentation-sensitive species (category 2 species) occurred much less frequently in narrow, linear habitat features (ca. 60 m wide and 250 m long) than a group of fragmentation-tolerant species (category 3 species), suggesting the sensitive species have more stringent corridor requirements and that their movements through the urban matrix are more constrained.

One of the striking features of Table 2 is the almost complete correlation of fragmentation-sensitivity with the inability to exploit the urban matrix. This is consistent with the urban matrix as a dispersal barrier for the fragmentation-sensitive species. Clearly, the urban matrix does not provide a barrier to the species that are able to reside there, and in general these species do not show fragmentation sensitivity.

The available evidence suggests that at least in part, fragmentation-sensitive patterns of members of the shrub avifauna are due to the isolating effects of the urban matrix. The matrix is not necessarily a complete barrier to dispersal but it appears to reduce colonization rates below extinction rates for a number of species (Crooks et al. 2001). More direct tests of this hypothesis in the form of dispersal studies or experimental introductions to unoccupied patches are needed.

Two studies have documented dispersal of banded California Gnatcatchers through fragmented landscapes. A banded juvenile was detected 1.3 km from its natal patch, having had to cross a lightly developed landscape of large wooded house lots and parkland (Atwood et al. 1995 cited in Bailey and Mock 1998). Bailey and Mock (1998) also document a number of dispersal events in a heterogeneous landscape in San Diego. A number of these apparently occurred from a large block of habitat through an archipelago of fragments separated by blocks of development up to 1 km wide. This study was conducted in the same landscape as Lovio (1996) with dense ornamental vegetation and sufficient relief to often provide line-of-sight between patches of habitat. This probably facilitates inter-patch movement. So although the California gnatcatcher does show area sensitivity, this may be more related to its large territory requirements (Preston et al. 1998) rather than a strict inability to recolonize isolated fragments. However, even though dispersal through the urban matrix is possible, colonization rates could still be in excess of extinction rates for this species.

Edge effects: habitat degradation/local habitat selection

Fragmentation and the creation of urban edge exposes CSS and chaparral habitat to increased levels of human-induced disturbance. The effect of increasing disturbance in the form of mechanical damage, fire, and exotic plant invasion on vegetation and birds in habitat fragments has not been thoroughly described. Alberts et al. (1993) found that fragments lose native shrub cover through time and native plant diversity declines while exotic plant diversity increases. Disturbance opens up the vegetation in fragments by causing internal fragmentation with stands of shrubs becoming separated by non-native grasses and forbs.

The effect of disturbance-induced changes in vegetation structure on bird communities has not been well-studied in this region. Sauvajot et al. (1998) found that chaparral bird species abundance did not respond to disturbance-induced changes in vegetation structure in chaparral, whereas Kristan et al. (in press) observed significant changes in vegetation, as well as "habitat," in CSS. Bird species clearly assort along a gradient of shrub density from grassland to open CSS to dense CSS and chaparral (Cody 1975, Bolger et al. 1997). By decreasing shrub cover, disturbance should move the bird community along this gradient. However, the relationship of this avifauna to disturbance-induced changes in shrub vegetation structure needs further quantification.

The effect of invasive non-native annual plants has been severe on coastal sage scrub and may be exacerbated by fragmentation. Coastal sage scrub has been exposed to several waves of grass and herbaceous invaders from the Mediterranean and Middle East beginning with species introduced by missionaries in the mid to late 1700s (Mooney et al. 1986, Minnich and Dezzani 1998). Most prominent among these invaders are grasses in the genera *Avena* and *Bromus,* and the annual forb *Brassica nigra.* These plants may invade as a consequence of soil disturbance and intense or frequent fires, and can invade undisturbed CSS from nearby disturbed areas (Zink et al. 1996). Once established these annuals resist native shrub recruitment (Eliason and Allen 1997). The increase in annual biomass increases rates of nutrient cycling (Jackson et al. 1988) and these annuals may decrease fire intervals by increasing fine fuel availability (Zedler et al. 1983).

Coastal sage scrub and chaparral are stable with fire intervals of ten years or more, but degrade to non-native grassland under more frequent fires or particular intense fires (Zedler et al. 1983). Both chaparral and CSS shrubs resprout after fire although resprouting is more complete in chaparral species. Germination from seed caches (*Salvia* spp.) or germination of small wind-dispersed seeds (*Eriogonum fasciculatum, Artemisia californica*) is a more important source of recovery in CSS shrubs than in chaparral species. Frequent fires can deplete the seed bank and stored carbohydrates of root-sprouting species and cause a vegetation type-conversion to non-native grassland.

