HOME-RANGE AND HABITAT SELECTION BY ADULT COUGARS IN SOUTHERN CALIFORNIA

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Abstract: Understanding the impact of habitat fragmentation, roads, and other anthropogenic influences on cougars (*Puma concolor*) requires quantitative assessment of habitat selection at multiple scales. We calculated annual and multiyear home ranges using a fixed-kernel (FK) estimator of home range for 13 adult female and 2 adult male radiotagged cougars that were monitored October 1986 through December 1992 in the Santa Ana Mountain Range of southern California, USA. Using compositional analysis, we assessed diurnal use of vegetation types and areas near roads at 2 orders of selection (second- and third-order; Johnson 1980). Mean annual and multiyear 85% FK home ranges for males were larger than those reported by previous studies in California. Mean wet-season 85% FK home ranges were significantly larger than those of the dry season. At both scales of selection and across seasons, cougars preferred riparian habitats and avoided human-dominated habitats. Grasslands were the most avoided natural vegetation type at both scales of selection. Although cougar home ranges tended to be located away from high- and low-speed 2-lane paved roads (second-order avoidance), cougars did not avoid roads within their home range, especially when roads were in preferred riparian areas. Protection of habitat mosaics that include unroaded riparian areas is critical to the conservation of this cougar population.

Persecution of North American cougars, overexploitation of their prey, and habitat loss across most of their historic range have relegated this species to habitats in the western states and southern Florida (Anderson 1983). Cougars persist in a wide range of ecosystems, including the hammock and swamp forests of southern Florida (Belden et al. 1988, Maehr and Cox 1995), the high deserts of southern New Mexico (Logan et al. 1996), and the northern Rocky Mountains (Williams et al. 1995). The vegetation and structural characteristics of these landscapes provide habitat for prey and cover for cub rearing, hunting, and stalking prey (Logan and Irwin 1985, Laing 1988, Koehler and Hornocker 1991, Beier et al. 1995, Williams et al. 1995). In California, an understanding of cougar distribution and habitat selection is relevant to managing the impact of hunting and trapping on cougars (Torres et al. 1996), cougar attacks on humans (Beier 1991), and habitat fragmentation (Beier 1993). Habitat fragmentation and road building are occurring at a rapid pace in the Santa Ana Mountains of southern California (Beier 1993).

Although some aspects of cougar ecology previously have been studied in California (Sitton and Wallen 1976, Neal et al. 1987, Hopkins 1989, Padley 1990, Beier and Barrett 1993, Pierce et al. 1999), these researchers did not quantitatively assess habitat selection. Only 4 previous studies have made quantitative assessments of cougar habitat use in the West (Logan and Irwin 1985, Laing 1988, Koehler and Hornocker 1991, Williams et al. 1995).

We used data from radiotagged cougars to quantify how adult cougars in the Santa Ana Mountains of southern California selected among vegetation types, topographic settings, and habitats with roads. We followed the framework developed by Johnson (1980) and Aebischer et al. (1993), in which animals make decisions about resource use at hierarchical stages, namely selection of a home range within a study area (second-order selection) and selection of patches within a home range (third-order selection). First-order selection (selection of a species' geographic range) was beyond the scope of this study. These orders of selection reflect a sequential process on the part of an individual animal. In locating its home range within 1 part rather than some other part of the Santa Ana Mountain Range, a cougar evaluates the resources (e.g., prey, ambush cover, water) and hazards (e.g., roads, human disturbance, other cougars) of various parts of the mountain range. Once this selection has occurred, the animal's day-to-day selection of sites within its home range is constrained by its

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previous selection of a home-range area. Important aspects of habitat selection could be masked by a study confined to only 1 level. For instance, an animal might spend 20% of its time in a habitat that composes 40% of its home range; a third-order study would interpret this as aversion to that habitat. However, the animal may have chosen that home range precisely for the high abundance of that habitat type; a second-order study would detect such selection. Conversely, a cougar might locate its home range away from areas of high density of paved roads (second-order aversion), but nonetheless suffer high risk of mortality if it does not avoid the few paved roads within its home range (third-order indifference). Although calculating home-range size was not our primary objective, delineation of home ranges is an integral part of the analysis of habitat selection and therefore became an important component of this study.

Our objectives were to (1) identify the seasonal, annual, and multiyear home-range characteristics for individual cougars; and (2) quantify habitat preferences at 2 orders of selection with respect to vegetation types, topography, and paved roads.

