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Use of corridor-like landscape structures by bird and small mammal species

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Abstract

We investigated the use of corridor-like structures by birds and rodents in coastal San Diego County, California, USA, in areas characterized by dense residential development and small remnant habitat fragments. In 1992 and 1993 we compared the use of remnant strips of coastal sage scrub habitat and revegetated highway rights-of-way (ROW) with that of larger remnant patches of coastal sage scrub habitat to which these strips were connected. Using live trapping we compared rodent species composition, percent of females reproducing, and recapture frequency among the three site types. Rodent species richness did not differ significantly among the three site types. One species, *Peromyscus eremicus* was significantly more abundant in ROW sites, while several other species, *Rheithrodontomys californicus*, *Chaetodipus californicus* and *C. fallax* showed a similar, though non-significant trend. *Peromyscus californicus* was most abundant in remnant strips while *Neotoma fuscipes* used ROW sites less than remnant strips or patches. No significant differences were detected among the three site types in recapture frequency or proportion of females in reproductive condition. Common bird species were a priori divided into two categories based on previous research in this region: fragmentation-sensitive and fragmentation-tolerant. Species richness in remnant strips of habitat was similar to that in remnant patches for both categories of species. Species richness of the fragmentation-sensitive species was significantly lower in ROW sites than in remnant strips or patches by a factor of 4–10. Species richness in fragmentation-tolerant species was significantly lower in ROW sites in 1993 by less than a factor of two. The greater reduction in fragmentation-sensitive species suggests they have more stringent corridor requirements than do fragmentation-tolerant species. The species richness per site for fragmentation-sensitive bird species was significantly correlated with the percent cover of native shrubs in 1993 in patch and remnant strip sites. Fragmentation-tolerant bird species showed no consistent trend with shrub cover. Rodent species richness trended higher with increasing shrub cover in five of six site-type/year combinations, but none of the correlations were significant. Within the range of width and length examined there was no correlation between bird or rodent species richness and length or width of these corridor-like structures. These results indicate that remnant strips of habitat and revegetated highway ROW have potential to serve as habitat linkages for native rodents and fragmentation-tolerant bird species, but only remnant habitat strips appear suitable for fragmentation-sensitive bird species. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Corridors; Fragmentation; Rodents; Birds; Southern California; Landscape ecology

1. Introduction

Habitat fragmentation is widely recognized as one of the principal threats to biological diversity (Wilcox, 1980; Wilcove et al., 1986; Meffe and Carroll, 1997). The isolation caused by fragmentation can lead to reduced rates of recolonization and thus lower species diversity in fragments and erosion of genetic diversity due to reduced gene flow. The provisioning of landscape corridors has often been suggested as mitigation for the isolation effect of fragmentation (Wilson and Willis, 1975; Saunders and Hobbs, 1991). However, the utility of this approach is controversial (Simberloff et al., 1992; Rosenberg et al., 1997). Experimental evidence of the success of corridors in reducing population extinction rate and maintaining genetic diversity is rare (Forney

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and Gilpin, 1989). Several studies do suggest that the presence of a corridor connection enhances population density relative to isolated patches (MacClintock et al., 1977; Fahrig and Merriam, 1985; La Polla and Barrett, 1993; Dunning et al., 1995; Haddad and Baum, 1999). However, corridors may be dominated by edge effects and thus could be mortality sinks for some species (Soulé and Gilpin, 1991; Simberloff et al., 1992). Even if corridors are useful for some species they may harm others in the landscape (Simberloff et al., 1992; Rosenberg et al., 1997).

These discrepancies notwithstanding, corridors continue to be important elements of regional conservation plans (Rosenberg et al., 1997). Obviously, to function as corridors, linear habitat features in the landscape must support movement or habitat use by the target species. In the absence of more detailed, long-term data on the effect of corridors on population density, extinction likelihood, and genetic diversity, a more modest goal is to estimate what species are likely to use linear landscape features as habitat and thus likely to use corridors if they are provided.

It is useful to differentiate two types of corridors: habitat linkages and movement corridors (Rosenberg et al., 1997; Lidicker, 1999). A habitat linkage supports resident individuals of the focal species and provides the resources needed for survival and reproduction. Thus, a habitat linkage between two patches creates one continuous population. To function as a movement corridor a landscape feature does not have to support resident individuals, but it must allow for movement between patches. Theoretically, relatively low rates of exchange between patches will homogenize gene pools (Crow and Kimura, 1970) and significantly reduce the risk of stochastic extinction (Fahrig and Merriam, 1994). In this study we investigated the use of linear landscape features as habitat by mammal and bird species of coastal sage scrub habitat in San Diego, CA.

The coastal sage scrub and chaparral plant communities of coastal southern California support rich native rodent (M'Closkey, 1972; Meserve, 1972, 1976a,b; Price and Waser, 1984) and bird communities (Bolger et al., 1997a; Rotenberry et al., unpublished). This area has undergone extensive urban and suburban development over the last fifty years which has resulted in a highly fragmented landscape (Soulé et al., 1988; Atwood, 1993; Atwood and Noss, 1994). Within the boundaries of the city of San Diego and adjacent communities are several hundred isolated fragments of coastal sage scrub habitat ranging in size from less than 1 ha to several hundred hectares. Many bird and rodent species occur in the partially developed landscape mosaic of urban San Diego, and show varying degrees of sensitivity to the isolation and edge effects resulting from habitat fragmentation (Soulé et al., 1988; Bolger et al., 1991, 1997a, b; Bolger, 2001). Declines in species richness of shrub habitat bird species and rodents have occurred in these fragments over time, apparently due to local extinction rates that are higher than colonization rates (Soulé et al., 1988; Bolger et al., 1991, 1997b; Crooks et al., 2001). If a desired management goal is to maintain populations of native birds and rodents in remnant habitat patches in this landscape, then landscape corridors linking remnant patches might be useful in combating the effects of isolation.