Non-native invasion is among the most serious threats to the conservation of native plant and animal communities in this region. For example, Minnich and Dezzani (1998) compared historical vegetation data (1929–1934) to recent survey data and concluded that loss of shrub cover of coastal sage scrub shrubs has been extensive in the Perris Plain of Riverside County. Modal shrub cover loss at 78 sites was 40%. This was particularly true on north-facing slopes, which supported high densities of non-native grasses (*Bromus* spp.). Loss of shrub cover occurred even in the absence of fire and grazing, suggesting a competitive exclusion by the non-native grasses, perhaps through competition for moisture (Minnich and Dezzani 1998).

A landscape analysis of the effect of fragmentation and edge on disturbance regimes in this region has not been attempted. Fragmentation and the creation of edge should increase the exposure of native plant communities to humans, exotic invaders, fire, and mechanical disturbance. It seems likely that habitat fragmentation has enhanced plant invasions by disturbing the native shrub vegetation and providing colonization sources of the exotic species. For example, Zink et al. (1996) documented the invasion of undisturbed coastal sage scrub by non-native annuals from a disturbed pipeline right-of-way. Although the effects of non-native annual plant invasion on native grasses, shrubs, and nutrient cycling have been examined, their effects on higher trophic levels has received little attention. The alteration of the physical structure of CSS and chaparral habitat, and changes in seed and arthropod food resources, could affect higher trophic levels including birds.

Landscape-scale habitat selection—patch size and isolation

Feasible observations and experiments to test this hypothesis are elusive, so the only support for this mechanism would be lack of evidence for other mechanisms. This mechanism is perhaps most feasible for the migrant species that would not be expected to have difficulty dispersing across the urban matrix (e.g., Lazuli Bunting). However, this hypothesized mechanism remains speculative.

Secondary effects: top-down—predation and brood parasitism

Morrison and Bolger (2002) found no evidence to suggest that the landscape pattern of the Rufous-crowned Sparrow results from top-down effects near edges. Nest predation rates and breeding productivity did not differ between edge and interior areas. The predation result is surprising considering that some putative nest predators (e.g., Western Scrub-Jays and Common Ravens, Table 1; California ground squirrels, D. Bolger, pers. obs.) are more abundant along edges. Video surveillance and direct observation documented ten predation events, nine of which were by snakes (seven by California kingsnakes, two by gopher snakes), suggesting that snakes are the principal predator on Rufous-crowned Sparrow nests. The rate at which snakes were encountered by field workers was equivalent in edge and interior areas (Morrison and Bolger 2002).

Top-down changes may be important in isolated habitat fragments. Crooks and Soulé (1999) found evidence for mesopredator release in fragments lacking coyotes. They report that the abundance of mesopredators (gray fox, opossum, striped skunk, and domestic cat), as revealed by track stations and scat transects, is negatively correlated with coyote abundance (after accounting for the potential confounding effects of area, age, and isolation). Moreover, mesopredator activity is also higher at times when coyote activity is lower. They found a significant positive correlation between the species richness of shrub-specialist birds and coyote presence and conclude that the presence of coyotes enhances survival and reproduction of these birds through the suppression of mesopredators. Bird species richness showed a non-significant negative trend with increasing mesopredator abundance.

Crooks and Soulé (1999) also presented evidence that the effect of coyotes on domestic cats is particularly marked. Their radio-collared cats often were killed by coyotes, 21% of coyote scat examined contained cat remains, and 46% of cat owners surveyed said they restricted their cats' activities when coyotes were present. The effects of cats can be severe. Based on owner surveys they estimate that a 20-ha fragment would be subject to predation by 35 outdoor cats that together would bring a total of 525 bird prey items to their owners each year. The authors do not report whether the prey items are predominantly common urban species or species residing predominantly in natural habitat.

Brown-headed Cowbirds have been shown to be another important top-down influence in fragmented forest habitat. However, they do not seem to be as significant an influence in fragmented coastal sage scrub vegetation (Ellison 1999). In four years (342 nests, Riverside and San Diego counties) in edge and interior habitat, S. Morrison and D. Bolger (2002; unpubl. data) found no brood parasitism by Brown-headed Cowbirds on Rufous-crowned Sparrows. In two years (same Riverside County site as Morrison and Bolger) Ellison (1999) observed cowbird parasitism in only 3 of 217 nests of Spotted and California towhees and Sage and Rufous-crowned sparrows collectively. Cowbirds were detected in my edge point counts in San Diego, but only infrequently.