STUDY AREA

At the time of the study, the Santa Ana Mountain Range study area (SAMR) contained approximately 2,060 km² of nonurban land. These wildlands included portions of Orange (38% of study area), Riverside (28%), and San Diego (34%) counties; over 1 million people lived in the cities and communities surrounding the SAMR (Beier 1993). Much of the potential cougar habitat in the area was protected within the Cleveland National Forest, Camp Pendleton Marine Corps Base, Fallbrook Naval Weapons Station, Caspers Regional Park, and several smaller reserves (Padley 1990, Beier and Barrett 1993). We delineated the study-area boundaries where potential cougar habitat met a major interstate highway, abutted coastline, or where human dwellings exceeded 4 residences per hectare. We assumed these landscape features to be effective barriers to selection by cougars beyond the core wildlands of the SAMR. Beier (1993, 1995) provides maps of the study area.

Common California plant communities present on the study area included chaparral, oak woodlands (*Quercus engelmannii* and *Q. agrifolia*), coastal scrub, annual grasses, and coniferous woodlands at higher elevations (Barbour and Major 1995). Citrus and avocado orchards and other nonnative vegetation types occurred in parts

of the area. While much of the study area remained undeveloped, human influence was widespread and included cattle grazing, orchards and agriculture, military training facilities, and public recreation areas. Maximum average daily temperature was 24 °C, and mean annual precipitation was 33 cm at lower elevations (Santa Ana Fire Station, Santa Ana, California; 1948–2000), with somewhat cooler and more mesic conditions at higher elevations. Precipitation in the form of fog drip was common during dry and wet seasons, and light snow accumulation was possible in winter at the higher elevations (Barbour and Major 1995). Elevations within the study area ranged from sea level at the coast to 1,717 m on Santiago Peak. The topography was rugged. Perennial streamflow was intermittent (Beier and Barrett 1993); however, springs, seeps, and other water sources were present and relatively common throughout the study area.

Other common carnivores included coyotes (*Canis latrans*), gray foxes (*Urocyon cinereoargenteus*), bobcats (*Lynx rufus*), raccoons (*Procyon lotor*), and striped skunks (*Mephitis mephitis*). Mule deer (*Odocoileus hemionus*) were common throughout the study area and were the most important prey species for cougars (Beier and Barrett 1993). Other prey included opossum (*Didelphis virginiana*), coyote, and raccoon (Beier and Barrett 1993).

METHODS

Radiotelemetry

Between October 1986 and December 1992, 13 adult (≥2 years old) female cougars and 2 adult male cougars were captured, radiocollared, and monitored on the SAMR study area (Padley 1990, Beier and Barrett 1993). Eighty-one percent of radiolocations were from ground-based triangulation conducted every 1 to 4 days, usually (85%) during daylight hours. Radiolocations were obtained from the ground using standard triangulation techniques (Mech 1983) conducted by a single observer. Because only a single observer was used and no network of precisely located receiving stations was available, we could not compute meaningful error polygons (White and Garrott 1990). Location errors were minimized by using only azimuths that differed by 60–120° and by getting close to the animal (White and Garrott 1990). Observers attempted to stay >100 m from the focal animal to avoid influencing its movement and <500 m away to obtain accurate locations; 76% of locations were determined

from within 500 m of the focal animal, and 87% were from within 1 km. The remaining 19% of locations were obtained by aerial homing from fixed-wing aircraft from flights conducted approximately once every 10 days, always during daylight. All locations were recorded as Universal Transverse Mercator (UTM) points and exported into a vector-based geographic information system (GIS; ArcView® 3.2a [ESRI, Redlands, California, USA]).

Home-Range Delineation

We calculated home-range sizes separately for the dry season (May–Oct), the wet season (Nov–Apr), and annual periods (seasons combined). We use the term "multiyear" to indicate a home range or analysis using data pooled across >1 year of observation; thus, a multiyear dry-season home range includes locations for 2 dry seasons for a particular animal. Using an animal movement analysis extension (Hooge and Eichenlaub 1997) in ArcView, we calculated annual 50%, 85%, and 95% FK home ranges (Worton 1989) with a level of smoothing selected by least-squares cross-validation (Worton 1995, Seaman and Powell 1996, Seaman et al. 1999) and a grid cell size of 30 m × 30 m. All home-range contours were clipped at the study-area boundary before subsequent analyses.

