ELSEVIER

Use of highway undercrossings by wildlife in southern California

Sandra J. Ng[a,b], Jim W. Dole[a], Raymond M. Sauvajot[b,*],
Seth P.D. Riley[b], Thomas J. Valone[c]

[a]*Department of Biology, California State University, Northridge, CA 91330-8303, USA*
[b]*National Park Service, Santa Monica Mountains National Recreation Area, 401 West Hillcrest Drive, Thousand Oaks, CA 91360, USA*
[c]*Department of Biology, St. Louis University, St. Louis, MO, USA*

Abstract

Roads, especially large highways, can have significant impacts on wildlife movement and survival. This is especially true for wide-ranging species, such as mammalian carnivores. Some of these impacts may be mitigated if wildlife can find and utilize passageways under highways. To determine if underpasses and drainage culverts beneath highways are used by wildlife as movement corridors, we monitored 15 such passages near Los Angeles, California using remotely triggered cameras and gypsum track stations. We found that passages were used by a variety of species, including carnivores, mule deer, small mammals, and reptiles. Many types of undercrossings were utilized, indicating that passages beneath highways, even when not originally designed for wildlife, can provide important safe avenues for animals to cross roads. For mammals of conservation concern, including native carnivores and deer, passage dimensions, surrounding habitat, and the extent of human activity were assessed to determine if these factors influenced passage use by these species. Our results show that while many native mammals used passages beneath highways, the presence of suitable habitat on either side of the passage was a particularly important factor predicting use. For deer and coyotes, passage dimensions were also important and should be considered with the presence of suitable habitat when wildlife passages are planned or evaluated. To increase the likelihood of utilization and to help prevent animals from crossing road surfaces, we suggest that simple improvements such as habitat restoration near crossing points and animal-proof fencing that serves to funnel wildlife to passages, can facilitate animal movement between fragmented habitats that are bisected by roads.
© 2003 Elsevier Ltd. All rights reserved.

Keywords: Wildlife corridor; Mammals; Carnivores; Habitat fragmentation; Culverts

1. Introduction

As roads and human development have extended into once pristine natural areas, habitat fragmentation has become an ever-increasing threat to the survival of many species (Wilcox and Murphy, 1985; Harris and Gallagher, 1989; Saunders et al., 1991). Perhaps most threatened are large mammals, such as carnivores and ungulates, that regularly move over great distances. It has been suggested that the adverse effects of habitat fragmentation by roads might be mitigated by constructing wildlife, or conservation, corridors (Soulé, 1991) connecting otherwise isolated patches of habitat

on opposite sides of roadways (Saunders and Hobbs, 1991; Beier and Loe, 1992). It is thought that drainage culverts, tunnels and freeway underpasses, though created for other purposes, may already serve this function (Noss, 1987a; Harris and Gallagher, 1989; Edelman, 1991; Soulé and Gilpin, 1991; Rodriguez et al., 1996; Rosenburg et al., 1997). However, few quantitative data are available on the extent to which such passages are used by wildlife (Simberloff et al., 1992). Likewise, the characteristics that promote and discourage the use of potential crossing points by wildlife—e.g., passage dimensions, surrounding habitat type, presence of fences, and the extent of nearby human activity—are poorly understood (Foster and Humphrey, 1995; Yanes *et al.,* 1995; Clevenger and Waltho 2000).

In California, especially in the southern coastal areas where urban sprawl has created a patchwork of developed and natural areas, determining the extent to which

* Corresponding author. Tel.: +1-805-370-2339.
E-mail address: ray_sauvajot@nps.gov (R.M. Sauvajot).

passages are used by wildlife has become a top conservation priority. In the vicinity of the Santa Monica Mountains National Recreation Area (SMMNRA) in western Los Angeles and eastern Ventura Counties, several relatively unspoiled natural regions, including three mountain ranges (Santa Monica, Santa Susana, San Gabriel), parts of two National Forests (Los Padres, Angeles) and the SMMNRA still support a rich diversity of vertebrate species. However, numerous multi-lane highways pass through the area, creating potential barriers between habitat patches. For this reason, it is widely acknowledged that habitat linkages are necessary to allow animals to cross major roadways between remaining patches of natural habitat (Lieberstein et al., 1987; Soulé, 1989; Santa Monica Mountains Conservancy, 1990; Edelman, 1991). In addition, information on wildlife movement relative to freeways in this area would be relevant for many other fragmented urban landscapes.