In this region, the habitat in which cowbirds are consistently a significant problem is riparian woodland. The endangered Least Bell's Vireo is significantly affected by cowbirds (Kus 1999) as have been other riparian breeding birds. This habitat is naturally patchy, but habitat loss due to development has increased the patchiness as well as patch isolation, and has exposed the habitat to a variety of disturbances. Because breeding habitat for riparian species occurs in relatively small, discrete patches, it has been possible to reduce the local density of cowbirds through trapping programs and reduce parasitism on the Least Bell's Vireo (Kus 1999).

Braden et al. (1997) reported that 32% of California Gnatcatcher nests suffered cowbird parasitism in coastal sage scrub habitat in southwestern Riverside County. Parasitism rates were not analyzed with respect to patch size or distance to edge so it is not possible to interpret these data with regard to fragmentation. However, at least two of Braden's study areas were adjacent to lakes that are fringed by riparian vegetation, which may have attracted the cowbirds (see below). Grishaver et al. (1998) found much lower rates (2%) of parasitism on gnatcatchers at a site in San Diego.

Cowbirds are noted for their large home ranges and the extensive distances they will fly between feeding, roosting, and host nesting areas (Thompson 1994, Robinson et al. 1995a). It is likely then that their abundance in southern California is related to factors distributed at a landscape or regional scale. The effect of urban fragmentation on cowbird abundance is unknown. If cowbirds can exploit resources in the urban matrix, such as seed from feeders, the urban landscape may be highly permeable to them and may enhance cowbird abundance in riparian areas that abut residential development. Further research on the landscape correlates and determinants of cowbird abundance in this region is needed.

Secondary effects: bottom-up

The effect of habitat fragmentation on bird food resources has been relatively understudied (Burke and Nol 1998, Robinson 1998). Bolger et al. (2000) found complex relationships between arthropods and fragment size, age, and edge proximity. Arthropods dwelling on California buckwheat (*Eriogonum fasiculatum*) generally decline in abundance and point diversity with decreasing fragment size and increasing fragment age. Thus food availability for foliage gleaners foraging on buckwheat is potentially lower in smaller and older fragments.

Reponses of the ground-dwelling arthropods are more varied, but are generally similar to the shrub insects. Interestingly, ground spiders increase in abundance and point diversity with decreasing area and increasing age (Bolger et al. 2000). The most abundant ground arthropods in habitat fragments are common non-native species: sowbug (*Armadillidium vulgare*), European earwig (*Forficula auriculatum*), and oriental cockroach (*Blatta orientalis*). There did not seem to be large differences between the edge and interior in the abundance and diversity of ground or shrub arthropods.

In contrast, ground arthropods are generally less abundant in the edge than the interior of large habitat blocks in San Diego (D. Bolger, unpubl. data). Grasshoppers, mites, spiders, jumping bristletails, and native ants were significantly less abundant in edge plots than in interior plots. Beetles, bees and wasps, and flies did not differ between edge and interior plots. No arthropod order was significantly more abundant in edge plots than in interior plots.

The arthropod taxa most vulnerable to fragmentation and edge are the native ants. In San Diego, the non-native Argentine ant (*Linepithema humile*) invades coastal sage scrub habitat from urban edges (Suarez et al. 1998). In isolated habitat fragments (Suarez et al. 1998) and in edge areas of large habitat blocks (D. Bolger, unpubl. data), the abundance and diversity of native ants is strongly negatively correlated with the abundance of the Argentine ant. Argentine ants are invasive human commensals and have become established in Mediterranean climates worldwide (Majer 1994). They have been implicated in the decline of native ants in a number of locations (Erickson 1971, Ward 1987, Majer 1994, Holway 1995, Cammell et al. 1996, Human and Gordon 1996). Argentine ants possess interference and exploitative competitive advantages over native California ants (Human and Gordon 1996, Holway et al. 1998, Holway 1999) and have higher worker densities possibly due to reduced intraspecific competition (Holway et al. 1998).

Several lines of evidence suggest that the availability of water from irrigation and runoff may allow the Argentine ants to invade along edges, and moisture limitation may prevent their invasion of undisturbed interior areas. Tremper (1976) found Argentine ants more vulnerable to desiccation than most native California ants. Also, Argentine ants are able to invade riparian habitat, but only if water flows year-round (Holway 1998a).

