Urban Ecosystems, 1998, **2**, 279–297

Patterns of human disturbance and response by small mammals and birds in chaparral near urban development

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We report on the extent of disturbance (including habitat alteration and road and trail proliferation) in chaparral near urban development and analyze the effects of disturbance on small mammal and resident bird species. Disturbance patterns were evaluated in a 6700 ha study area in southern California; effects on mammals and birds were investigated by analyzing relationships between vegetation structure and animal species richness and abundance. Disturbance was prevalent throughout the study area and included extensive human-altered habitat (from past human activities such as vegetation clearing, human-caused fires, refuse dumping, and vegetation trampling) and 157 km of roads and trails. A nonsignificant trend was found between human-altered habitat and proximity to development, but human-altered habitat was significantly associated with roadway proximity. Trails were also more frequent near urban development and roads. Small mammals responded strongly to disturbance-related vegetation changes, while birds showed little or no response. Mammals endemic to chaparral vegetation were less diverse and abundant in disturbed sites, whereas disturbance-associated species increased in abundance. Close proximity of urban development to natural areas resulted in alteration of natural habitat and proliferation of roads and trails. Variation in life history traits between birds and mammals may affect response to disturbance and influence persistence if disturbance continues. Conservation efforts must recognize the potential for habitat damage and associated declines in native animal species caused by disturbance near urbanization and implement strategies to reduce these threats.

Keywords: urban edge; habitat disturbance; small mammals; birds; chaparral

Introduction

Land conversion, habitat fragmentation, and human activities continue to increase in and around natural communities (Murphy, 1988; Lubchenco *et al*., 1991; Hannah *et al*., 1994). As a consequence, natural habitats often exist as only small, isolated patches. Because human activities and land uses may facilitate

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the movement of human impacts into previously undisturbed sites (Janzen, 1986), the protection of native biota in these human-altered landscapes will require an understanding of the interactions between human-modified lands and adjacent natural areas (Schonewald-Cox, 1988; Saunders *et al*., 1991).

A number of effects and mechanisms have been proposed that may influence natural areas near human development. For example, natural areas may be subjected to the introduction of exotic species from surrounding areas (MacDonald *et al*., 1988), invasion by competitors, nest predators, or nest parasites (Brittingham and Temple, 1983; Wilcove, 1985; Sieving, 1992; Paton, 1994), and the alteration of microclimatic conditions near clear-cut lands (Lovejoy *et al*., 1986; Chen *et al*., 1993). These influences, often generally referred to as edge effects (Lovejoy *et al*., 1986; Harris, 1988) or generated edge effects (Schonewald-Cox and Bayless, 1986; Schonewald-Cox, 1988), can reduce the conservation value of remaining natural areas by negatively affecting the native biota within (Noss, 1987; Murcia, 1995). At the same time, the consequences of edge effects can vary widely depending on the type of effect (e.g., microclimatic, interspecific), the vegetation community, and the species of interest (Murcia, 1995; Buechner and Sauvajot, 1996). In general, effects become less apparent with increasing distance from the edge.

One important category of interactions between natural lands and nearby human developments is direct habitat alteration that can occur in natural areas exposed to human activities (Buechner and Sauvajot, 1996). The proximity of natural lands to human development facilitates access and opportunities for humans to disturb natural habitats. Disturbances can include increased fire frequencies (Sauvajot, 1995), damaging vegetation management practices, trail proliferation (Bolger *et al*., 1997a), off-road vehicle use (Boyle and Samson, 1985), poaching and plant collecting (Dawson, 1996), refuse dumping, and vegetation trampling (Schonewald-Cox and Buechner, 1992). Although these influences may occur along edges of human development, they may also extend into the interiors of natural areas following access routes or occurring near sites of concentrated human activity (Buechner and Sauvajot, 1996). Although the ecological consequences of human disturbance near development may be severe, only limited research has addressed disturbance changes along a gradient and how these effects influence animal communities (Dickman and Doncaster, 1987; Matson, 1990; Blair, 1996).

Effects of human-caused disturbance on natural areas of southern California and other Mediterranean-type ecosystems are important because development is rapidly fragmenting sensitive ecological communities (Keeley, 1993; Hannah *et al*., 1995). Expansive natural areas have become altered, fragmented, and surrounded by dense urban development (Scott, 1995), and a number of the wildlife species that depend on these areas are becoming rare, threatened, or endangered (Dobson *et al*., 1997). In addition, otherwise widely distributed chaparral small mammals and resident birds are prone to extinction in urban-isolated habitats and may be sensitive to human disturbance effects (Soulé *et al*., 1988; Soulé *et al*., 1992; Bolger *et al*., 1997a). Protection of native species in rapidly developing urban/wildland interface areas requires evaluating the spatial extent and ecological influence of human-caused habitat disturbances in remaining open space.

This study reports on patterns of human-caused habitat disturbance in chaparral near urban development in the Santa Monica Mountains of southern California and analyzes the effects of this disturbance on small mammals and resident birds. Specific objectives were (1) to describe the extent of human-caused disturbance in a specific study area near urban development; (2) to analyze relationships between disturbance patterns and proximity to urban development and public roadways; (3) to evaluate the effects of habitat disturbance on the richness and abundance of small mammals and resident birds; and (4) to assess the implications for conservation management.

Methods

Study area

We conducted our research within a 6700 ha study area in the Santa Monica Mountains of southern California (Fig. 1). Specific study area boundaries for disturbance analysis were defined by identifying

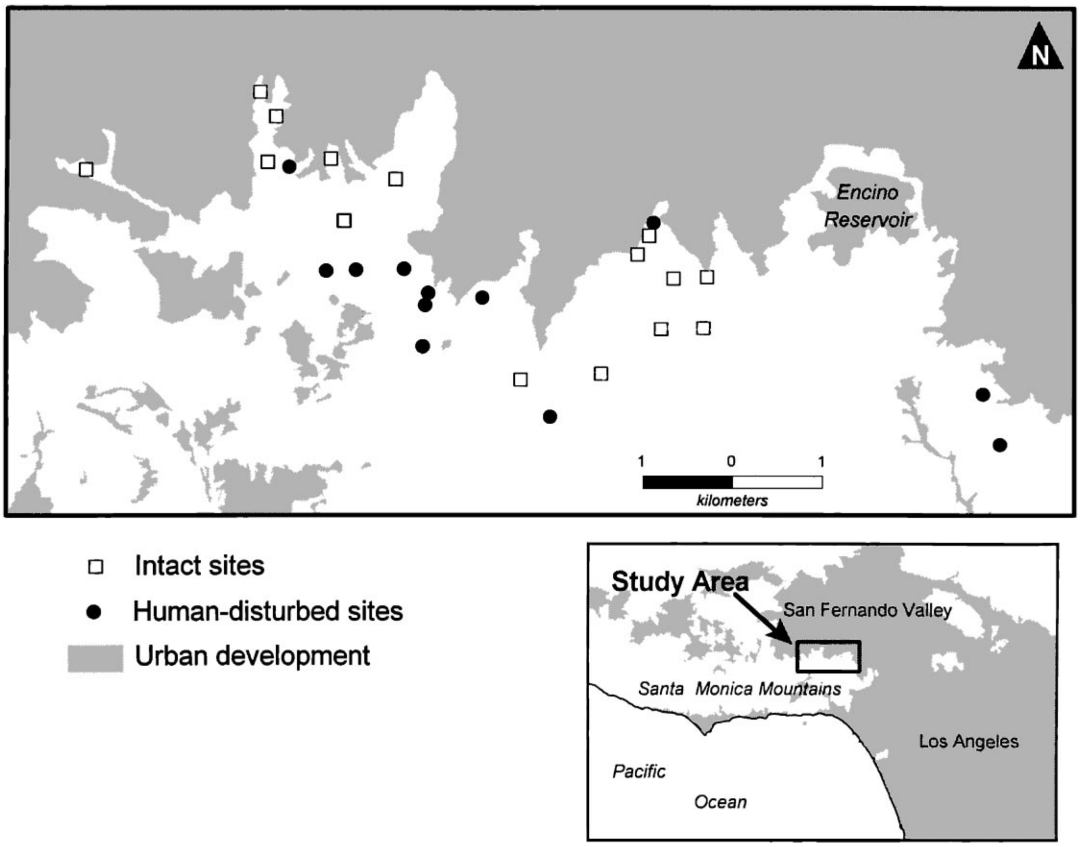


Figure 1. Location of study area and 27 sample sites in the Santa Monica Mountains of southern California.