The purpose of this study was to obtain quantitative data on the extent to which passages beneath highways in this fragmented landscape are used by wildlife. Our specific objectives were: (1) to evaluate animal use of selected underpasses, tunnels, and drainage culverts that cross beneath three major highways; and (2) to assess characteristics of the passages most frequented by species of conservation concern, including native carnivores and mule deer, and domestic cats and dogs. As habitat fragmentation continues in areas occupied by native carnivores and deer, these species become increasingly threatened because they move over great distances to find food and mates, and to disperse. Carnivores are especially threatened because of their low population densities and large home range requirements. Domestic carnivores such as cats and dogs, on the other hand, can have adverse effects on wildlife through direct predation (Churcher and Lawton, 1987; Soulé et al., 1988), harassment, and the spread of disease. Thus, knowledge of passage attributes that can facilitate desired movement by deer and carnivores as well as possible use by non-native carnivores is a top conservation concern and has important management value. In addition, the limited data now available on whether or not species of conservation concern even utilize existing passages to cross roadways is of great interest among conservationists and land and transportation planners.

2. Study area and methods

2.1. Study area

The study was conducted along three major highways located on the eastern edge of Ventura County, California, just west of the San Fernando Valley and adjacent to the Los Angeles metropolitan area (Fig. 1). The three highways—US Highway 101, State Route 23, and US Highway 118—border the Simi Hills on the south, west, and north, respectively. US 101 and 118 act as potential barriers to animal movements to and from surrounding wilder regions, the Santa Susana Mountains
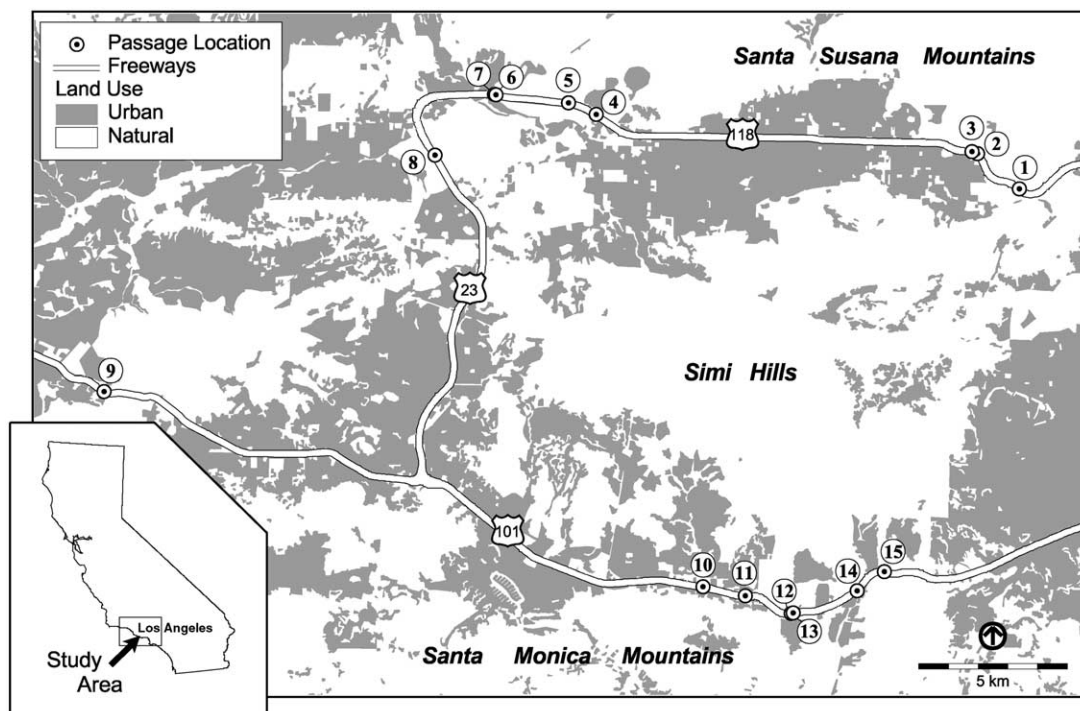

Fig. 1. Map showing natural habitat and urban development, highways and the 15 passages studies. Adjacent passages are indicated by a single point.

to the north and the Santa Monica Mountains to the south (Soulé, 1989; Santa Monica Mountains Conservancy, 1990; Edelman, 1991).

The region through which these highways pass is a complex of low hills and flat-bottomed valleys. The Simi Hills and the Santa Monica Mountains are a mixture of highly urbanized and relatively natural lands. In contrast, the Santa Susana Mountains consist of mostly intact natural landscapes, with urbanization encroaching along its fringes, and they link to the north and east to two extensive wild regions: the Los Padres National Forest in the western Transverse Mountain Range and the Angeles National Forest in the San Gabriel Mountains.

The natural areas support a diversity of biological communities, including chaparral vegetation (*Adenostoma fasciculatum, Ceanothus* spp., *Rhamnus ilicifolia*), coastal sage scrub (*Artemisia californica, Salvia leucophylla, Malosma laurina*), coast live oak (*Quercus agrifolia*) woodland, and riparian woodlands (*Salix lasiolepis, Platanus racemosa*).