Argentine ants are generally smaller than the native ant species they replace, suggesting that they may not be adequate replacements in the diet of ant-eating birds and lizards. Suarez et al. (2000) demonstrated that the ant-specialist coastal horned lizard showed a strong prey preference for native ants over the Argentine ant. Ants frequently appear in lists of prey consumed by ground-foraging birds, but their relative dietary importance is unclear. Several studies have reported negative correlations of Argentine ants, or other exotic ants, with non-ant arthropods (Porter and Savigno 1990, Cole et al. 1992, Human and Gordon 1997, Bolger et al. 2000), while others have found no relationship (Holway 1998 b). Bolger et al. (2000) found significant partial negative correlations between the abundances of Argentine ants and several non-ant arthropod taxa. The magnitude of the correlations, however, were generally small suggesting the effect of Argentine ants on non-ant arthropods is less severe than their effect on native ants.

Taken together these studies demonstrate that arthropod communities change greatly with fragmentation and edge. In general arthropod abundance and diversity declines in isolated fragments and near the edge of large habitat blocks. Unfortunately, at this time we do not know how these changes in arthropod communities affect bird foraging, reproductive success, and habitat selection.

CONCLUSIONS

The studies reviewed indicate that a significant portion of the avifauna of coastal sage scrub and chaparral habitats in coastal southern California display patterns of abundance that suggest sensitivity to edge and fragmentation caused by urban development. Area, age, and edge sensitivity in bird abundance and presence/absence have been demonstrated in a broad spectrum of the avifauna (Table 1; Soulé et al. 1988, Lovio 1996, Bolger et al. 1997, Crooks et al. 2001). However, so little research has been conducted on mechanisms that it is difficult at this time to generalize about the forces shaping these distributions. Area exerts an influence through an initial sampling effect (Bolger et al. 1991). It may also affect extinction rates through its effect on population size; extinction rates are higher in smaller fragments (Crooks et al. 2001). The available evidence suggests that elevated predation and parasitism along edges are not involved (Morrison and Bolger 2002; P. Mock, pers. comm.). Correlational evidence suggests mesopredator release affects bird species persistence in isolated habitat fragments. However, an effect of mesopredator abundance on nest predation rate or adult or juvenile survival has yet to be demonstrated. Arthropod community composition and abundance varies strongly with fragmentation and edge suggesting that food availability could play a role in shaping these abundance patterns (Suarez et al. 1998, Bolger et al. 2000; D. Bolger, unpubl. data).

The characteristics of the urban matrix and bird species responses to it may be very important. Dispersal limitation imposed by the urban matrix may explain area sensitivity in many fragmentation-sensitive species. Extinction rates of fragmentation-sensitive species exceeded colonization rates in fragments (Crooks et al. 2001). These species generally are not observed to occur in the urban matrix (Table 2). Species that are able to exploit the urban matrix do not show fragment area sensitivity or edge sensitivity (Table 2). Clearly, as shown by the California Gnatcatcher's ability to disperse through developed landscapes, this is not the case for all fragmentation-sensitive species.

The relationship between habitat degradation and extinction and colonization rates in habitat fragments needs clarification. Is fragmented habitat sufficiently degraded to lead to local extinction or cause dispersing birds to pass up fragments? Many fragments lacking particular bird species do not differ in gross habitat characteristics from those that do support them (D. Bolger, pers. obs.). Crooks et al. (2001) found no relationship between extinction rates and percent native shrub cover, an index of habitat degradation. I suspect that, except for the most degraded patches, the absence of species in the "moderately sensitive" category (Table 2) from fragments is due in large part to the inability of these species to successfully disperse through the urban matrix and colonize patches frequently enough to counteract extinction processes. However, studies of dispersal in a variety of species are needed, as are demographic studies in habitat fragments and reintroduction experiments to test the suitability of unoccupied fragmented habitat.

CONTRASTS WITH FRAGMENTATION STUDIES IN THE EAST AND MIDWEST

Several features of the research reviewed here appear in contrast to the work done in the East and Midwest where top-down effects appear to be the most important consequences of fragmentation. Studies in those regions have often documented strong effects of nest predation and brood parasitism near edges or in more fragmented landscapes (Robinson et al. 1995a, Donovan et al. 1997). The evidence for top-down effects in southern California is mixed. Morrison and Bolger (2002) found that rates of nest predation or parasitism were not elevated along developed edges in the Rufous-crowned Sparrow, although Crooks and Soulé (1999) find evidence for mesopredator release in isolated fragments.