Roads are a major feature of the landscape in developed countries and have a variety of negative consequences for adjacent biodiversity including fragmentation of habitat and populations, pollution, and disturbance by noise, movement and light (see review in Forman and Alexander, 1998). A number of studies have focused on the possible negative effects of highways on bird density in adjacent habitat (Ferris, 1979; Van Der Zande et al., 1980; Adams and Geis, 1981; Reijnen and Foppen, 1991; Reijnen et al., 1995), but few have focused on the possible utility of rights-of-way (ROW) as corridors for birds and other vertebrates (Getz et al., 1978). Highways in the southern California landscape cause extensive habitat fragmentation, but rights-of-way are also one of the few features in the landscape which have the geometric attributes to potentially function as corridors.

In this study we compared the use of linear habitat features in this landscape by bird and rodents species. In most cases the landscape structures we examined were peninsula-like strips of habitat connected to larger habitat patches on only one end. They included revegetated highway ROW strips, and strips of remnant habitat. We used these peninsula-like strips because true corridors of coastal sage scrub habitat are uncommon in this landscape. We make the assumption that the use of these corridor-like strips as habitat should be similar to the use of true corridors of similar length, width and habitat composition. If this is true, these results estimate the utility of similar landscape features as habitat linkages.

We tested the null hypothesis that the habitat suitability of ROW and remnant strips is equal to that of remnant habitat patches. This hypothesis predicts that relative abundance, and reproductive and residence status should be the same in the three site types. We compared these characteristics in birds and rodents occupying remnant habitat and highway ROW strips to those in remnant habitat patches to which they were connected. An alternative hypothesis is that landscape elements in which the habitat is more similar to undisturbed habitat will have higher suitability. Thus suitability should rank: remnant patches > remnant strips > ROW. We tested the following specific predictions of this alternative hypothesis: (1) Rodent and bird species richness and the abundance of individual rodent species varies among the three site types; (2) Rodents are transient rather than resident in the corridor-like structures. This hypothesis is tested by comparing the frequency of recapture and the proportion of females in reproductive condition in these structures to that in the remnant patches; (3) Fragmentation-sensitive bird species use corridor-like structures less than fragmentation-tolerant species. This should be true if fragmentation-sensitivity results from a relative inability to disperse through the urban matrix (Bolger, 2001). Difficulty in moving through the landscape mosaic would suggest an inability or reluctance to use human-modified or impacted landscape elements and predicts that corridor requirements would be more stringent for the fragmentation-sensitive group; and (4) Use of corridor-like structures by birds and rodents is affected by corridor structure, including degree of native shrub cover, and corridor width and length.

2. Methods

Appropriate study areas were identified by inspection of 1:10 000 aerial photographs and on-the-ground inspection. Each study area contained two landscape elements (Fig. 1): one or two remnant patches and one or two habitat strips (remnant and/or ROW). The remnant and ROW strips were all contiguous with at least one remnant patch. Most of the remnant and ROW strips were not truly corridors in that they did not connect two patches of habitat. A peninsula would be a better geographic analogy as they were connected to a remnant patch on one end and extended for some distance before terminating at a road or housing development. The development of the landscape in this region has not produced many true corridors, thus we were limited to these peninsula-like strips of habitat. Despite not being functional corridors, these sites were appropriate to evaluate the use of narrow strips of habitat in urban landscapes by birds and rodents. For the sake of simplicity we will sometimes use the term corridor to refer to these landscape features in this paper. Bird and rodent presence was assessed at a number of points within the remnant patch and the ROW or remnant strip.

Highway sites were chosen in ROW that had been revegetated with native shrubs. Remnant corridor sites were remnant strips of native vegetation in the landscape that were not associated with highways. The vegetation in most sites was coastal sage scrub, although some sites contained patches of chaparral vegetation. Most remnant corridors were narrow drainages or slopes that were bordered by housing on either side, or housing on one side and a surface road on the other. Thus they resembled ROW in shape, but they were not adjacent to a highway and their vegetation was remnant