2.2. Animal use

Along the three highways, 15 potential wildlife passages in the form of underpasses (surface roads or wide streams crossing under the highway), drainage culverts (square or pipe culverts) and livestock tunnels, were monitored (Fig. 1). Some of the potential crossing points had been previously identified as potential "wildlife corridors" (Santa Monica Mountains Conservancy, 1990; Edelman, 1991) but none was made specifically to facilitate wildlife movement. Other passages were identified from flood control maps provided by the Public Works agencies of Ventura and Los

Angeles Counties. Passage size varied considerably (Table 1). On average, square culverts were 97 m long, 4.2 m wide and 3.7 m high, pipe culverts were 176 m long, 2.6 m wide and 2.9 m high, and underpasses were 44 m long, 42 m wide and 5.2 m high.

Each passage was monitored for four consecutive days each month from 1 July 1999 through 30 June 2000, with the exception of passage 15. Passage 15 was filled with water during January and February at the height of the rainy season, and could not be monitored during that period. The order in which passages were sampled each month was determined randomly.

Two techniques were used to monitor animal use, remotely triggered cameras (Rappole et al., 1986; Carthew and Slater, 1991; York et al., 2001) and gypsum powder track stations (methods modified from Crooks and Soulé, 1999; Haas, 2000). Passive infrared trail monitoring units (TrailMaster TM550: Goodson and Associates, Inc., 10614 Widmer, Lenexa, KS 66215) were used at four passages (8, 12, 14, 15) where the probability of vandalism was judged to be minimal and where heavy water flow in the rainy season precluded monitoring animal tracks. Each unit consisted of an automatic flash camera triggered by the body heat or motion of an animal passing within 20 m and within a horizontal arc of 20° and a vertical arc of 4° of the infrared sensor. Sensors operated continuously, but were set to take only one photograph per minute. At each of the four passages with camera systems, at least three camera units were used to ensure adequate monitoring in the middle of the passage and at each entrance.

Where the probability of vandalism was judged high (passages 1–7, 9–11, 13), cameras were not used.

Table 1

Attributes of the 15 passages monitored in this study. Habitat type is the percentage of habitat within a 250-m semi-circle around both ends of each passage

Attributes	Tunnels, culverts and underpasses														
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Crossing type	□	⊞	◸	⊞	◸	□	□	⊞	□	◸	□	⊞	◸	□	⊞
Dimensions															
Length (m)	58.3	144.9	45.1	196.1	48.9	73.5	249.6	133.4	45.0	84.4	54.3	189.2	44.3	98.9	218.1
Width (m)	4.6	3.9	47.6	2.1	41.8	3.2	4.3	2.2	2.5	30.0	5.5	1.6	46.7	4.8	3.0
Height (m)	4.7	3.8	5.0	2.2	4.9	4.6	3.2	2.6	2.6	6.0	2.9	1.6	4.9	4.0	4.3
Cross-sect. area (m^2)	21.6	11.6	238.0	3.6	204.8	14.7	13.8	4.5	6.5	180.0	16.0	2.0	228.8	19.2	10.5
Habitat type (%)															
Natural	100	54	38	50	100	38	38	100	69	8	0	46	46	50	60
Landscaped	0	8	20	23	0	12	12	0	0	15	0	0	0	0	0
Developed	0	38	42	27	0	50	50	0	31	77	100	54	54	50	40
Human activity															
No. of crossings	120	46	331	0	38	49	2	0	0	482	17	0	491	0	0

Human activity includes all human crossings whether on foot, on horseback or by vehicle. Passage type: □ = square culvert/ tunnel; ⊞ = drainage culvert; ◸ = spanning bridge underpass.

Instead, passage use was monitored by placing three strips of agricultural gypsum powder across the floor of each passage to capture animal tracks. The strips of gypsum, each about 3 mm thick and 1 m wide, were laid across the entire width of each passage by sifting the powder through a mesh colander. We placed one strip in the middle of each passage and one at each entrance in order to detect both visits and crossings. As with the cameras, tracks in the gypsum were monitored for four days per month. Each day all tracks were identified (Murie, 1974), recorded and erased with a feather duster to prevent recount. We also recorded the direction of travel and, to further assist with species identification, the prints' length and width, and for canid and felid tracks, stride (the distance between two consecutive tracks) and straddle (the distance separating the outermost sides of the left and right track). To verify track identifications, one passage (8) was monitored simultaneously with both cameras and gypsum. All track identifications at this passage were in agreement with accompanying photographs.

From each set of tracks or photographs, we categorized the animal's use as: (1) a verified crossing, (2) a probable crossing, or (3) an assessment of the entrance only. When tracks or photographs of an animal were present at both ends of the passage and in the middle, the animal's use of the passage to traverse the width of the roadway was considered verified. When tracks or photographs were recorded at both end stations, but not in the middle, or at the middle station and at one of the ends, completion of the traverse was judged probable. In most such instances all tracks were in a single direction, suggesting that the animal had not turned back and that the missing tracks had been lost due to wind or human disturbance. When tracks or photographs were obtained at one end of a passage only, an animal was considered to have assessed the passage but not to have passed through it. Because our intent was to detect utilization and not to evaluate absolute levels of use by any particular species, we did not attempt to distinguish between individual animals. Hence, it is likely that some individuals were counted more than once.