the largest rectangular area within which we could obtain appropriate aerial photography data and which contained all 27 vegetation and animal sample sites (see below). Within the study area, urban development immediately abutted open space (i.e., nondeveloped areas) along clearly identifiable boundaries. Within the 6700 ha study area, 3360 ha included undeveloped open space, much of it protected as public park land. Substantially more natural habitat (toward the south) and urban development (toward the north) are contiguous with the study area.

Open space in this study area was comprised primarily of chaparral habitat dominated by several species of shrubs including chamise (*Adenostoma fasciculatum*), black sage (*Salvia mellifera*), and laurel sumac (*Malosma laurina*). Human disturbances altered portions of the natural habitat, resulting in patches of modified habitat interspersed within areas of intact chaparral. The disturbed areas consisted of a variety of cover types including recovering chaparral shrubs, exotic annual forbs and grasses (e.g., *Brassica* spp., *Avena* spp., and *Bromus* spp.), disturbance-associated shrub species (e.g., *Lotus scoparius*), and bare ground.

Patterns of human disturbance

To evaluate patterns of human disturbance, we identified and mapped disturbed areas that contained reduced native shrub cover and extensive bare ground using 1:9600 scale 1992 true color aerial photographs. We also mapped human-constructed trails and vehicle roadways within the study area. Patches of disturbed habitat were identified based on knowledge of past human uses of the area and by visually inspecting vegetation conditions from aerial photographs and site visits. If necessary, we visited sites to confirm that disturbances were human rather than naturally occurring (e.g., landslides, native grasslands, and other natural features were not mapped). Human disturbance mechanisms included vegetation clearance for fire protection, off-road vehicle use, increased fire frequencies, refuse dumping, and general vegetation trampling from heavy use. Human-constructed trails were divided into two categories: single-track trails up to three m wide and double-track trails wider than three m. We also mapped public park boundaries, and land use and ownership in the study area. Data were digitized at 1:9600 scale and entered into Arc/Info geographic information system (GIS) software (Environmenal Systems Research Institute, Inc., 1995, Revision 7.0.3).

We used GIS to calculate the number and area of disturbed patches, total lengths of roads and trails, and distribution of disturbed features with respect to land cover categories. We used log-liklihood ratio goodness of fit tests to statistically compare these variables between land cover categories. To assess relationships of human disturbance and trail frequency with respect to urban development and roadway proximity, we combined GIS analyses with statistical techniques. Seven successive 200 m buffer zones were established from urban development and public road edges (where chaparral habitat begins), along with an eighth buffer zone 1400 m or more from the edge to encompass the remainder of the study area (i.e., buffer zones were 0–200 m, 200–400 m, etc., up to 1400+ m from urban and road edges). We calculated the percentage of disturbed area and the frequency of trail length (length per unit area) within each of these buffer zones. Pearson product moment correlations were then used to statistically assess relationships of disturbed areas and trail length to distances from urban development and road edges. Although correlation analyses do not imply cause and effect relationships, they can indicate trends associated with such relationships. When needed, arcsine transformations ($Y' = \arcsin(Y)^{-1}$) were applied to percentage data (Zar, 1984, p. 239).

Effects of disturbance on small mammals and birds

We chose small mammals and year-round resident birds as focal species because their year-round dependence on local resources and relatively short generation times may lead them to respond rapidly to human disturbance. In addition, some bird and small mammal species may be sensitive to edge effects and habitat fragmentation (Gates and Gysel, 1978; Wilcove, 1985; Mills, 1995; Friesen *et al*., 1995), particularly small mammals and resident birds in southern California chaparral (Soulé *et al*., 1988; Soulé *et al*., 1992; Bolger *et al*., 1997a; Bolger *et al*., 1997b).

Small mammal species included 10 native chaparral rodents and three rodent species often associated with more open or disturbed areas (Table 1). Bird species included 15 year-round residents, ranging from chaparral dependents to urban associates (Table 1). Although several species of nonnative birds and small mammals are known to occur in nearby urban areas, the only nonnative species encountered in the study area during sampling was the rock dove (*Columba livia*).

To evaluate the effects of disturbance on small mammals and birds, we censused species in 27 sites across undeveloped open space in the study area (Fig. 1). Fifteen sites were located in intact chaparral and 12 sites were located in areas that had been disturbed to varying degrees by past human activities. We identified specific site locations using a stratified random procedure to ensure that locations were broadly distributed across the study area and at varying distances from the urban edge (Sauvajot, 1997). To ensure that sites exhibited similar geographic and potential vegetative characteristics, we located all sites along north–south ridge line trails within similar chaparral. Sites were limited to lands available for study (usually public lands).

We sampled small mammals, birds, and vegetation in each site from July through early September, 1992. Sampling dates were randomized to control for potential within-season variation. Chaparral rodents were

Table 1. Small mammal and year-round resident bird species studied[a]

Scientific name	Common name
Chaparral mammal species[b]	
Peromyscus boylii	Brush mouse
Peromyscus californicus	Parasitic (California) mouse
Peromyscus truei	Piñon mouse
Peromyscus maniculatus	Deer mouse
Neotoma fuscipes	Dusky-footed woodrat
Neotoma lepida	Desert woodrat
Perognathus californicus	California pocket mouse
Disturbance-associated mammal species	
Microtus californicus	California meadow vole
Reithrodontomys megalotus	Harvest mouse
Dipodomys agilis	Pacific kangaroo rat
Chaparral bird species[c]	
Callipepla californica	California quail
Thryomanes bewickii	Bewick's wren
Chamaea fasciata	Wrentit
Toxostoma redivivum	California thrasher
Pipilo maculatus	Spotted towhee
Other resident bird species	
Columba livia	Rock dove
Zenaida macroura	Mourning dove
Calypte anna	Anna's hummingbird
Aphelocoma californica	Western scrub-jay
Corvus corax	Common raven
Baeolophus inornatus	Oak titmouse
Psaltriparus minimus	Bushtit
Mimus polyglottos	Northern mockingbird
Pipilo crissalis	California towhee
Carpodacus mexicanus	House finch

[a]Nomenclature follows Jameson and Peeters, 1988; American Ornithologists' Union, 1998.
[b]Differentiation between chaparral and disturbance-associated mammal species based on habitat preferences in California chaparral (see Jameson and Peeters, 1988; Quinn, 1990).
[c]Differentiation of chaparral bird species based on habitat preferences in California chaparral (see Garrett and Dunn, 1981; Ehrlich *et al*., 1988; Soulé *et al*., 1988).

sampled using mark–recapture techniques (Davis, 1982). Fifty Sherman live traps ($7.5 \times 9 \times 23$ cm) were baited with peanuts and set in two parallel trap lines 150 m long and 10 m apart, with 25 traps spaced 6 m apart along each trap line. Each site was sampled on five consecutive nights, with individual animals marked using nontoxic permanent markers and released at the site of capture. Small mammal relative abundance at each site was estimated from the total number of individuals captured at a site (i.e., the trap-revealed population or minimum number known alive). For the study overall, 6750 small mammal trap-nights were logged in 1992.