Fragment isolation appears to be a more important influence in southern California. In the Midwest, regional-scale dispersal appears to maintain populations of neotropical migrants in extensive landscape sink areas (Robinson et al. 1995a). In contrast in San Diego, isolation on the scale of 100's of meters appears to prevent rescue of populations of some species in fragments. Either the fragmentation-sensitive species in southern California are poorer dispersers, or they are much better at recognizing and avoiding sink habitat than the neotropical migrants of the Midwest. Of course, it has not been demonstrated that fragments are demographic sinks in southern California as they are for a number of species in the Midwest.

The avifauna in southern California is predominantly composed of year-round resident species as opposed to the neotropical migrant species that dominate the eastern and midwestern avifauna. The generally shorter dispersal distances of residents compared to migrants (Paradis et al. 1998) may help explain the relative importance of isolation. The nature of the intervening urban matrix may also play a role. The urban matrix could be more hostile to dispersal than the agricultural matrix of the Midwest.

Habitat degradation may be a more powerful consequence of fragmentation and edge in the arid West than in the Midwest and East. This degradation may be reflected in changes in physical habitat structure or food availability in habitat fragments. The effect of fragmentation on woody vegetation structure has not been the focus of studies of fragmentation in the East and Midwest, but one study has demonstrated lower food availability in fragments (Burke and Nol 1998).

INFORMATION NEEDS

In addition to those already mentioned there are a number of gaps in our knowledge that limit our ability to understand, predict, and manage the effects of fragmentation on birds in this region. Our understanding of the trophic effects of fragmentation is hindered by the lack of basic autecological data on bird foraging and diet, including adult and nestling food. Nest predation must be investigated on a range of bird species to discover whether the results on the Rufous-crowned Sparrow are generalizable to other species nesting in different strata and with differing landscape sensitivities. We know little about the non-mammalian predator community in fragments. Snakes appear to be quite rare in habitat fragments (D. Bolger, unpubl. data). If this is true what effect does this have on species that are vulnerable to snake predation? Are predation rates lower in fragments or does the effect of increased mammalian mesopredators or other predators compensate for reduced snake predation?

We also need to understand how edge effects scale with the percentage of the local landscape that is developed (Donovan et al. 1997). Do isolated habitat fragments experience more intense edge effects than larger habitat blocks? Similarly, how does the predation regime in isolated fragments compare with predation in the edge and interior of large habitat blocks? A virtually untouched question is the source status of the urban matrix for bird species that occur in both the urban matrix and natural habitat. Bolger et al. (1997) found elevated densities of some native urban-exploiting birds up to 1km into habitat blocks. The consequences of this density augmentation on avian communities deserves further study.

A landscape perspective on disturbance regimes is urgently needed. How do fragmentation and edge affect non-native plant invasion, fire, and other disturbance regimes. These are among the most severe threats to conservation in this semi-arid region as demonstrated by Minnich and Dezzani's (1998) work. Physical gradients (soil moisture, air temperature, etc.) along edges have not been investigated in this system and may be important. Also the effect of ENSO (El Niño-Southern Oscillation) driven variation in rainfall is essential to understanding avian population fluctuations (Morrison and Bolger in press) that may have important implications for extinction rates in fragments.

CONSERVATION IMPLICATIONS

There is an extensive conservation planning effort ongoing for coastal southern California under the state's Natural Communities Conservation Planning program (NCCP). The reserve system that ultimately results from this effort will by necessity be set within a predominantly urban matrix. A species-by-species evaluation of the conservation implications of the findings reviewed here is beyond the scope of this paper and would require a region-wide evaluation of the abundance and distribution of these species on protected lands (J. Rotenberry et al., unpubl. data). There are, however, a number of general conclusions that can be drawn that are relevant to the management of reserves in these landscapes.

The studies reviewed here suggest that highly isolated shrub habitat patches less than 100 ha provided little conservation value for fragmentation-sensitive species over the long term. However, they do support other members of the regional fauna in abundance (Soulé et al. 1988, Crooks et al. 2001). The limitations of fragmented habitat for conservation are acknowledged in the NCCP reserve selection guidelines that emphasize large, contiguous blocks of habitat (Atwood and Noss 1994). Denser archipelagos of fragments probably would support more interpatch movement and higher abundance of these species as suggested by a comparison of Soulé et al. (1988) and Lovio (1996). However, since we do not know whether fragments are sink or source habitat for most species it seems unwise to design landscape to encourage dispersal to fragments from source habitat.