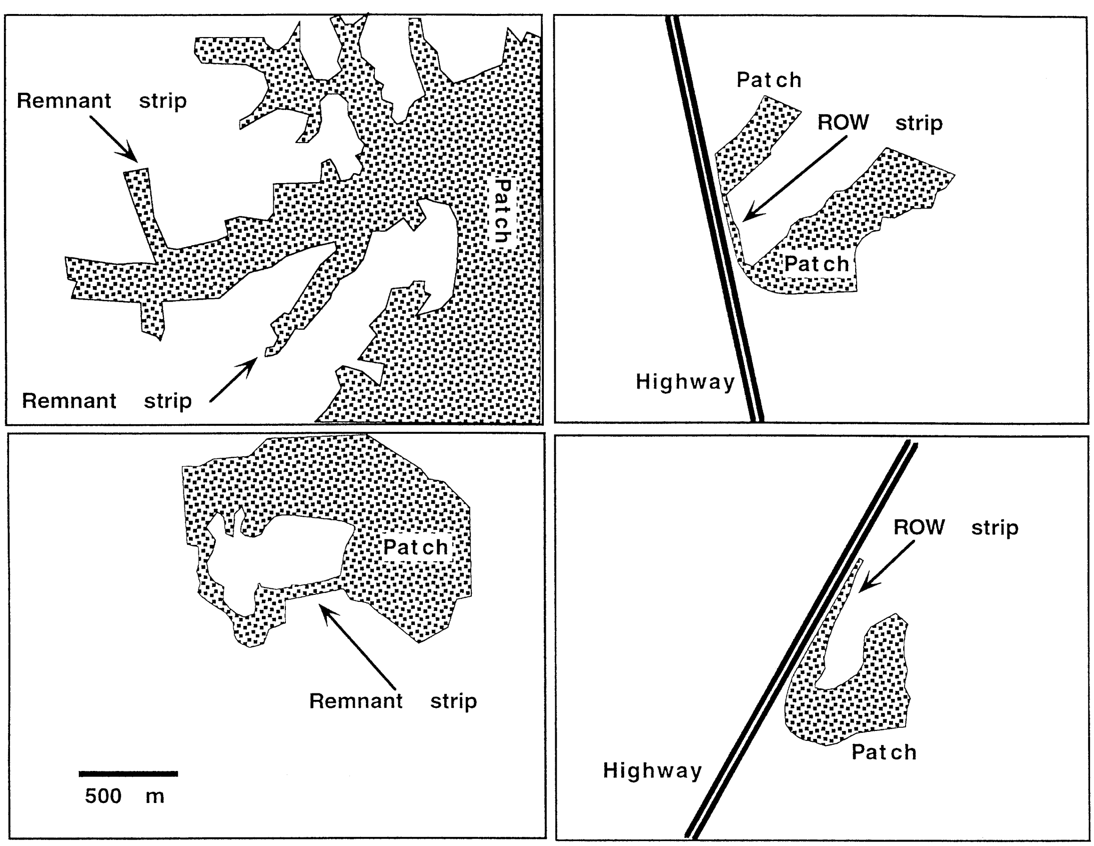

Fig. 1. Maps of four corridor study sites in San Diego, CA. Two sites are remnant strips of habitat and two are highway right-of-way strips. Remnant habitat and revegetated right-of-way is shown as stippled and residential development is shown in white.

natural vegetation not restored vegetation as in the ROW sites. Remnant strips were not a perfect match for the ROW sites in physical dimensions, however, since they were usually somewhat longer (mean of 367 m compared to 189 m) and wider (mean of 91 m compared to 39 m). Remnant patches exceeded the remnant and ROW strips several-fold in width and area. Patches ranged from 1 to 260 ha in area, with a mean of 48 ha (median = 25 ha).

ROW sites were also not a perfect match to remnant habitat in terms of shrub species composition. In general, species diversity was obviously lower in ROW strips than in remnant habitat. The dominant shrub species in ROW sites were typically three coastal sage scrub species, *Artemisia californica*, *Eriogonum fasciculatum*, and *Encelia californica*. These three species are often used to revegetate ROW. However, other typical remnant coastal sage scrub species including *Malosma laurina* and *Salvia mellifera* were relatively rare in ROW sites. In remnant habitat, chaparral shrub species (e.g. *Adenostoma fasciculatum*, *Quercus dumosa*, *Cercocarpus betuloides*) contribute to diversity in remnant habitat but these also rarely occurred in ROW sites. Because of these inherent differences we could not separate differences in shrub species composition from site type and so could not examine the role of species composition in determining corridor suitability. Instead, we focused on vegetation structure in terms of percent shrub cover at the sites. At each site the total cover of native shrubs was estimated visually employing a Braun-Blanquet categorical scale (Mueller-Dombois and Ellenberg, 1974).

2.1. Rodents

Two different rodent studies were conducted. The first was carried out in both 1992 and 1993. Rodent abundance was sampled by live-trapping in the three site types: highway ROW strips, remnant habitat strips, and patches. In 1992 trapping was conducted at 11 ROW sites, seven remnant strips, and 12 patch sites. In 1993 this was increased to 13 highway ROW sites, 14 remnant corridor sites, and 17 patch sites. Each site was trapped once per year. Trapping was conducted between May 12 and June 27 in 1992, and between April 5 and July 16 in 1993. The presence of rodent species was surveyed by live-trapping with small Sherman traps baited with bird seed. Traps were set in the early evening and recovered the next morning. We identified captured rodents to species, assessed sex and reproductive status and released them. Thirty-six traps were set at each site in a 6×6 grid with 6 m between grid points. The order in which sites were trapped was randomized within each year.

The second study was a mark-recapture study done at two patch-ROW complexes in 1993 and 1994. The purpose of this study was to further assess the usefulness of highway ROW as rodent habitat. At each site multiple trapping grids were located in the ROW and the adjacent patches. In 1993 trapping occurred at just one patch-ROW complex. Five plots, three in patches and two in ROW, were trapped four times each, twice on non-consecutive days (7–21 days in between trappings) in early to mid-April, and twice on non-consecutive days in mid- to late-June. In 1994 trapping was carried out at two patch-ROW complexes and seven plots were trapped, three in patches and four in ROW. Each plot was trapped from five to seven times from June 3 to August 20. Most plots were trapped on three consecutive nights in the period mid-June to mid-July, and 2–3 consecutive nights in early to mid-August.

In this latter study, each grid consisted of 48 traps arranged in eight rows of six traps. Traps were placed 6 m from one another except for the first and eighth rows, which were placed 12 m from the adjacent rows. Each individual captured was identified to species and sex, reproductive state of females determined, weighed, individually marked by toe-clipping or metal ear tags, and released. Females were judged to be in reproductive state if nipples or vagina were swollen, or if there were obvious signs of pregnancy.