We surveyed resident birds within each site using transect counts (Emlen, 1971). A trained observer walked a 150-m transect recording all bird species observed by sight and call during a 20-minute sampling period. Observations were limited to birds detected within 50 m of either side of the observer. Birds were surveyed on five consecutive mornings between 7:00 and 9:00 a.m. To control for potential biases between observers, individual bird surveys were randomized between different observers across sites and mornings.

We estimated the relative abundance of birds as the sum of the maximum number of individuals for each species observed in one day at each site over the five-day sampling period.

Line point methods (Heady *et al*., 1959) were used to measure vegetation structure and composition at each site. We sampled fifty points spaced 1.5 m apart using a range pole along two 150 m parallel transects. We determined total vegetation cover, woody vegetation cover, forb and grass cover, mean vegetation height, woody species richness, and woody cover volume (% cover of woody vegetation $*$ mean height of woody vegetation) for each site. Vegetation data were used as indicators of the effects of disturbance on habitat and, in combination with the animal data, to assess the effects of disturbance on small mammals and birds.

Pearson product moment correlation analyses were used to statistically evaluate relationships between vegetation structure measures (i.e., disturbance indicators) and animal richness and abundance. Although many other factors in addition to vegetation structure may be associated with or affect animal communities (see below), we felt that a correlative analysis was appropriate for investigating the important variable of habitat structure. Because a continuous range of vegetation structure occurred between sites (see below), we combined intact and human-altered sites for correlation analyses. In addition, prior to analysis, seven mammal and five bird species were categorized as chaparral species, with a preference for intact chaparral (Table 1). Three species of small mammals were categorized as disturbance-associated, with a preference for disturbed or open habitats. Ten species of birds are commonly known from chaparral habitats and urban areas and were therefore differentiated from the chaparral species.

We tested simultaneous correlation hypotheses between single measures of animal richness and abundance and multiple measures of vegetation structure (e.g., mammal species richness vs., woody cover, forb and grass cover, vegetation height). A sequential Bonferroni adjustment was used for between-group comparisons (Miller 1966; Holm, 1979; Rice, 1989). Specifically, each group of simultaneous comparisons between one animal richness or abundance variable and several measures of vegetation structure was considered a single family of tests with a group-wide significance level (alpha) of 0.05. To carry out the test, p-values for the family of tests were ranked from smallest to largest. If the smallest p-value (p_1) was $< 0.05/k$ (where $k =$ the number of simultaneous tests), then that p was considered significant at the family-wide alpha-level of 0.05. If p_1 was significant, the second smallest p-value (p_2) was considered significant if $p_2 < 0.05/(k-1)$. If p_2 was significant, the third smallest p-value (p_3) was considered significant if $p_3 < 0.05/(k-2)$, and so forth. If any inequality was not met, then that test was declared insignificant and all larger p-values were also considered insignificant at the family-wide alpha-level of 0.05.

Results

Patterns of human disturbance

Human habitat disturbance was prevalent throughout the study area (Fig. 2). In particular, across the 3360 ha of undeveloped open space, 256 ha (7.6%) were composed of human-altered habitat. Of this disturbed area, 138 ha occurred on “protected” park land, or 9.7% of all park land in the study area, and undeveloped open space was intersected by more than 157 km of roads and trails, including 77.6 km of single-track trails, 58.4 km of double-track trails, and 21.8 km of publicly accessible vehicle roadways (road lengths in developed areas were not included). Overall, a substantial human presence was apparent in and around remaining habitat, with over half of all open space located ≤ 600 m from urban development, roads, and trails.

Most disturbed patches were less than one ha, but one patch was nearly 80 ha in size (Fig. 2). Average patch size was 4.13 ha (SD $= 10.5$ ha, $N = 62$). Disturbed patches were variable in shape, but were often characterized by extensive edges relative to patch interiors. Disturbed areas also contained significantly greater ($p < 0.001$) frequencies of all types of roads and trails (Fig. 3).

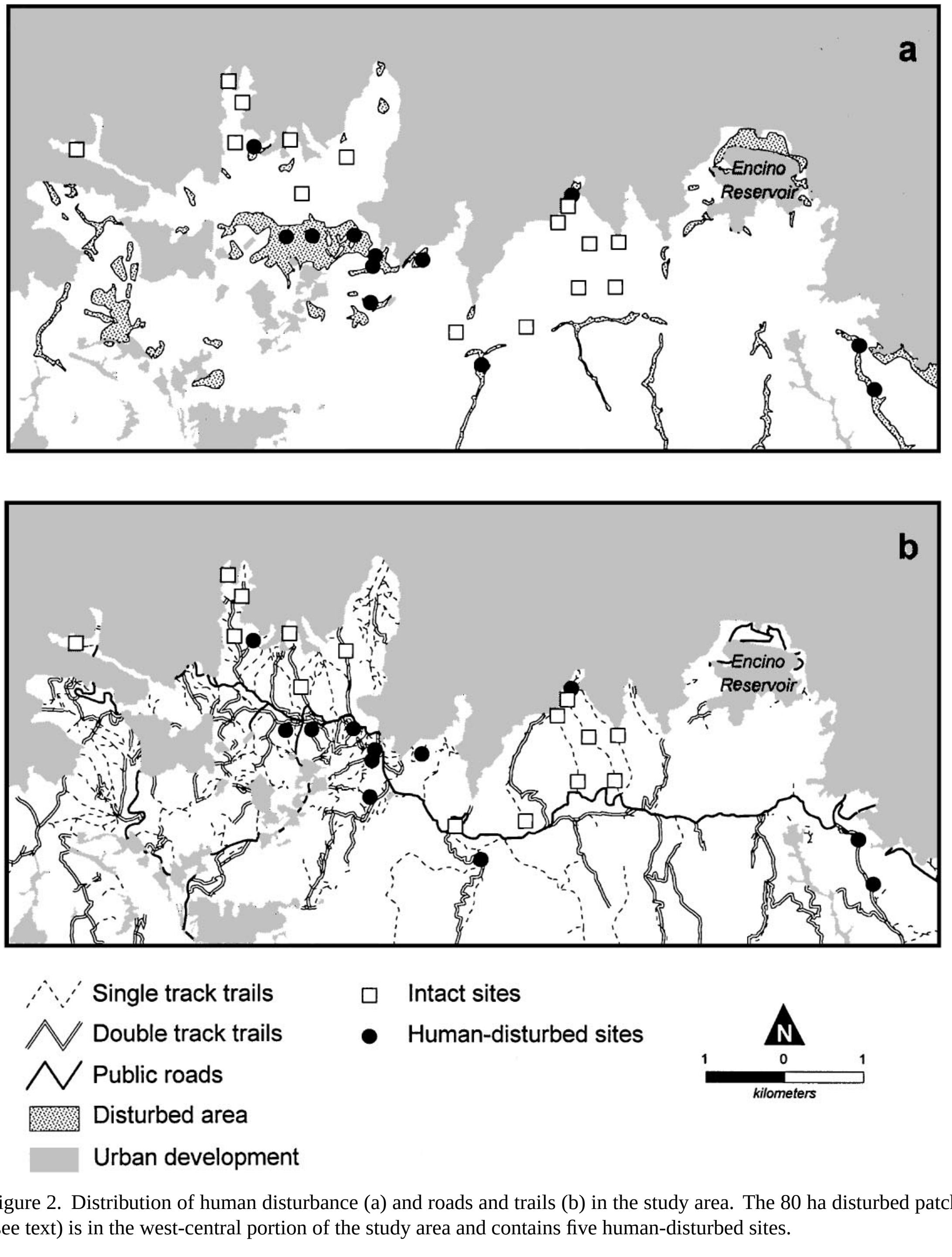


Figure 2. Distribution of human disturbance (a) and roads and trails (b) in the study area. The 80 ha disturbed patch (see text) is in the west-central portion of the study area and contains five human-disturbed sites.