Nonparametric kernel estimators can estimate densities of any shape (Seaman and Powell 1996) and are not influenced by effects of grid size or placement (Silverman 1986). We report the 50% home range as an area of core utilization and the 85% home range as an area of ecological importance to a cougar. We report the 95% home range as a commonly referenced contour, but agree with Seaman et al. (1999) that it is of little biological significance and unreliable, regardless of the home-range estimator used. Seasonal home ranges were calculated only for individual adult cougars that were monitored for >91 days of a 182 day season and that yielded >50 locations in a season. We tested for differences in seasonal 85% home-range sizes using a Wilcoxon signed-rank test (T = test statistic).

Compositional Analysis of Habitat Selection

We use the term "habitat composition" to refer to a vector of proportions of habitat classes (as defined by vegetation type and other classifying factors) used by or available to an animal; each habitat composition necessarily sums to 100%. Rettie and McLoughlin (1999) demonstrated that the use of point data (e.g., ignoring location error) increases the risk of drawing erroneous

conclusions about relative preference because of the bias associated with assigning a point to a specific patch of habitat. To account for error in assigning an individual radiolocation to a particular class (e.g., vegetation type), our analysis assumed that a cougar used all classes within a 200-m radius of a radiolocation in proportion to the area of that class within the circle. We chose a 200-m-radius buffer to encompass triangulation error in estimating animal locations (Beier et al. 1995) and to encompass errors inherent in the digital coverages used to analyze selection. Equally important, this buffer allows our analysis to detect the potential importance of habitat mosaics in the selection process (see Rettie and McLoughlin 1999). To evaluate second-order selection, we compared the habitat composition of the study area to the averaged habitat compositions of individual cougar radiolocations. For third-order selection, we compared the habitat composition of an individual's multiyear 85% home range to the averaged habitat composition of the radiolocations of that individual captured in that multiyear 85% home range.

At both scales of selection, we used compositional analysis to develop a ranking of habitat preference (Aitchison 1986, Aebischer and Robertson 1992, Aebischer et al. 1993). Compositional analysis correctly uses the individual animal, not the radiolocation, as the sampling unit and avoids statistical problems arising from non-independence of proportions within a habitat composition (Aebischer et al. 1993).

Because 6 animals are the minimum for statistical inferences from compositional analysis (Aebischer et al. 1993) and we had data for only 2 males, we pooled males and females. At both scales of analysis, we analyzed only those habitat classes available to all cougars.

Compositional analysis compares use of each habitat class to an arbitrary reference class k by the log-transformed ratio of habitat proportions for each animal (Aitchison 1986):

$$y_{ij} = \ln(x_{ij}/x_{ik}) \, (i = 1, \dots, n; \, j = 1, \dots, D; \, j \neq k),$$

where x_{ij} describes proportional use by an individual i of the jth of D habitat types, and n = number of individual animals. When an individual's proportional utilization of a habitat was 0, we replaced this value with a number less than 0.1 times the smallest observed value for that habitat (Aebischer et al. 1993). The differences between used and available habitat log-ratios for each indi-

vidual formed a single row of a difference matrix with n rows and $D - 1$ columns. To test the null hypothesis that utilization was random (difference matrix = 0), we constructed a residual matrix from the matrix of log-ratio differences and computed the Wilks' lambda statistic:

$$\lambda = \frac{|R1|}{|R2|} \ ,$$

where $R1$ is the matrix of mean corrected sums of squares and cross-products, and $R2$ is the matrix of raw sums of squares and cross-products. Following the procedure proposed by Aebischer et al. (1993), we transformed λ into the test statistic:

$$- N \times 1n(\lambda),$$

which approximates a chi-square distribution with $k - 1$ degrees of freedom, and where N is the number of individuals in the sample and k = the number of habitat classes. When habitat use was significantly nonrandom ($P < 0.05$), we calculated the mean and standard deviation for all log-ratio differences and constructed a matrix ranking habitat types in their order of use. To assess differences between ranks, we used a paired t-test to compare mean utilization between all pairs of habitats.