2.2. Birds

Based on the results of Soulé et al. (1988) we a priori categorized our focal bird species as fragmentation-sensitive or fragmentation-tolerant (species are listed in Table 5). The species in both categories are all common resident breeders in coastal sage scrub, chaparral or mixed habitats (Unitt, 1984). Species listed as fragmentation-sensitive show area-sensitivity and many have been shown to experience local extinction in isolated habitat fragments (Soulé et al., 1988, Bolger et al., 1991; Crooks et al., 2001). The fragmentation-sensitive birds have been shown to have reduced abundance in fragmented habitat compared to large blocks of habitat (Crooks et al., 2001) and are only rarely observed in urban areas in San Diego (Lovio, 1996; Crooks et al., 2001). Fragmentation-tolerant bird species, in addition to being common in chaparral and coastal sage scrub habitat, are also frequently observed in highly modified and urban habitats (Unitt, 1984; Lovio, 1996; Crooks et al., unpublished data). Given these differing characteristics we thought it likely that these two groups of species would respond to potential corridors differently and so should be analyzed separately.

Bird occupancy was assessed with variable distance point counts (Ralph et al., 1993) in the spring of 1992 and 1993. Point counts were performed at 31 stations in 1992 (11 in patches, 12 remnant strips and eight ROW) and 44 in 1993 (16 in patches, 14 remnant strips and 14 ROW). Three counts were performed per station per year. The duration of counts was 5 min in 1992 and was expanded to 8 min in 1993. Counts were conducted between April 20 and June 11, 1992 and between May 13 and June 12, 1993.

2.3. Analysis

Normality of the dependent and independent variables was assessed by inspection of frequency histograms. If data appeared non-normal, non-parametric methods were used, otherwise parametric analyses were employed. In most cases 1992 and 1993 data were analyzed separately. Rodent species richness was compared among site types using Kruskal–Wallis analysis of variance (ANOVA) as was capture frequency per trap-night for each species.

The number of bird species recorded per point count site was compared among the three site types with ANOVA. Species richness was a simple count of the species from each species group that were detected at least once within 50 m of the point count location within a given year. Because of the possible bias in detection caused by the greater noise levels in the highway ROW we repeated the analyses with only detections within 30 m. The relative differences among site types were generally constant between the 30 and 50 m analyses, but fewer of the results were significant due to the generally lower number of detections, so the 50 m results are presented here.

To further examine the use of habitat strips by birds we compared the species present in patch sites to the species found in the adjoining corridor sites. That is, of the species present in the patch how many also appeared in the strips of habitat. A species' propensity to use habitat strips was represented as the ratio of the number of remnant strip or ROW sites in which it was observed, to the total number of potential sites (the number of remnant strip or ROW sites adjoining patch sites at which the species occurred). These ratios were totaled for the fragmentation-sensitive species and the fragmentation-tolerant species and tested among site types and between species groups using a three-way contingency table.

Spearman rank correlation was used to test for a significant relationship between bird and rodent species richness and the percent native shrub cover at each site. Linear regression was used to quantify the relationship between bird and rodent species richness and the width and length of the remnant or ROW strip. Since the purpose of this analysis was to determine if species richness in corridors declines with increasing distance from the adjoining patch, the measure of length used was the distance from the sampling point to the junction of the habitat strip with the adjoining patch rather than the entire length of the structure.

For the rodents captured in the mark-recapture study the proportion of females in reproductive condition and the frequency of recapture of marked individuals was compared among site types. If rodents use ROW strips transiently (or if mortality is high) then recapture of animals in ROW sites should be less frequent than in remnant patches. The frequency of recapture of individual rodents was compared between ROW and patch sites in the two mark-recapture study sites. Data were pooled between 1993 and 1994 to increase our power to detect a difference between highway and mainland sites. The mean number of times each individual was captured was compared between site types with Mann–Whitney U-tests. Since the number of nights of trapping differed between grids and years we standardized this measure of recapture frequency by dividing the number

Table 1
The mean number of captures (per 36 trap-nights) of nine native rodent species are compared among the three types of study sites in 1992–1993[a]

	1992				1993			
	Patch	Remnant strip	ROW	P	Patch	Remnant strip	ROW	*P*
Number of sites	12	7	12		18	14	12	
Peromyscus californicus	1.75	3.00	1.00	0.05	1.24	2.71	1.46	0.39
Peromyscus eremicus	3.00	0.14	4.30	0.03	1.47	0.79	2.39	0.04
Peromyscus maniculatus	1.41	1.86	2.42	0.51	0.77	0.43	0.54	0.58
Neotoma fuscipes	1.42	1.86	0.25	0.06	0.71	0.14	0.23	0.24
Neotoma lepida	0.17	0.29	0.33	0.80	0.12	0.21	0.00	0.22
Reithrodontomys megalotis	0.08	0.14	0.33	0.80	0.00	0.07	0.23	0.09
Microtus californicus	0.17	0.00	0.17	0.74	0.06	0.00	0.00	0.45
Chaetodipus californicus	0.33	0.00	0.75	0.39	0.35	0.14	0.77	0.06
Chaetodipus fallax	0.17	0.00	0.50	0.34	0.00	0.07	0.15	0.26
Species richness	2.67	2.29	2.67	0.72	2.18	1.86	2.85	0.09
% Cover of native shrubs	74	71	56	0.35	72	70	50	0.09

[a] Also compared are the mean number of species caught per site, the total number of individuals captured, and the percent native shrub cover. The probabilities result from one-way Kruskal–Wallis ANOVAs comparing capture frequency among the three site types. The probabilities for the species richness comparisons are from one-way ANOVA. ROW, right-of-way.

of times each animal was captured by the total number of nights of trapping at that grid in that year. Contingency tables were used to test among site types for differences in the proportion of females showing signs of reproduction.