2.3. Passage characteristics as predictors

For each passage, three dimensions (length, width, height), the nature of the surrounding habitat, and the amount of human activity were recorded as predictor variables for animal use (Table 1). From width and height, cross-sectional area of each passage was calculated. At each passage, photographs and tracks of humans, horses, bicycles, and other vehicles were also counted. Collectively, these served as a measure of human activity.

Habitat surrounding each passage was quantified by sampling within a 250-m semicircle around each entrance. For this purpose, habitat was placed into three categories: (1) natural, which consisted of intact vegetation (both native and naturalized); (2) developed or urban areas; or (3) landscaped, which consisted of human-altered areas without buildings, e.g. golf courses and landfills. For passages along US 101 and State Route 23, habitat type was determined from Digital Orthophoto Quarter Quadrangles (DOQQ), from which aerial percent coverage of each habitat category was determined. Because DOQQ coverage did not extend to US 118, Satellite Pour l'Observation de la Terre (SPOT) images were used to obtain the percent cover for passages along this freeway. Because some landscapes were being altered during the study period, at each site percentages were verified in the field by estimating the predominant habitat type (i.e. natural, developed, or landscaped) at 15° intervals within a 250-m semicircle surrounding each passage entrance. An overall percentage of each habitat category at the passage was then calculated by dividing the total number of observed dominant habitat types by 24 (the total number of bearings). Where percentages of the DOQQ and SPOT images differed from those obtained from field verifications, the percentages obtained in the field were used to determine habitat cover at the passage.

Before analyzing animal use data, we first searched for confounding associations among the various passage attributes using correlation analysis. Passage use by each species was approximated to a normal distribution via an arcsine square-root transformation. Spearman's rank correlation was used to quantify the relationship between the use of passages by wildlife and predictor variables. Low number of observations precluded statistical analyses for mountain lions. Where logical, analyses were conducted on records of several species grouped into classes, e.g. (a) large carnivores (coyotes, bobcats, and mountain lions) and (b) mid-sized mammals (raccoons, opossums, and striped and spotted skunks). Because sample sizes were small and non-parametric tests were used, we adopted $\alpha = 0.10$ as a measure of statistical significance.

3. Results

3.1. Animal use

During the year of study, 2723 detections were recorded as tracks and photos (Table 2). Of these records, 531 (19.5%) were of native large and mid-sized mammals, 1640 (60.2%) were of humans, 155 (5.7%) were of domestic animals, and 397 (14.6%) were of small mammals. Wild mammals known to have passed through one or more passages at least once included: deer mice (*Peromyscus* spp.), woodrats (*Neotoma* spp.), ground squirrels (*Spermophilus beecheyi*), cottontail rabbits

(*Sylvilagus auduboni*), opossums (*Didelphis virginianus*), striped skunks (*Mephitis mephitis*), spotted skunks (*Spilogale putorius*), raccoons (*Procyon lotor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), mountain lions (*Puma concolor*), and mule deer *(Odocoileus hemionus)*. For large and mid-sized mammals (excluding domestic species), we recorded 391 (73.6%) verified or probable crossings and 140 (26.4%) assessments of the entrance. For species of conservation interest, passage use varied between sites and species (Table 3). Raccoons were most commonly detected using passages and used all sites except one. Coyotes, bobcats, and domestic dogs and cats each used about half of the 15 sites studied. Deer and mountain lions were only detected at a few sites.

3.2. Passage attributes as predictors of wildlife use

There were four significant correlations between the various passage attributes. Length was negatively correlated with cross-sectional area ($r_s = -0.639$, $P < 0.01$).

Table 2
Nature and frequency of use of culverts, tunnels and underpasses, all passages combined

Species	Crossings			Investigations	Total records	Verified and probable crossings (as % of total records)
	Verified	Probable	Total			
Human	1332	36	1368	59	1427	95.9
Bike	156	12	168	5	173	97.1
Vehicle	36	0	36	0	36	100.0
Horseback	4	0	4	0	4	100.0
Total human activity	1528	48	1576	64	1640	96.1
House cat	24	10	34	25	59	57.6
Dog	57	8	65	18	83	78.3
Cow	12	0	12	1	13	92.3
Total domestic animals	93	18	111	44	155	71.6
Mountain lion	1	0	1	0	1	100.0
Bobcat	31	5	36	17	53	67.9
Coyote	49	10	59	12	71	83.1
Deer	26	0	26	2	28	92.9
Total large mammals	107	15	122	31	153	79.7
Raccoon	127	80	207	58	265	78.1
Opossum	17	7	24	5	29	82.8
Striped skunk	12	11	23	11	34	67.6
Spotted skunk	0	5	5	2	7	71.4
Cottontail rabbit	1	9	10	33	43	23.3
Total mid-sized mammals	157	112	269	109	378	71.1
Total rodents	133	106	239	158	397	60.2