Edge effects on bird abundance (Table 2; Bolger et al. 1997) and the penetration of Argentine ants along edges (Suarez et al. 1998; D. Bolger, unpubl. data) are of concern even in large reserves. We still do not have an adequate understanding of the variety of ecological mechanisms generating edge effects, the extent of their spatial penetration into blocks of habitat or the time course of these effects. Edge effects such as reduced or enhanced abundance of bird species, Argentine ant invasion, and changes in arthropod communities appear to penetrate reserves on the scale of hundreds of meters. Thus these effects can significantly reduce the effective area of even large reserves.

To effectively conserve the coastal southern California biota, it will be necessary to identify the effects of urban fragmentation and understand their ecological mechanisms. There is an understandable desire among land managers and conservation planners for simple geographic answers from ecologists: prescriptions for minimum area requirements, buffer and edge effect distances. However, easy answers are misleading, for although fragmentation and edge effects have a geographic dimension, that is they can be mapped to some degree of resolution, they are primarily community ecological and population ecological phenomena. As such, they are dynamic processes and their spatial dimension is dependent upon the makeup of the local community as well as time. For example, Crooks et al. (2001) demonstrated that area sensitivity is not static but is a function of time. It is likely that the spatial penetration of edge effects is also not static.

Ecologists will only be able to make robust management prescriptions about fragmentation and edge effects when we have more fully examined the range of ecological mechanisms generating these effects. Even then, they will not be simple answers expressed in meters and hectares, but will be time-dependent and conditional on the composition of the local community. So, minimum area requirements will be expressed in general terms for a given range of fragment age and will depend on the condition of the vegetation in the fragment and the composition of the predator community. These answers will not be easy to map, or to explain to policy-makers, but they will be ecologically valid. Of course geographic tools such as buffer distances will continue to be important conservation planning tools. But we cannot allow that fact to convince policy-makers, the public, and ourselves, that conserving the native biota of coastal southern California in the face of a large and growing human population will be as simple as creating buffers of a fixed distance around reserves. Instead, it we will require understanding and actively managing populations and processes, and we are a long way from possessing the necessary knowledge and management capabilities to accomplish that.

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APPENDIX. Scientific Name of All Vertebrate Species Mentioned in Text or Tables

Birds	
California Quail	*Callipepla californica*
Mourning Dove	*Zenaida macroura*
Lesser Nighthawk	*Chordeiles acutipennis*
Costa's Hummingbird	*Calypte costae*
Anna's Hummingbird	*Calypte anna*
Bell's Vireo	*Vireo bellii*
Western Scrub-jay	*Aphelocoma coerulescens*
Common Raven	*Corvus corax*
American Crow	*Corvus brachyrhynchos*
Common Bushtit	*Psaltriparus minimus*
Bewick's Wren	*Thryomanes bewickii*
Wrentit	*Chamaea fasciata*
Blue-gray Gnatcatcher	*Polioptila caerulea*
California Gnatcatcher	*Polioptila californica*
Northern Mockingbird	*Mimus polyglottos*
California Thrasher	*Toxostoma redivivum*
European Starling	*Sturnus vulgaris*
Lazuli Bunting	*Passerina amoena*
Spotted Towhee	*Pipilo maculatus*
California Towhee	*Pipilo crissalis*
Rufous-crowned Sparrow	*Aimophila ruficeps*
Sage Sparrow	*Amphispiza belli*
Black-chinned Sparrow	*Spizella atrogularis*
Grasshopper Sparrow	*Ammodramus savannarum*
Lark Sparrow	*Chondestes grammacus*
Brown-headed Cowbird	*Molothrus ater*
Western Meadowlark	*Sturnella neglecta*
House Finch	*Carpodacus mexicanus*
Lesser Goldfinch	*Carduelis psaltria*
Reptiles	
coastal horned lizard	*Phrynosoma coronatum*
California kingsnake	*Lampropeltis getula*
gopher snake	*Pituophis melanoleucus*
Mammals	
Virginia oppossum	*Didelphis virginiana*
California ground squirrel	*Spermophilus beechyi*
striped skunk	*Mephitis mephitis*
coyote	*Canis latrans*
grey fox	*Urocyon cinereoargenteus*
domestic cat	*Felis catus*