3. Results

3.1. Rodent species richness and relative abundance

Native rodents were frequently trapped in remnant patches and both remnant and highway ROW strips (Table 1). All species were captured in all three site types. There were no significant differences in rodent species richness among site types in 1992 or 1993 (Table 1).

The frequency with which most rodent species were trapped did not differ significantly among site types. Two species, the woodrats *Neotoma fuscipes* and *N. lepida*, showed a trend toward lower trapping frequency in ROW sites. *N. fuscipes* had a nearly significant ($P=0.06$) difference among site types in 1992. Trapping frequency for *P. eremicus*, *Rheithrodontomys megalotis*, *Chaetodipus californicus*, and *C. fallax* was highest in highway ROW sites. Those differences were significant for *P. eremicus* in 1992 and 1993, and nearly significant ($P=0.06$) for *Chaetodipus californicus* in 1993. *Peromyscus californicus* showed marginally significant variation ($P=0.01$) among site types in 1992 and reached its highest trap frequency in remnant habitat strips.

3.2. Rodent reproduction and recapture frequency

The proportion of females in reproductive condition did not differ significantly between site types (Table 2) for the three species (*P. californicus*, *P. eremicus and P. maniculatus*) for which we had sufficient data. Similarly, we found no significant difference for any species in the frequency of recapture of marked individuals (Table 3). Although none of the differences were significant, mean recapture frequency was higher in ROW sites than in remnant patches for seven of the eight species.

Table 2
The ratio of females showing signs of reproductive activity, to total females captured at patch, remnant strip, and highway right-of-way (ROW) sites[a]

Species	Patch	Remnant strip	Highway ROW	Chi-square	*P*
Neotoma fuscipes	4/12	1/1	3/7		
Neotoma lepida	1/6	1/1	2/5		
Peromyscus californicus	5/10[b]	9/15[b]	7/16[b]	0.83	0.66
Peromyscus eremicus	25/44[b]	4/5	19/36[b]	0.13	0.72
Peromyscus maniculatus	9/15[b]	0/1	6/11[b]	0.08	0.78
Reithrodontomys megalotis	5/8	0/0	4/17		
Chaetodipus californicus	1/6	0/2	0/6		
Chaetodipus fallax	0/4	1/1	2/32		

[a] Remnant strip data were collected only in 1993, ROW and patch data were collected in 1993 and 1994. For each species, data were pooled among sites and years. Chi-square tests were performed on species for which sufficient data were available to test for differences in frequency of reproduction among site types. Only site types for which sufficient captures were available were included in these analyses.
[b] Data used in the Chi-square test on that species.

Table 3
Frequency of recapture of marked rodents at the Tierra Santa and Encinitas mark-recapture study sites[a]

Species	Number trapped	Patch mean	Number trapped	ROW mean	*P*
Neotoma lepida	7	0.407	7	0.354	0.48
Neotoma fuscipes	13	0.328	8	0.374	0.74
Peromyscus californicus	4	0.305	11	0.408	1.00
Peromyscus maniculatus	20	0.358	11	0.455	0.26
Peromyscus eremicus	62	0.385	56	0.417	0.61
Reithrodontomys megalotis	24	0.279	48	0.295	0.15
Chaetodipus californicus	13	0.288	11	0.439	0.13
Chaetodipus fallax	10	0.299	67	0.405	0.13

[a] Data were pooled between 1993 and 1994. Because the number of nights of trapping differed among grids and years, recapture frequency was standardized by dividing the number of times each animal was captured by the total number of nights of trapping at that grid in that year. Mann–Whitney *U*-tests were used to test for a significant difference in this measure of recapture frequency between highway right-of-way (ROW) and patch sites for each species.

Table 4
ANOVA results comparing bird species richness (estimated by point counts) in two species groups (fragmentation-sensitive and -tolerant) among the three site types[a]

Species group/year	Mean species richness			d.f.	*F*	*P*
	Patch	Remnant strip	Right-of-way			
Fragmentation-sensitive — 1992	1.3	1.3	0.3	2, 29	4.16*	0.03
Fragmentation-tolerant — 1992	3.8	3.6	2.1	2, 29	2.77	0.08
Fragmentation-sensitive — 1993	2.1	2.7	0.2	2, 38	21.0	< 0.0001
Fragmentation-tolerant — 1993	5.6	6.6	3.6	2, 38	15.1**	< 0.0001

[a] See Table 5 for a list of bird species in each category. If the ANOVA was significant, pairwise post-hoc comparisons were made using the Scheffe *F*-test. Means not connected with underlining are significantly different.
$^{*}P<0.05$.
$^{**}P<0.001$.

3.3. Bird species richness

There was significant variation in the number of species recorded per point count location among the three site types for fragmentation-sensitive bird species in both 1992 and 1993 and for fragmentation-tolerant bird species in 1993 (Table 4). A posteriori tests revealed that species richness in both groups was higher in remnant strips and patches of habitat than in highway ROW sites, but patches and remnant strips were indistinquishable. Fragmentation-sensitive species were very rare in ROW sites (mean species richness per location of 0.3 in 1992 and 0.2 in 1993).