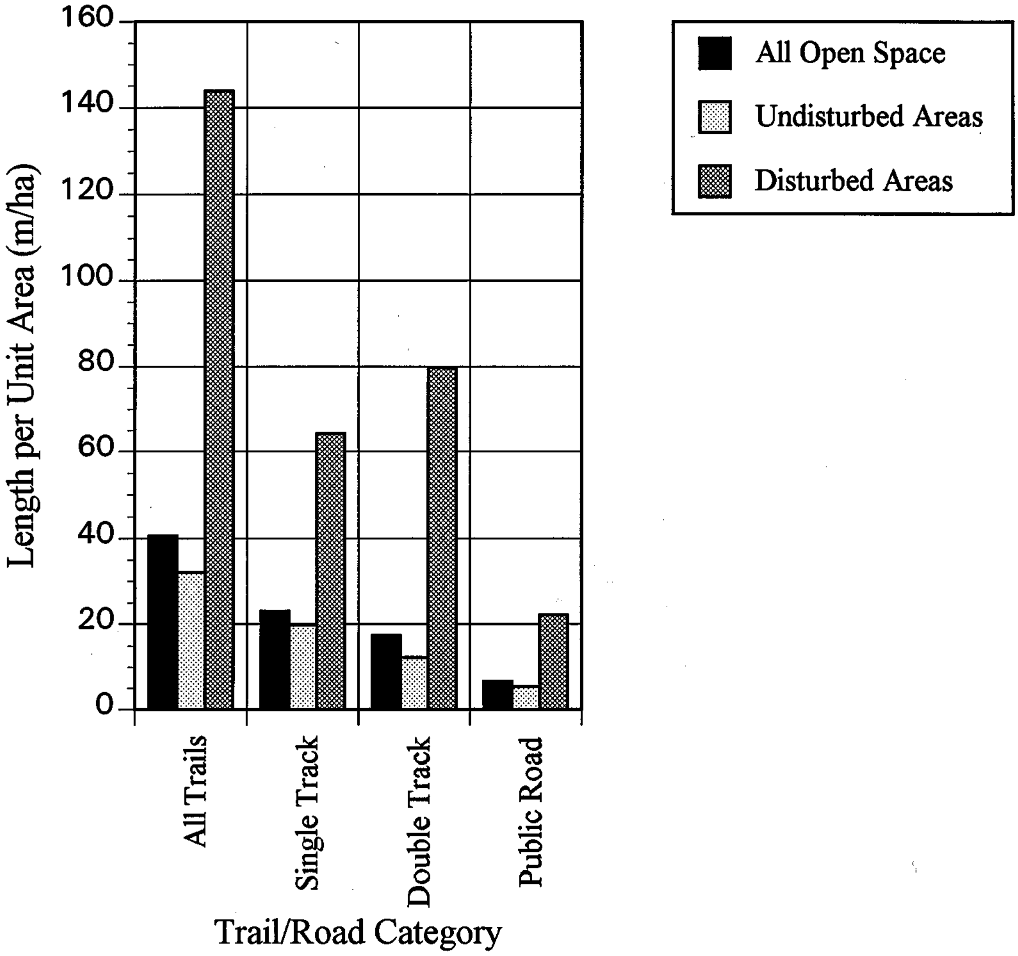


Figure 3. Length per unit area of trails and roads within all undeveloped open space, undisturbed open space, and human-disturbed open space in the study area. Categories include all trails combined, single-track trails less than three m wide, double-track trails wider than three m, and publicly accessible vehicle roadways. Comparisons are significant for all categories ($p < 0.001$, log-likelihood ratio goodness of fit tests).

Human disturbance was not significantly correlated with urban development (Fig. 4a). Nevertheless, a trend is apparent suggesting that human disturbance occurred more frequently within 400 m of an urban edge. Beyond 400 m, the frequency of disturbed habitats was variable, with some disturbed areas over 1400 m away from development (e.g., close to 4% of the study area greater than 1400 m from urban development was human-altered habitat). Overall, it appeared that while most disturbance was concentrated closer to the edge, low levels of disturbance occurred regardless of the distance from development.

A clear relationship was found between the amount of disturbed habitat and proximity to the roadways (Fig. 4b). Disturbance dropped off steadily to 600 m from the edge and remained fairly constant beyond this distance threshold. In areas > 600 m, a fairly constant level of disturbance ($\sim$ 2.5%) was found, with no obvious increasing or decreasing trend.

Similar analyses were conducted for trail frequencies in the study area (Fig. 5). All trails combined and single-track trails were distributed significantly closer to urban development than further away