Table 3
Frequency of passage use by species, including verified and probable crossings

Species	Passages															Total Passages Used
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	
Deer	2	0	0	0	9	0	0	0	0	0	0	0	15	0	0	3
Coyote	13	19	1	0	20	2	0	1	0	0	0	0	3	0	0	7
Bobcat	8	1	0	0	6	2	0	16	0	0	1	0	0	2	0	7
Mountain lion	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Raccoon	3	12	0	9	1	7	17	1	1	87	22	19	2	15	11	14
Opossum	0	1	5	0	0	7	2	1	5	1	0	2	0	0	0	8
Spotted skunk	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	1
Striped skunk	2	3	0	0	2	4	0	0	0	0	0	12	0	0	0	5
House cat	4	6	11	0	1	3	0	0	0	1	7	0	1	0	0	8
Domestic dog	9	4	36	0	7	3	0	1	0	0	1	0	4	0	0	8

Table 4
Spearman's rank correlation coefficient matrix for predictor variables and frequency of crossings through passages, probable and verified crossings combined

Species	Length	x.s.Area	Natural	Developed	Human activity
Coyote	−0.405	0.442	0.414	−0.454 *	0.553 **
Bobcat	−0.124	0.107	0.476 *	−0.462 *	−0.005
All large carnivores	−0.373	0.404	0.451 *	−0.442	0.372
Raccoon	0.523 **	−0.211	−0.559**	0.676 ***	−0.094
Opossum	−0.030	−0.176	−0.288	0.123	−0.055
Spotted skunk	0.247	−0.433	−0.094	0.281	−0.287
Striped skunk	0.068	−0.143	0.166	−0.117	0.122
All mid-sized mammals	0.447 *	−0.242	−0.665 ***	0.674 ***	−0.073
Deer	−0.523 **	0.551 **	0.367	−0.235	0.490 *
Rodents	−0.075	−0.291	0.528 **	−0.463 *	−0.114
Domestic dog	−0.571 **	0.619 **	0.172	−0.299	0.659 ***
House cat	−0.514 **	0.635 **	−0.318	0.154	0.765 ***

Statistically significant relationships are indicated with asterisks (*$P < 0.10$, **$P < 0.05$, ***$P < 0.01$).

Human activity was negatively correlated with length ($r_s = -0.531$, $P < 0.05$) and positively correlated with cross-sectional area ($r_s = 0.806$, $P < 0.01$). Not surprisingly, human activity was largely restricted to shorter passages with large cross-sectional areas (underpasses and tunnels) and was rarely associated with culverts. Because culverts are typically long and underpasses much shorter, the strong negative correlation between length and cross-sectional area was expected.

Three larger carnivore species—mountain lions, bobcats and coyotes—traversed the passages. Coyote use showed a significant positive correlation with human activity (Table 4). However, for both bobcats and coyotes, we observed negative relationships ($0.05 < P < 0.10$) between passage use and percentage of developed habitat, suggesting a tendency by these animals to avoid passages surrounded largely by developed habitat (Table 4). Moreover, for bobcats the relationship between passage use and percentage of natural habitat was positive and statistically significant. The single record of a mountain lion precluded a statistical test. For all three native carnivore species combined, the relationship between passage use and extent of natural habitat was again positive ($0.05 < P < 0.10$).

Raccoon use of the passages was negatively correlated with extent of natural habitat and positively correlated with both extent of developed habitat and with passage length (Table 4). No statistically significant relationships were found between passage attributes and activity of opossums or either of the two skunk species, presumably the result of small sample sizes. For all mid-sized mammals (raccoons, opossums, and skunks) passage length and passage use were positively correlated ($0.05 < P < 0.10$).

Mule deer only used three large passages and never used small passages, such as culverts, even though some small passages were large enough for their use. Mule deer use of passages was negatively correlated with passage length and positively correlated with cross-sectional area (Table 4). No statistically significant relationship was found between mule deer use of passages and habitat type. However, of the three sites used by deer, all were characterized by significant amounts of nearby natural habitat (Table 1).

For both domestic dogs and cats, the use of passages was negatively correlated with passage length and positively correlated with both cross-sectional area and the amount of human activity (Table 4). Corridor use by dogs and cats was not significantly related to habitat.