When the species in the patch were compared to the species in the attached ROW or remnant strips at each site, a similar pattern was evident. Birds of both species groups were more likely to be present in an attached corridor site if it was a remnant strip versus a ROW (Table 5). However, for the fragmentation-sensitive species this difference was large, a roughly 20-fold difference between the two site types in the proportion of sites occupied in 1992 and 1993 (Table 6). The only non-significant log-linear model that could be fit to the frequency data was a saturated model that included the three-way interaction: site type×species type×present/absent (Table 6). This demonstrates an interaction between the species groups and their frequency in the different site types. In other words, the difference in frequency of occurrence between ROW strips as compared to patches and remnant strips was significantly greater for fragmentation-sensitive species than for the fragmentation-tolerant species.

In some cases a species that was not recorded from a patch was detected in the connected corridor sites. We refer to such instances as "additional sightings". Consistent with the previous findings, additional sightings were much more common in remnant strips than in ROW strips, and fragmentation-sensitive species were less likely to be observed in a corridor unless they were recorded in the attached patch than were the fragmentation-tolerant species (Table 5).

3.4. Shrub cover

There were no significant rank correlations between rodent species richness and the percent of native shrub cover at a site. Five of the six trends were positive (Table 7) with the strongest trend in the ROW sites.

Bird species richness in the fragmentation-tolerant group was uncorrelated with shrub cover in all site types and years (Table 7) and no consistent trends were evident. Fragmentation-sensitive bird species showed a significant rank correlation with shrub cover in patches and remnant strips in 1993 and a non-significant trend in highway ROW in 1992 ($P=0.08$). The sign of the correlation coefficient was positive for all six year/site type comparisons for the sensitive species. Fragmentation-sensitive species were never recorded from a highway ROW site with less than 40% native shrub cover.

3.5. Width and length of habitat strip

In most cases there was no significant dependence of bird or rodent species richness on the length or width of the remnant or ROW strip (Table 8). The *R*-squared values are generally very low and the *P* values high, giving little suggestion of a trend. The one exception was a significant positive regression of fragmentation-sensitive bird species richness on ROW width in 1993. However, the significance of this result was due to a single influential observation. When this point was removed from the analysis *P* increased from 0.02 to 0.23.

4. Discussion

4.1. Potential utility of ROW and remnant habitat strips as habitat linkages for rodents

Our results suggest that both remnant habitat strips and ROW can serve as habitat linkages for native rodents. Most species were caught as frequently in ROW and remnant strips as they were in remnant

Table 5
Distribution of fragmentation sensitive and fragmentation tolerant birds species in different types of sites[a]

Species	Patch		Remnant strip		ROW		Additional sightings	
	Present/total	Proportion	Present/total	Proportion	Present/total	Proportion	ROW	Remnant
1992 — Fragmentation sensitive species								
California Quail (*Callipepla californica*)	2/11	0.18	2/4	0.50	0/3	0.00	0	2
Bewick's Wren (*Thryomanes bewickii*)	3/11	0.27	3/5	0.60	0/4	0.00	0	2
California Thrasher (*Toxostoma redivivum*)	4/11	0.36	1/5	0.20	0/2	0.00	0	0
Wrentit (*Chamaea fasciata*)	11/11	1.00	11/12	0.92	1/8	0.13	0	0
California Gnatcatcher (*Polioptila californica*)	0/11	0.00	0/0	0.00	0/0	0.00	2	0
Spotted Towhee (*Pipilo crissalis*)	8/11	0.73	9/10	0.90	0/3	0.00	0	1
Mean		0.273		0.286		0.021	0.0	0.3
1992 — Fragmentation tolerant species								
Mourning Dove (*Zenaida macroura*)	4/11	0.36	1/4	0.25	2/6	0.33	1	3
Anna's Hummingbird (*Calypte anna*)	7/11	0.64	7/10	0.70	2/5	0.40	1	2
Black Phoebe (*Sayornis nigricans*)	1/11	0.09	0/0	0.00	0/1	0.00	0	2
Scrub Jay (*Aphelocoma coerulescens*)	8/11	0.73	9/10	0.90	2/3	0.67	0	0
Common Bushtit (*Psaltriparus minimus*)	5/11	0.45	3/6	0.50	1/5	0.20	0	6
Northern Mockingbird (*Mimus polyglottos*)	2/11	0.18	1/2	0.50	1/4	0.25	0	4
Lesser Goldfinch (*Carduelis psaltria*)	3/11	0.27	0/2	0.00	1/1	1.00	2	5
House Finch (*Carpodacus mexicanus*)	9/11	0.82	7/7	1.00	3/8	0.38	0	2
California Towhee (*Pipilo fuscus*)	6/11	0.55	4/5	0.80	3/6	0.50	1	1
Song Sparrow (*Melospiza melodia*)	9/11	0.82	6/9	0.67	4/8	0.50	0	1
Mean		0.455		0.507		0.389	0.4	2.3
1993 — Fragmentation sensitive species								
California Quail	6/16	0.38	7/10	0.70	0/1	0.00	1	0
Bewick's Wren	11/16	0.69	6/11	0.55	0/7	0.00	0	2
California Thrasher	4/16	0.25	3/7	0.43	0/0	0.00	1	0
Wrentit	9/16	0.56	12/12	1.00	0/8	0.00	1	0
California Gnatcatcher	5/16	0.31	2/4	0.50	1/6	0.17	0	1
Spotted Towhee	10/16	0.63	8/12	0.67	0/8	0.00	1	0
Mean		0.406		0.524		0.028	0.5	0.5
1993 — Fragmentation tolerant species								
Mourning Dove	14/16	0.88	11/12	0.92	12/14	0.86	0	2
Anna's Hummingbird	13/16	0.81	14/14	1.00	4/12	0.25	1	0
Black Phoebe	4/16	0.25	3/6	0.50	1/1	1.00	1	2
Scrub Jay	9/16	0.56	8/10	0.80	0/5	0.00	2	2
Common Bushtit	12/16	0.75	11/12	0.92	3/9	0.33	3	2
Northern Mockingbird	9/16	0.56	12/12	1.00	4/7	0.57	1	0
Lesser Goldfinch	13/16	0.81	8/11	0.73	9/12	0.75	0	1
House Finch	16/16	1.00	14/14	1.00	14/14	1.00	0	0
California Towhee	15/16	0.94	14/14	1.00	9/13	0.69	1	0
Song Sparrow	14/16	0.88	9/12	0.75	6/14	0.43	0	0
Mean		0.656		0.769		0.503	0.9	0.7