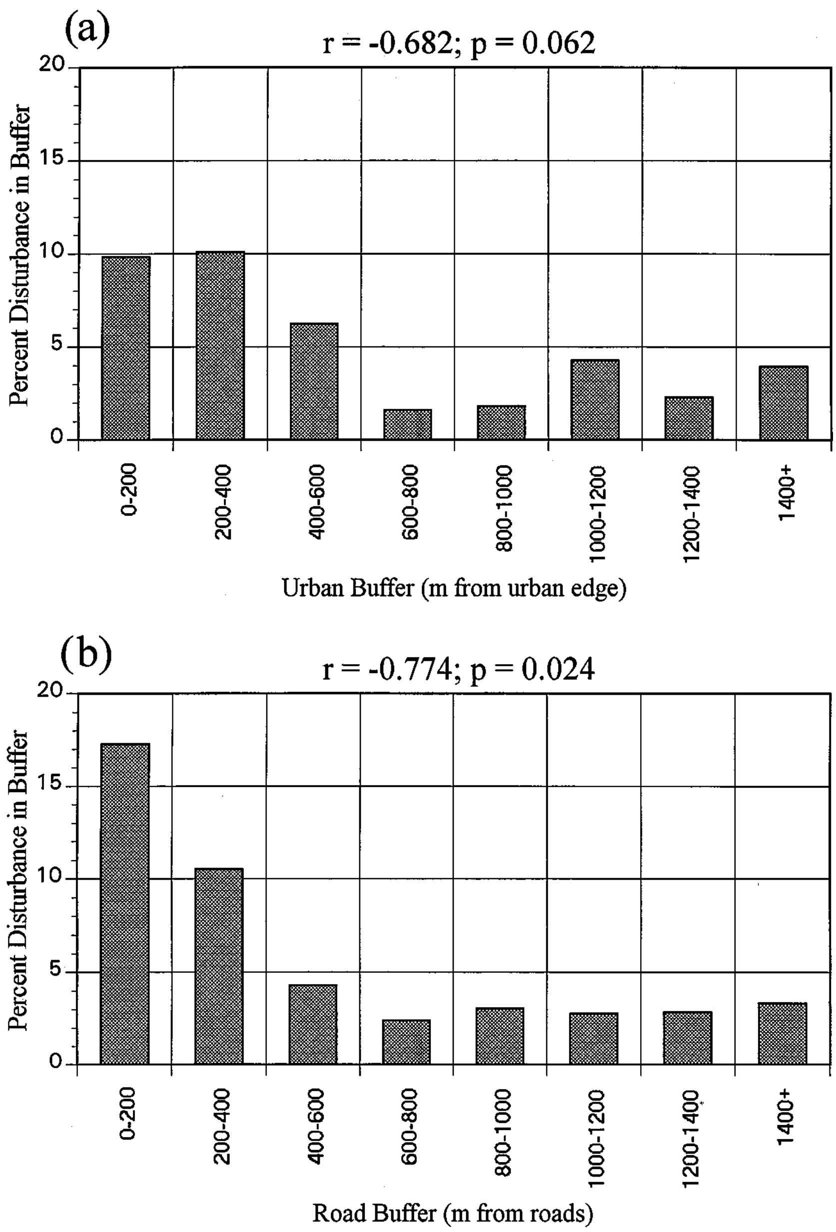
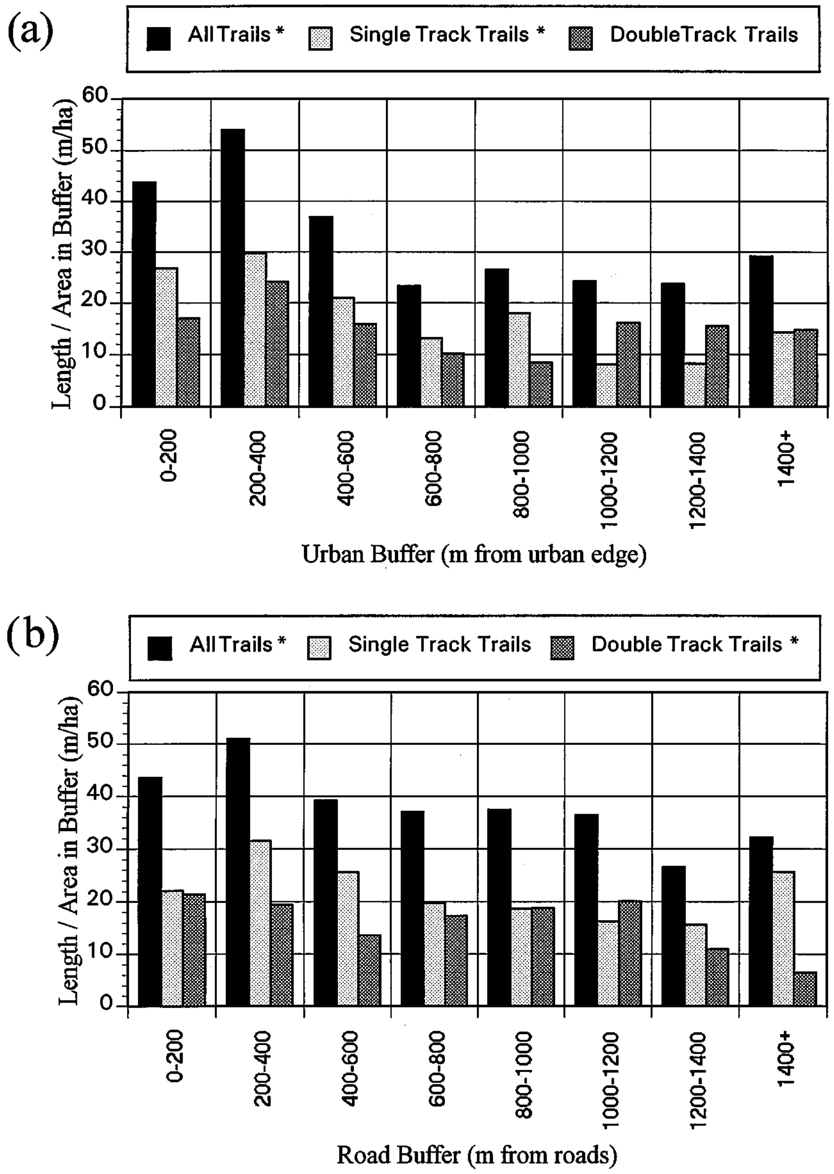


Figure 4. Percentage of disturbed area in the study area within successive 200 m buffer zones from the urban edge (a) and publicly accessible vehicle roadways (b). Each bar indicates the percentage of specified buffer area composed of human habitat disturbance. 1400+ buffer includes all open space in the study area greater than 1400 m from urban development (a) or roads (b). Pearson correlation coefficients and p-values are indicated. Percentage data were arcsine transformed prior to analysis. (Roads within urban areas are not included.)



* Statistically significant ($p < 0.05$).

Figure 5. Length per unit area of trails in the study area within successive 200 m buffer zones from the urban edge (a) and publicly accessible vehicle roadways (b). Each bar indicates m/ha of trail within the specified buffer for all trails combined, single track trails, and double track trails. 1400+ buffer includes all open space in the study area greater than 1400 m from urban development (a) or roads (b). (Roads within urban areas are not included.)

Table 2. Means ± SD of vegetation structure measurements for sample sites and t-test results between undisturbed and human-disturbed sites

Vegetation measure	All sites	Undisturbed sites	Disturbed sites	t	p-value
Total cover (%)	91.7 ± 10.8	95.6 ± 3.81	86.8 ± 14.5	2.06	0.062
Woody cover (%)	63.7 ± 33.5	89.3 ± 7.92	31.7 ± 23.7	8.08	<0.0001
Forb & grass cover (%)	40.5 ± 31.1	20.5 ± 19.3	65.5 ± 24.4	−5.22	<0.0001
Vegetation height (m)	0.921 ± 0.503	1.27 ± 0.370	0.480 ± 0.205	7.07	<0.0001
Woody spp. richness	7.26 ± 3.05	9.07 ± 2.37	5.00 ± 2.17	4.63	0.0001
Woody cover volume[a]	81.2 ± 59.5	126 ± 36.8	24.5 ± 18.0	9.43	<0.001

[a]Woody cover volume = (% cover of woody vegetation)∗(mean height of woody vegetation [m]).

($r = -0.748$; $p = 0.033$; and $r = -0.829$; $p = 0.011$); however, double-track trails were not significantly associated with urban proximity ($r = -0.369$; $p = 0.368$). For road proximity, all trails combined were distributed significantly closer to roads ($r = -0.842$; $p = 0.009$), as were double-track trails ($r = -0.708$; $p = 0.049$); the relationship for single-track trails, however, was not significant ($r = -0.449$; $p = 0.264$). In summary, whereas trails overall were more likely to occur closer to urban development and roadways, single-track trails occurred more often near urban edges, whereas double-track trails occurred closer to roadways.

Effects of disturbance on small mammals and birds

Human activities modified chaparral vegetation in a fairly predictable manner. Although total vegetation cover was not significantly different between disturbed and undisturbed sites, vegetation structure varied significantly: disturbed areas had substantially less woody vegetation cover, more forb and grass cover, lower average vegetation height, less woody species richness, and lower woody cover volume (Table 2). Disturbed areas had lower heights and less cover (Fig. 6), but a continuum of vegetation variation also existed between disturbed and undisturbed sites. Therefore, all 27 disturbed and undisturbed sites were combined in correlation analyses between animal data and vegetation structure measures.