4. Discussion

Our data clearly demonstrate regular use of underpasses and drainage culverts beneath highways by wildlife, including species of conservation concern. We suggest that maintaining or modifying passages can be important for protecting native species in areas bisected by high-speed roadways. Although culverts are typically installed to accommodate water flow, installation of such passages solely for wildlife use may also be justified, particularly where no other passages exist and habitat is suitable. If this is done, consideration must be given to passage dimensions, especially if the passage is intended for use by deer. However, protecting suitable habitat in the vicinity of crossing points is especially important, particularly for larger carnivores and deer. In general, a culvert or underpass, regardless of its dimensions, is of little value as a wildlife corridor if it does not connect suitable habitat.

In this study, we demonstrated use of corridors by wildlife and not benefits associated with that use. Corridor use alone does not necessarily impart conservation

value, and some have suggested that corridors can even be detrimental to wildlife conservation efforts (Simberloff and Cox, 1987; Simberloff et al., 1992). However, because the species we monitored are susceptible to fragmentation impacts and because roadways within their habitats are significant sources of mortality (Ng, 2000; Riley et al., 2003), we believe that the ecological benefits of highway undercrossings will outweigh possible impacts in our study area.

A significant aspect of the corridor debate focuses on whether or not animals will actually use corridors, if they are provided (Simberloff and Cox, 1987; Noss, 1987b; Simberloff et al., 1992; Hess, 1994; Beier and Noss, 1998). Much recent empirical work has adopted an experimental approach and focused on small-bodied species (e.g. Dunning et al., 1995; Andreassen et al., 1996; Haddad, 1999; Haddad and Baum, 1999; Danielson and Hubbard, 2000). Our work, examining road undercrossing use by large-bodied species in natural landscapes, complements this literature by demonstrating that large and medium-sized carnivores, deer, and other species will regularly use passages beneath highways. Larger carnivores, specifically bobcats and coyotes, traversed passages of a wide variety of sizes, from the largest spanning bridge underpasses to the smaller pipe culverts (Table 3). Assuming that corridors do impart conservation value, these findings are important for conservation by clearly demonstrating wildlife use of underpasses.

Coyote use of passages was significantly and negatively correlated with development. At the same time, though, we also found coyotes most likely to use passages associated with high degrees of human activity. Indeed, we commonly recorded coyotes using passages that had trails or roads within them, and that were regularly frequented by people. However, encounters between humans and coyotes are probably limited, since coyotes are most likely to frequent the passages at times when humans are least likely to be there. In fragmented landscapes, coyotes are often seen in urban areas that are immediately adjacent to natural habitat (Atkinson and Shackleton, 1991; Rosmos, 1998; Sauvajot et al., 2000; Riley et al., 2003). Consequently, our findings probably reflect coyote prevalence on urban fringes and a willingness to use areas of human activity rather than an attraction to them.

We had one record of a mountain lion using passage 1. Although a single record does not allow us to make conclusions about habitat or dimensions, it documents the potential use of passages for facilitating movements of these animals. The numbers and movement patterns of mountain lions in the Los Angeles area are not well understood (but see Beier, 1993), and more information about the status and distribution of mountain lions in this region is critical to understand the effects of roads and habitat connectivity on this species.

Raccoons, opossums, and skunks are opportunistic species that live in a wide variety of habitats, including in suburbs and cities (Rosatte et al., 1990; Riley et al., 1998). These species may benefit from human activities, both because of the addition of anthropogenic food sources and the increased availability of water. In our study, raccoons were detected at the passages more frequently than any other wild mammal species and were more common in passages surrounded by human development than in those adjoining wild land. The prevalence of raccoons was in part because they actually used the passages as foraging habitat and not necessarily as movement corridors. Many raccoons were encountered in culverts that contained water and sometimes entire families were photographed foraging in the water.

Consistent with other studies (Reed, 1981; Foster and Humphrey, 1995; Crooks and Jones, 1998; Haas, 2000), we found that passage dimensions significantly influenced passage use by deer. All mule deer crossings occurred at spanning bridge underpasses with large cross-sectional areas. Although we found no statistically significant correlation between deer use and habitat, deer were only encountered at passages surrounded largely by natural habitat. Crooks and Jones (1998) also found deer using underpasses with more natural habitat and less residential development.

We found house cats using underpasses and culverts in or near urbanization. Thus, while underpasses may be used by native carnivores, they can also provide access for house cats which in turn may have deleterious impacts on other native species. For example, in areas of high human density, domestic animals, particularly house cats, have been associated with the decline and extinction of bird and small mammal populations in fragmented habitats (Soulé et al., 1988; Bolger et al., 1997; Crooks and Soulé, 1999).

Overall, our results indicate that underpasses, culverts, and other cross-highway structures facilitate wildlife attempting to cross major roads. We believe that such structures, even if not originally designed for wildlife, can be important parts of regional conservation strategies. We also observed numerous instances of animals being killed while attempting to cross road surfaces (Ng, 2000; Riley et al., 2003). To increase the likelihood of passage use by wildlife and to keep animals off roadways, we recommend installing animal-proof fencing to funnel animals away from road surfaces and into crossing structures. Although our results demonstrate that existing passages will be used, more effective crossing structures could certainly be developed if wildlife movement was the primary design objective.