[a] Data are the number of sites a species was present in/the total number of sites, and the proportion. Data for the right-of-way (ROW) and remnant strip sites are represented as the ratio of the number of sites that a species was recorded in to the total number of sites that were connected to patches in which the species was present. Additions are cases where a species was detected in an ROW or a remnant strip but not in the connected patch.

habitat patches (Table 1). The degree to which rodent species appear to reside in highway ROW is striking. Although a few species (*N. fuscipes* and *P. californicus*) were trapped less frequently in ROW sites, several others (*P. eremicus*, *Chaetodipus californicus*, *C. fallax*, and *Reithrodontomys megalotis*) were captured more frequently in ROW sites than in remnant habitat.

Several results strengthen the inference that ROW serve as habitat to native rodents. The mark-recapture studies indicate that residency of rodents in these ROW strips over the duration of our study was similar to that in habitat patches (Table 3). The high proportion of females in ROW sites that were reproducing (Table 2) suggests that these landscape features are more than

Table 6
Contingency table analysis of the use of remnant strips of habitat and highway ROWs by fragmentation-tolerant and sensitive bird species[a]

Species group	Site type	Present	Absent	Chi-square	*P*
1992					
Fragmentation-sensitive	Remnant strip	26	10	6.83	0.009
	ROW	1	19		
Fragmentation-tolerant	Remnant strip	38	17		
	ROW	19	28		
1993					
Fragmentation-sensitive	Remnant strip	38	18	8.18	0.004
	ROW	1	29		
Fragmentation-tolerant	Remnant strip	104	13		
	ROW	58	39		

[a] Presence and absence is scored at point count sites that are in sites contiguous with fragments that contain the species. Chi-square values are from log-linear three-way contingency models for 1992 and 1993 data: site type×species group×presence/absence. Chi-square and *P* values are from models with all two-way interactions included, the significance of which demonstrates that presence/absence is dependent on both species group and site type.

Table 7
Spearman rank correlations of bird and rodent species richness and the percent shrub cover at point count sites

Species group/year	Patch	Remnant strip	Right-of-way
Fragmentation-sensitive — 1992	0.32	0.44	0.62*
Fragmentation-tolerant — 1992	−0.29	−0.23	−0.27
Fragmentation-sensitive — 1993	0.74***	0.58**	0.43
Fragmentation-tolerant — 1993	0.13	−0.11	0.18
Rodents — 1992	0.14	0.32	0.33
Rodents — 1993	0.10	−0.01	0.33

*$P<0.10$.
**$P<0.05$.
***$P<0.01$.

Table 8
Regressions of bird and rodent species richness per site in highway right-of-way (ROW) strips and remnant habitat strips on the width and length of the strips[a]

	Remnant strips			ROW		
	n	*R*-squared	*P*	*n*	*R*-squared	*P*
Birds						
1992 — Length						
Sensitive species	12	0.03	0.58	10	0.18	0.22
Tolerant species	12	0.01	0.82	10	0.02	0.68
1992 — Width						
Sensitive species	12	0.07	0.39	10	0.10	0.38
Tolerant species	12	0.06	0.45	10	0.12	0.32
1993 — Length						
Sensitive species	14	0.00	0.94	14	0.07	0.36
Tolerant species	14	0.05	0.44	14	0.00	0.94
1993 — Width						
Sensitive species	14	0.11	0.25	14	0.38	0.02
Tolerant species	14	0.03	0.54	14	0.02	0.66
Rodents						
1992						
Length	7	0.24	0.27	11	0.02	0.70
Width	7	0.38	0.14	11	0.00	0.98
1993						
Length	14	0.03	0.59	13	0.01	0.81
Width	14	0.07	0.57	13	0.11	0.27

[a] Rodent species number is the number of species trapped in 36 trap-nights. Bird species counts result from detections within 50 m of the point count station station.

movement corridors or dispersal sinks for these species. These results support the view that similar landscape features have significant potential as habitat linkages for a range of native rodent species.

The variation among rodent species in the extent of ROW use relative to remnant habitat strips may be due to differing habitat preferences. In comparison to the other rodent species, the four species that were more abundant in ROW sites prefer habitat that is relatively open, with less shrub cover and more grass and forb cover, and rocky or bare ground (Rotenberry et al., unpublished). The highway sites have a lower native shrub cover than the remnant strips (Table 1). However, other factors, including resource availability and predation pressure, may also affect relative abundance of rodent species in ROW strips.