Small mammals responded strongly to changes in vegetation structure (Table 3). This was particularly true when chaparral species and disturbance-associated species were analyzed separately. Although total species richness was not associated with vegetation structure, chaparral species richness was strongly related to all measures of vegetation structure. Disturbance-associated species richness exhibited opposite but statistically insignificant effects. Total small mammal abundance also was significantly associated with most measures of vegetation structure, although chaparral species and disturbance species showed opposite effects. Overall, chaparral mammal richness was less and abundance reduced in the more disturbed sites. These effects were reversed for mammals preferring disturbed habitats.

These patterns are consistent with analyses of small mammal richness and abundance and woody cover volume (Fig. 7). Chaparral mammal richness and abundance increased significantly with higher levels of woody cover volume, whereas disturbance-associated mammals showed opposite effects. Again, higher levels of disturbance, which reduces woody cover volume, negatively affected chaparral mammals but favored species preferring open or disturbed habitats.

Relationships for resident birds contrast sharply with those found for small mammals (Table 3). For bird species, the only significant correlation was a negative relationship between total bird abundance and forb and grass cover. Similar results were found in analyses of bird richness and abundance and woody cover volume (Fig. 8). For both chaparral birds and all species combined, no significant relationships occurred.

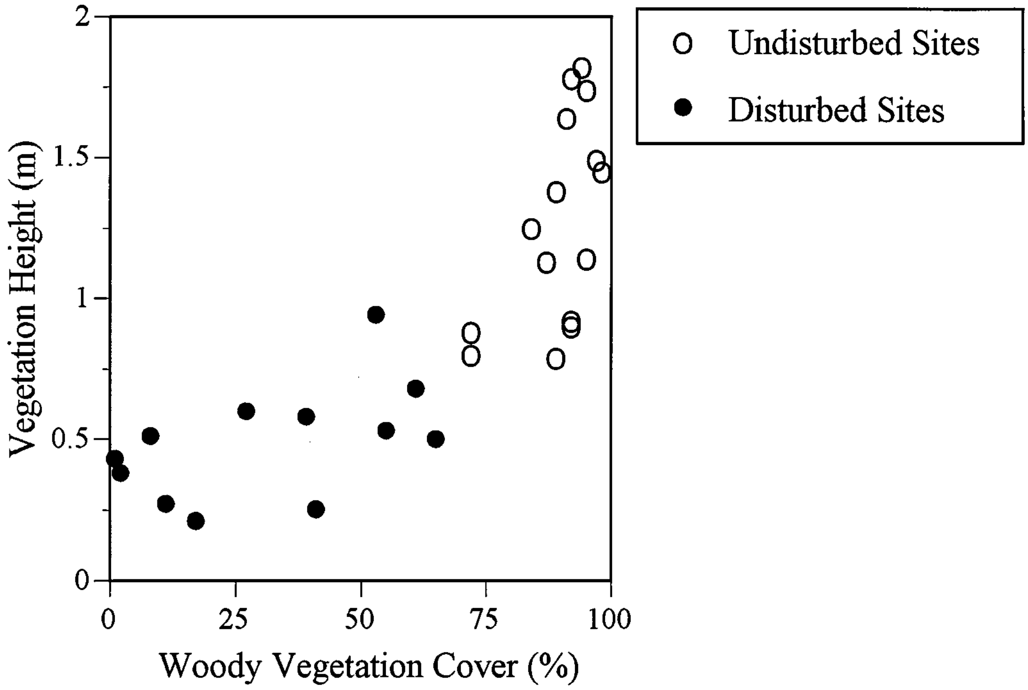


Figure 6. Relationship between mean vegetation height and woody vegetation cover for undisturbed and human-disturbed sites.

Table 3. Results of correlation analyses between mammal and bird species richness and abundance data and measures of vegetation structure. Simultaneous correlations between a bird or mammal variable and the four measures of vegetation structure were considered a single family of tests with group-wide -level of 0.05 (see text)

	Woody cover	Forb & grass cover	Vegetation height	Woody spp. richness
Mammal species				
Total spp. richness	0.363	−0.240	0.369	0.377
Chaparral spp. richness	0.643*	−0.450*	0.658*	0.615*
Disturbance-associated spp. richness	−0.440	0.336	−0.457	−0.366
Total individuals	0.557*	−0.313	0.620*	0.602*
Chaparral individuals	0.747*	−0.499*	0.763*	0.785*
Disturbance-associated individuals	−0.556*	0.485*	−0.470*	−0.553*
Bird species				
Total spp. richness	0.199	−0.204	0.256	0.201
Chaparral spp. richness	0.236	−0.134	0.369	0.369
Total individuals	0.379	−0.470*	0.178	0.228
Chaparral individuals	0.273	−0.349	0.044	0.269

*Correlation coefficient significant at a family-wide -level of 0.05 after sequential Bonferroni adjustment.