Acknowledgements

the Preservation of the Santa Susana Mountains; and the University Corporation and Office of Graduate Research at California State University, Northridge. Logistic support, vehicles, and cameras were provided by the National Park Service, Santa Monica Mountains National Recreation Area (SMMNRA). Access to study passages was provided by the Rancho Simi Recreation and Parks District, California Department of Transportation (Caltrans), the Los Angeles and Ventura County Flood Control Districts, and the Simi Valley Landfill. We are extremely grateful for help provided by E. York, C. Haas, D. Jones, P. Schiffman, P. Wilson and by the many dedicated interns and volunteers of the National Park Service, SMMNRA: L. Lee, L. Kellogg, C. Thompson, M. Hanson, L. Bragg, L. Aschim, K. Asmus, J. Chraft, P. Roby, S. Breidenthal, A. Paden, and G. Pasrich. Finally, we acknowledge helpful comments on earlier drafts of this manuscript from two anonymous reviewers and from M. Schwartz.

References

Andreassen, H.P., Halle, S., Ims, R.A., 1996. Optimal width of movement corridors for root voles: not too narrow and not too wide. Journal of Applied Ecology 33, 63–70.

Atkinson, K.T., Shackleton, D.M., 1991. Coyote, *Canis latrans*, ecology in a rural urban environment. The Canadian Field-Naturalist 105, 49–54.

Beier, P., 1993. Determining minimum habitat areas and habitat corridors for cougars. Conservation Biology 7, 94–108.

Beier, P., Noss, R.F., 1998. Do habitat corridors really provide connectivity? Conservation Biology 12, 1241–1252.

Beier, P., Loe, S., 1992. A checklist for evaluating impacts to wildlife movement corridors. Wildlife Society Bulletin 20, 434–440.

Bolger, D.T., Alberts, A.C., Sauvajot, R.M., Potenza, P., McCalvin, C., Tran, D., Mazzoni, S., Soulé, M.E., 1997. Responses of rodents to habitat fragmentation in coastal southern California. Ecological Applications 7, 552–563.

Carthew, S.M., Slater, E., 1991. Monitoring animal activity with automated photography. Journal of Wildlife Management 55, 689–692.

Churcher, P.B., Lawton, J.H., 1987. Predation by domestic cats in an English village. Journal of Zoology 212, 439–455.

Clevenger, A.P., Waltho, N., 2000. Factors influencing the effectiveness of wildlife underpasses in Banff National Park, Alberta, Canada. Conservation Biology 14, 47–56.

Crooks, K.R., Jones, D., 1998. Monitoring Program for Carnivore Corridor Use in the Nature Reserve of Orange County. The Nature Reserve of Orange County (Unpublished Report).

Crooks, K.R., Soulé, M.E., 1999. Mesopredator release and avifaunal extinctions in a fragmented system. Nature 400, 563–566.

Danielson, B.J., Hubbard, M.W., 2000. The influence of corridors on the movement behavior of individual *Peromyscus polionotus* in experimental landscapes. Landscape Ecology 15, 323–331.

Dunning Jr., J.B., Borgella, J.R., Clements, K., Meffe, G.K., 1995. Patch isolation, corridor effects, and colonization by a resident sparrow in a managed pine woodland. Conservation Biology 9, 542–550.

Edelman, P., 1991. Critical Wildlife Corridor/habitat Linkage Areas between the Santa Susana Mountains, the Simi Hills and the Santa Monica Mountains. The Nature Conservancy (Report).

Foster, M.L., Humphrey, S.R., 1995. Use of highway underpasses by Florida panthers and other wildlife. Wildlife Society Bulletin 23, 95–100.

Haas, C.D., 2000. Distribution, Relative Abundance, and Roadway Underpass Responses of carnivores throughout the Puente-Chino Hills. MS Thesis, California State Polytechnic University, Pomona, CA. 110 pp.

Haddad, N.M., 1999. Corridor and distance effects on interpatch movements: a landscape experiment with butterflies. Ecological Applications 9, 612–622.

Haddad, N.M., Baum, K.A., 1999. An experimental test of corridor effects on butterfly densities. Ecological Applications 9, 623–633.

Harris, L.D., Gallagher, P.B., 1989. New initiatives for wildlife conservation: the need for movement corridors. In: Mackintosh, G. (Ed.), Preserving Communities and Corridors. Defenders of Wildlife, Washington DC, pp. 11–34.

Hess, G., 1994. Conservation corridors and contagious disease: a cautionary note. Conservation Biology 8, 256–262.

Lieberstein, T., Nava, K., Crother, J, Galieti, J., Morgenstern, E., Robinson, M., Bathker, C., 1987. Wildlife corridor design: A case study for Los Angeles and Ventura Counties. In: Hardy, D.F., McIntire, E. (Eds.), Part III in the series: biogeography and the zoo. California State University, Northridge, CA.