4.2. Potential utility of ROW and remnant habitat strips as habitat linkages for birds

With one exception all bird species considered were recorded in both remnant habitat strips and ROW strips (Table 5). The exception, the Bewick's wren, was not recorded in ROW strips. Remnant habitat strips were indistinguishable from habitat patches in terms of species richness for both species groups (Table 4). This suggests they have significant potential as habitat linkages for both species groups.

Most bird species were less likely to use highway ROW strips than remnant strips or patches of habitat (Table 5). Furthermore, fragmentation-sensitive bird species were significantly less likely to be recorded in

ROW sites than were fragmentation-tolerant species (Table 6). Species richness of fragmentation-tolerant birds was significantly lower in ROW than remnant habitat strips and patches in both 1992 and 1993, but species richness of fragmentation-tolerant species was only significantly lower in 1993 (Table 4). Species richness of fragmentation-sensitive species was lower in ROW than remnant strips by a factor of 4–10 while tolerant species richness differed only by a factor less than two.

Bolger (2001) concluded that that the fragmentation sensitivity among the sensitive species group is due at least in part to their relative inability to disperse across the urban matrix. This is supported by the fact that these species experience higher rates of extinction than colonization in isolated fragments (Crooks et al., 2001) and the lack of a significant relationship between fragment isolation and the occurrence of these species (Soulé et al., 1988; Crooks et al., 2001). Also, these species are not commonly observed in human-modified habitat (backyards, parks, golf courses; Unitt 1984; Lovio 1996; Crooks et al., 2001). We hypothesize that their rarity in ROW sites is caused by the same avoidance of non-coastal sage scrub landscape elements that causes their fragmentation sensitivity. The fragmentation-tolerant species, however, are more tolerant of modified habitat and many of these species do occur in the urban matrix (Unitt, 1984; Lovio, 1996; Crooks et al., unpublished data).

The greater habitat sensitivity of the fragmentation-sensitive species is also suggested by their dependence on the habitat structure of the site. Fragmentation-sensitive bird species richness was positively correlated with native shrub cover in remnant habitat patches and remnant habitat strips. The trend was the same in highway ROW sites but was not significant (possibly because fragmentation-sensitive species did not appear in ROW sites frequently enough to allow a very powerful test). Fragmentation-tolerant species showed no relationship with shrub cover. Our results suggest that in addition to being more sensitive to fragmentation this group of species has more stringent corridor requirements. Highway ROW strips as presently constituted do not appear to frequently support resident individuals of fragmentation-sensitive species and thus have limited potential as habitat linkages for these species.

4.3. Research needs

Our results still leave unanswered several important questions about the utility of corridors in these landscapes. Would real corridors increase focal species density, promote gene flow and reduce extinction rates compared to isolated patches? An answer to this question requires either long-term population studies or careful comparisons among connected and unconnected patches. Are narrow habitat strips mortality sinks for birds and rodents (Heinen and Merriam, 1990; Soulé and Gilpin, 1991)? This could be a problem particularly in the ROW strips; highway traffic is a well-know cause of mortality for many animal species (Forman and Alexander, 1998). Our data on residency in rodents suggests that ROW strips are not sinks for rodents. However, survival would need to be measured over at least an entire year to adequately assess that potential. How vulnerable are these strips to degradation by edge effects? An examination of habitat quality in a chronosequence of corridors could help answer this question. Although ROW strips do not support habitat use by fragmentation-sensitive bird species, do they function as movement corridors for this group? This could be assessed through studies of color-marked individuals in patch-corridor-patch complexes.

4.4. Management and conservation implications

Within the range of corridor length and width addressed in our study, our results indicate that remnant strips of habitat have significant potential as corridors for the rodent and bird species addressed here. Highway ROW strips appear to have significant potential as habitat linkages for native rodents. Although they are also used by the fragmentation-tolerant bird species, highway ROW strips, as currently constituted, appear to have limited utility for fragmentation-sensitive bird species.

Our data do not allow us to determine the cause of the difference in use of ROW strips and remnant strips by fragmentation-sensitive bird species. However, the generally low abundance of these species in ROW strips suggests that even with higher shrub cover, the utility of ROW as habitat for these species may be limited. Other characteristics of the ROW strips may make them undesirable to these species including the ROW width, shrub species composition, or the high noise levels, motion, and evening lighting produced by passing vehicles and overhead lights. Within the range examined we saw no evidence of a relationship between use and ROW width. Although the available ROW sites had a narrow range (<114 m), we found no evidence of a relationship between width and use. It would, however, be instructive to examine the use of wider ROW strips by fragmentation-sensitive bird species if such ROW sites could be located.

Native shrub cover appears to be important in promoting use of remnant strips and ROW strips by fragmentation-sensitive birds and possibly rodents. Fragmentation-sensitive bird species were more numerous in sites with higher native shrub cover. Rodents showed a similar, though non-significant, trend. These results suggest that revegetation of ROW strips or other putative corridors should mimic the natural shrub communities, in terms of percent native shrub cover, to enhance their use as habitat. However, the diverse habitat preferences of the focal species need to be considered. For instance, among the native rodent species, several prefer more open habitat while others favor a higher shrub cover (Price and Kramer, 1984; Price and Waser, 1984; Rotenberry et al., unpublished). Therefore, a mosaic pattern of shrubs and grass/forbs may promote use of these corridors by the greatest number of rodent species. We did not examine the effect of shrub species composition on corridor use, but this could clearly be important for some species and warrants further investigation. Most existing ROWs in San Diego County have little if any native shrub cover. Our data suggest that these would be poor habitat linkages for rodents and fragmentation-sensitive bird species (Table 7).

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