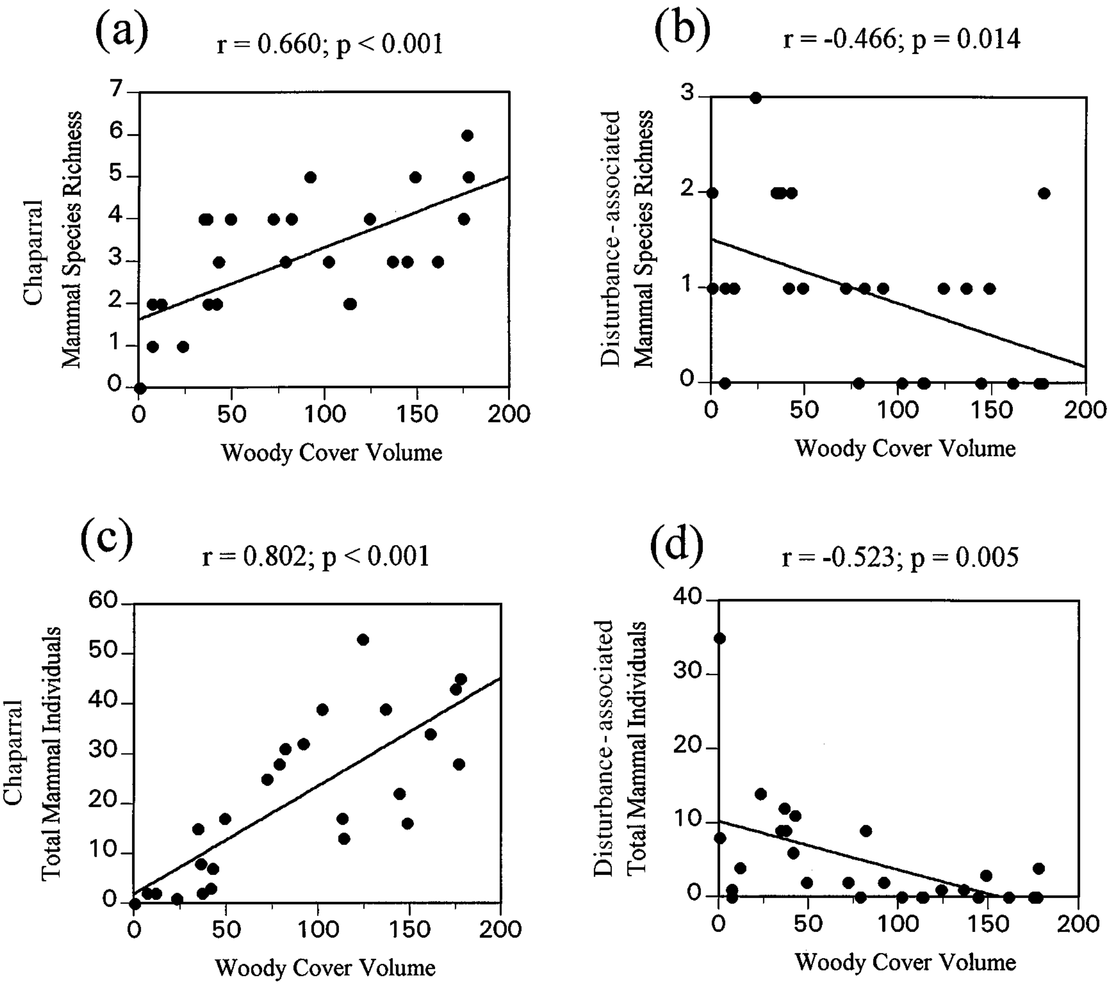


Figure 7. Relationship between woody cover volume [(% woody cover)∗(mean height of woody vegetation in m)] and chaparral mammal richness (a), disturbance-associated mammal richness (b), chaparral mammal abundance (c), and disturbance-associated mammal abundance (d). Pearson correlation coefficients, p-values, and least-squares regression lines are shown. Mammal abundance indicated as the total number of individuals captured at a site.

Discussion

Direct habitat alteration caused by human activities was widespread throughout the study area. Human-altered habitat patches occurred across study area open space, and roads and trails were apparent throughout the region. In general, the proximity of extensive urban development and human activities resulted in the alteration of animal communities and vegetation.

Spatial distribution of disturbed habitat patches were associated with urban proximity and roadways, but the strength of the relationships varied. Although disturbance was associated with proximity to development, the relationship was not statistically significant. At the same time, there was a trend suggesting disturbance was more concentrated near the edge (e.g., within 400 to 600 m). The relationship of disturbance with urban proximity was further complicated by the distribution of human-altered patches well into habitat interiors (e.g., beyond 1400 m, see Fig. 2a). Proximity to roads, on the other hand, was significantly

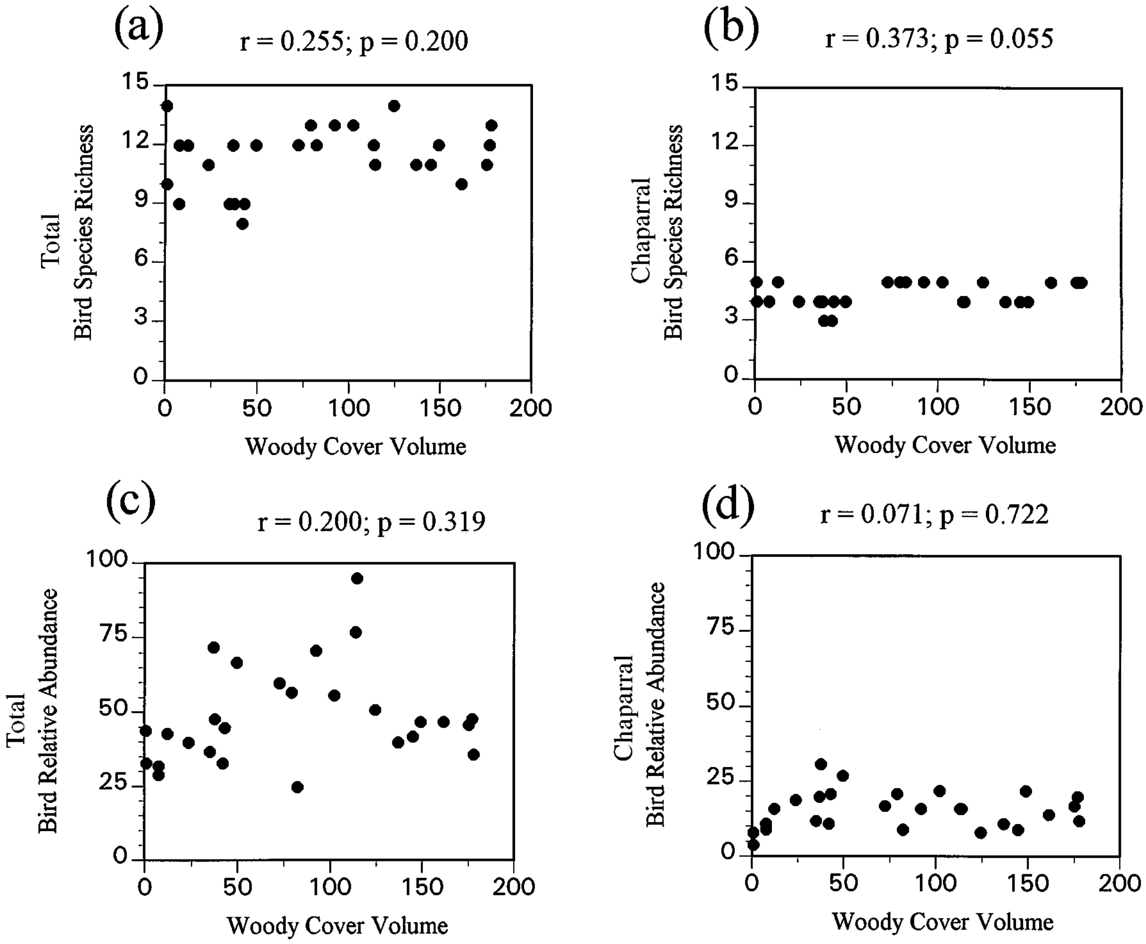


Figure 8. Relationship between woody cover volume [(% woody cover)∗(mean height of woody vegetation in m)] and total bird richness (a), chaparral bird richness (b), total bird abundance (c), and chaparral bird abundance (d). Pearson correlation coefficients and p-values are shown. Bird relative abundance indicated as the sum of the maximum number of individuals observed at a site over the 5-day sampling period.

correlated with patches of human disturbance. Disturbed area frequency was much greater near vehicle roadways, particularly within 400 to 600 m of a road (Fig. 4b). Road access has been previously identified as a potentially significant conduit for habitat disturbance mechanisms (Noss, 1987; Schonewald-Cox and Buechner, 1992), and in this study area, disturbance was strongly associated with road proximity. It is likely that in chaparral and other similarly dense vegetation types, physical openings in the habitat (e.g., roads) can greatly facilitate the spread of additional disturbance across the landscape (Buechner and Sauvajot, 1996). On the other hand, because urban developments often back up against natural areas and afford limited access (other than for individual residents), proximity to urban areas may facilitate less habitat damage than roads or other public access points.

Trail frequencies were associated with proximity to both urban areas and roads; however, single-track trails were more frequent near urban development, whereas double-track trails were more frequent near roads. It is possible that access by urban residents (most often on foot) leads to narrower single-track trails close to urban developments, while roadways facilitate intensive uses (such as off-road vehicle activity), leading to double-track trails near roads. Apparently, interactions between accessibility and the mechanism of disturbance can influence patterns of habitat alteration across the landscape.

Human activities modified chaparral habitat by substantially reducing woody cover and richness and replacing it with often exotic annual forbs and grasses. These disturbance effects are common across southern California and can pose significant threats to remaining natural habitats (Soulé *et al*., 1992; Scott, 1995; Bolger *et al*., 1997a). In addition, disturbance mechanisms do not act independently (Sauvajot, 1995). For example, road access can increase the probability of human-ignited fires, which in turn open habitats to off-road vehicle use, trail proliferation, and exotic species invasions.