Murie, O.J., 1974. A field guide to animal tracks, second ed. Houghton Mifflin Company, Boston.

Ng, S.J. 2000. Wildlife use of underpasses and culverts crossing beneath highways in southern California. M.S. Thesis. California State University, Northridge. Northridge, CA. 58 pp.

Noss, R.F., 1987a. Protecting natural areas in a fragmented landscapes. Natural Areas Journal 7, 2–13.

Noss, R.F., 1987b. Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology 1, 159–164.

Rappole, J.H., Navarro-Lopez, D., Tewes, M., Everett, D., 1986. Remote trip cameras as a means for surveying nocturnal felids. In: Nocturnal mammals: techniques for study. Pennsylvania State University School of Forestry Research, pp. 45–52 (paper 48. p157).

Reed, D.F., 1981. Mule deer behavior at a highway underpass exit. Journal of Wildlife Management 45, 542–543.

Riley, S.P.D., Sauvajot, R. M., Fuller, T.K., York, E.C., Bromley, C., Kamradt, D.A., Wayne, R.K., 2003. Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. Conservation Biology 17, 566–576.

Riley, S.P.D., Hadidian, J., Manski, D.A., 1998. Population density, survival, and rabies in raccoons in an urban national park. Canadian Journal of Zoology 76, 1153–1164.

Rodriquez, A., Crema, G., Delibes, M., 1996. Use of non-wildlife passes across a high speed railway by terrestrial vertebrates. Journal of Applied Ecology 33, 1527–1540.

Rosatte, R., Power, M.J., MacInnes, C.D., Lawson, K.F., 1990. Rabies control for urban foxes, skunks, and raccoons. In: Davis, L.R., Marsh, R.E. (Eds.), Proceedings of the 14th Vertebrate Pest Conference, Sacramento, CA, 6–8 March, 1990. Univeristy of California, Davis, pp. 160–167.

Rosmos, J.S., 1998. Home Range, Habitat Use, and Movements of Coyotes in a Southern California Urban Environment. MS Thesis, Humboldt State University.

Rosenburg, D.K., Noon, B.R., Meslow, E.C., 1997. Biological corridors: Form, function, and efficacy. BioScience 47, 677–687.

Santa Monica Mountains Conservancy. 1990. Preserving the Critical Link: A Discussion of the Wildlife Corridor from the Santa Susana Mountains to the Santa Monica Mountains via the Simi Hills (Unpublished Report).

Saunders, D.A., Hobbs, R.J., 1991. Nature Conservation 2: The Role of Corridors. Surrey Beatty, Chipping Norton, Australia.

Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 18–32.

Sauvajot, R.M., York, E.C., Fuller, T.K, Kim, H.S., Kamradt, D.A., Wayne, R.K., 2000. Distribution and status of carnivores in the Santa Monica Mountains, California: preliminary results from radio telemetry and remote survey cameras. In: Keeley, J.E., Baer-Keeley, M.B., Fotheringham, C.J. (Eds.), Second interface between Ecology and Land Development in California. US Geological Survey, Sacramento, CA, pp. 113–123.

Simberloff, D., Cox, J., 1987. Consequences and costs of conservation corridors. Conservation Biology 1, 63–71.

Simberloff, D., Farr, J.A., Cox, J., Mehlman, D.W., 1992. Movement corridors: Conservation bargains or poor investments? Conservation Biology 6, 493–504.

Soulé , M.E., 1989. USDI-National Park Service Proposed Land Exchange: Wildlife Corridors. Envicom Corporation (Report. 18-332-101).

Soulé, M.E., 1991. Theory and Strategy. In: Hudson, W.E. (Ed.), Landscape Linkages and Biodiversity. Island Press, Washington DC, pp. 91–104.

Soulé, M.E., Gilpin, M.E., 1991. The theory of wildlife corridor capability. In: Saunders, D.A., Hobbs, R.J. (Eds.), Nature conservation 2: the roles of corridors. Surrey Beatty and Sons, Chipping Norton, NSW, Australia, pp. 3–8.

Soulé, M.E., Bolger, D.T., Alberts, A.C., Sauvajot, R.M., Wright, J., Sorice, M., Hill, S., 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology 2, 75–92.

Wilcox, B., Murphy, D., 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist 125, 879–887.

Yanes, M., Velasco, J.M., Suárez, F., 1995. Permeability of roads and railways to vertebrates: the importance of culverts. Biological Conservation 71, 217–222.

York, E.C., Moruzzi, T.L., Fuller, T.K., Organ, J., Sauvajot, R.M., DeGraff, R.M., 2001. Description and evaluation of an inexpensive remote camera and triggering system for monitoring carnivores. Wildlife Society Bulletin 29, 1228–1237.