The effects of human disturbance on small mammals were substantial. Chaparral mammal richness and abundance were reduced in more disturbed sites, while disturbance-associated mammals were more abundant in these sites. Apparently, habitat preferences of the individual species are important determinants of their response to habitat alteration. These results are consistent with studies of small mammals in other disturbed habitats. For example, Dickman and Doncaster (1987) found that small mammal abundance was strongly correlated to vegetation density, and that the most highly disturbed sites had the fewest number of mammals. In remnant habitat fragments in San Diego County, native small mammals disappeared in part because of ongoing degradation of chaparral and coastal sage scrub habitat (Bolger *et al*., 1997a). Similar results have been found for small mammals in tropical forests (Stephenson, 1993), where reduced species richness was associated with increased habitat alteration and human presence. In general, small mammals seem to respond strongly to habitat alteration and exhibit species-specific responses depending on their habitat requirements. Persistent habitat disturbance will likely lead to ongoing declines of chaparral mammals. If disturbance patterns continue to spread, it is possible that chaparral species could become locally extinct, particularly if recolonization sources are not available or are widely separated. Although some small mammal species are known to disperse across inhospitable habitats (e.g., up to 500 m, Dickman and Doncaster, 1989), greatly separated source populations combined with urban-associated habitat fragmentation and disturbance can lead to small mammal extinctions (Bolger *et al*., 1997a). Increased habitat alteration may favor the persistence of disturbance-associated species. For all species combined, however, small mammal abundance was less in disturbed sites, suggesting that increased habitat alteration across the study area will result in an overall decline in small mammal abundance. From a conservation perspective, maintenance of chaparral small mammal populations will require controlling the spread of habitat alteration by humans.

Resident bird species were much less affected by human disturbances. Although bird species are known to respond to variation in vegetation structure (MacArthur and MacArthur, 1961; Cody, 1981), resident bird richness and abundance were not associated with disturbance-related vegetation changes in this study. First, it is possible that the bird species studied were in fact resistant to habitat disturbance effects. Disturbed sites contained some vegetation cover and probably useful resources to resident birds. As a result, disturbed sites with similar richness and abundance to undisturbed chaparral may have been occupied by resident birds because disturbed areas provided some useful habitat. The resilience of some bird species to urban encroachment effects and habitat disturbance has been documented (e.g., Friesen *et al*., 1995 for resident birds near urbanization and Hutto, 1989 for migratory land birds in tropical deciduous forests), although the patterns are complex and depend strongly on the species considered. Certainly, bird species also respond negatively to human disturbances (Friesen *et al*., 1995; Blair, 1996; Jullien and Thiollay, 1996), and different results might have been obtained if other bird species were included in the analysis (e.g., migratory birds).

A more likely explanation for observed bird distributions is that, because all disturbed sites were relatively close to undisturbed areas (e.g., no disturbed site was more than 150 m from intact chaparral), and because disturbed patches were generally quite small, birds were able move between disturbed and undisturbed areas. In other words, the increased vagility of the bird species may have allowed them to persist in disturbed and undisturbed areas, even if preferred habitats were in intact chaparral. Similar mechanisms have been proposed for bird persistence in other human-altered landscapes, where individuals from surrounding areas supplement populations in suboptimal regions (e.g., Riffell *et al*., 1996; Jullien and Thiollay, 1996). This explanation is also consistent with the small mammal results, where a species group with less mobility was strongly affected by human disturbance in the study area.

Will resident chaparral birds persist if habitat alteration continues? If vagility plays a significant role and disturbed areas reflect suboptimal habitats for bird species, it is possible that increased disturbance will lead to declines for chaparral birds. For example, while chaparral birds may currently occupy the "marginal" human-disturbed habitats through emigration from surrounding "source" populations in intact chaparral (e.g., Pulliam, 1988; Howe *et al*., 1991), as habitat alteration spreads, chaparral birds may decline as the "source" habitats become degraded and further separated (Doak, 1995). This effect would be compounded for species with limited dispersal abilities and if disturbed habitats served as population "sinks" for birds (Buechner, 1987). In general, information on dispersal abilities and population demographics in disturbed and undisturbed sites will be necessary to evaluate this hypothesis and evaluate long-term persistence of chaparral birds if habitat alteration continues.

Several conservation and management recommendations are suggested by this research. First, because human habitat alteration can be significant in natural areas near development and disturbance patterns can affect wildlife distribution, management efforts should focus on reducing habitat disturbance by humans in remaining habitats. Managing human behavior may substantially reduce disturbance impacts and can include increasing public education, redistributing human activities into less sensitive areas, and restricting human access (Jim, 1989). Active park management, public education, and enforcement of park regulations have been implemented in this study area, and a number of formerly human-altered sites are already showing signs of recovery. Specific techniques can be as simple as erecting regulatory signs, installing roadside barricades, and controlling park uses (e.g., limiting vehicle access, enforcing fire regulations, realigning trails). In addition, habitat restoration may serve an important role in highly disturbed sites, and anecdotal observations from this study suggest that restoration efforts can contribute to chaparral recovery. Distribution of patches of disturbed habitat and the frequency of trails across the study area suggest that the accessibility of disturbance to natural areas is critical for controlling disturbance spread. Vehicle roadways may be important conduits of disturbance because they not only represent disturbed habitat but provide access into habitat interiors for other disturbance mechanisms (Schonewald-Cox and Buechner, 1992; Buechner and Sauvajot, 1996). Management attention should be directed at those areas with high potential access to natural habitats, such as along roads or at public access points.

Results from this study also indicate the importance of separating effects of habitat alteration from proximity to development. Although development proximity may be correlated with habitat alteration, intact chaparral near urban edges can still provide important conservation value (Sauvajot and Buechner, 1993). The key to developing effective conservation strategies is to identify all mechanisms responsible for habitat and wildlife changes near developed edges, especially those associated with human disturbance (Murcia, 1995). In this study area, habitat alteration from human activities, which can penetrate deep into remaining open space, appears to be a primary conservation concern, more so than proximity to urban environments (Sauvajot and Buechner, 1993; Sauvajot, 1997).

Finally, because the potential for disturbance is constant and disturbance mechanisms can interact, ongoing vigilance will be necessary to identify and mitigate human disturbance threats. Certainly, in some instances, disturbance impacts will be difficult to control. For example, access restrictions may be difficult to enforce, and some disturbances are almost impossible to prevent (e.g., human-caused fires). However, because of the substantial resource values at risk (Dobson *et al*., 1997) and the amount of habitat alteration that has already occurred, particularly in southern California and other Mediterranean-type ecosystems (Hannah *et al*., 1995), a constant effort will be required to protect biological diversity in chaparral communities and other regions near human-developed areas.

Acknowledgments

We wish to thank Jim Quinn and Dirk Van Vuren for valuable help and advice on this research. Tracy Dudman provided GIS assistance and digitized geographic data. Field assistance was provided by Andor Czigeledi, Maren Stauber, Keith Lewis, Laura Wertz, and Rachael Knapp. Funds were provided by the UC Davis Public Service Research Program, The Nature Conservancy through a grant to the Santa Monica Mountains Conservancy, the UC Davis Cooperative Park Studies Unit, and the Los Angeles County Fish and Game Commission. Additional support was provided by the Santa Monica Mountains National Recreation Area, the Mountains Education Program, and the William O. Douglas Outdoor Classroom. Comments from two anonymous reviewers substantially improved the manuscript.

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