Vegetation Types

We obtained digital vegetation coverages from Orange, Riverside, and San Diego counties. Vegetation polygons available on the study area were identified by county personnel during 1990, 1992, 1993, and 1995 using LANDSAT Thematic Mapper and SPOT 2 satellite imagery, digital aerial photographs, and field vegetation mapping surveys (ground-based and aerial). County personnel digitized vegetation boundaries "on-screen" using the airphotos and satellite imagery as background layers and georeferenced the resulting polygons using terrain-corrected satellite data. These polygons were then digitally coded and projected into UTM zone 11 (North American Datum of 1927). These methods resulted in a mean spatial accuracy of approximately 25 m and a minimum mapping unit between 0.2 and 2.0 ha. In some cases, narrow riparian areas were more accurately delineated using the near infrared band of a SPOT image, which can detect greater leaf moisture content, or by using hydrographic data layers. All vegetation types were categorized and classified by the 3 counties based on modifications to the Holland classification system (R. F. Holland.

1986. Preliminary descriptions of the terrestrial natural communities of California. California Department of Fish and Game, Nongame Heritage Program, Sacramento, USA, unpublished report). Initially, we identified 16 broad vegetation types and interpolated these across the 3 counties. We further consolidated infrequent vegetation types into 9 more general vegetation types: scrub, chaparral, grassland, riparian, forest, woodland, agriculture, developed, and disturbed (Dickson 2001). Lakes, rivers, wetlands, vernal pools, beaches, and artificial watercourses (totaling 0.70% of the study area) were classified within the riparian vegetation type. Cliff and rock habitats (totaling 0.04%) were most often adjacent to chaparral vegetation types and so were reclassified as such. Coastal dunes (totaling 0.01%) often were associated with scrub vegetation and were grouped within this type.

Topography

Within the GIS, we merged 26 USGS 1:24,000 digital elevation models (DEMs) to describe elevation, slope, and aspect of the entire study area and individual 85% home ranges. The slope (in degrees) of a cell location was derived from the DEM by calculating the maximum rate of change between neighboring cells. The aspect (in degrees) of a cell location was derived from the DEM by calculating the steepest down-slope direction to its neighboring cells. We reclassified aspect into 4 cardinal direction categories: north (315°–45°), east (45°–135°), south (135°–225°), and west (225°–315°). We assessed cougar use of elevation, slope, and aspect by calculating the average of all 30 m × 30-m cell values captured within 200 m of an individual radiolocation. We used a z-test (z = Test Statistic) to test for significant differences between utilized and available calculations of elevation and slope. For each individual cougar, we calculated the proportion of radiolocations that fell into each of the 4 aspect categories.

Roads

To assess the response of cougars to roads on the SAMR, we obtained 1995 U.S. Bureau of the Census TIGER (Topologically Integrated Geographic Encoding and Referencing) digital data coverages for all roads on the 3 counties. We modified these coverages based on paper maps on which field crews had indicated accurate road location and condition (e.g., paved, dirt, unusable, absent) of mapped roads. We did not analyze cougar response to multi-lane freeways (because they occurred at the periphery of only 3

Table 1. Mean multiyear home range areas (km^2) for 13 adult female (F1–F19) and 2 adult male (M2, M9) cougars in the Santa Ana Mountain Range, California, USA, 1986–1992, using a fixed-kernel estimator.

Animal ID	No. years	Multiyear home range				Dry-season home range				Wet-season home range			
		No. locations	50%	85%	95%	No. locations	50%	85%	95%	No. locations	50%	85%	95%
F1	3	433	20	80	158	211	14	68	122	222	19	74	157
F2	4	718	14	52	89	360	10	45	84	358	21	65	114
F3	2	590	7	42	82	306	7	33	67	284	16	58	96
F4	3	537	4	37	92	260	3	25	72	277	18	67	123
F5	4	251	51	151	264	147	41	146	252	104	70	195	334
F6	3	267	10	90	234	149	14	79	218	118	21	167	245
F9	2	213	16	52	95	84	11	43	78	129	17	58	96
F10	3	380	27	85	140	247	27	84	128	133	15	74	142
F11	5	357	7	75	147	171	7	48	120	186	26	128	201
F12	3	304	9	44	77	192	7	35	68	112	15	59	99
F15	1	131	17	77	139	77	9	43	105	54	25	145	265
F18	2	70	45	148	350	—	—	—	—	—	—	—	—
F19	1	130	33	114	225	88	24	88	186	—	—	—	—
Female mean	—	337	20	81	161	191	14	61	125	180	24	99	170
M2	2	290	51	412	671	115	59	291	543	175	105	544	735
M9	2	129	100	527	854	72	80	579	898	57	184	574	791
Male mean	—	210	75	470	763	94	69	435	721	116	144	559	763

home ranges) or dirt roads (because they were ubiquitous in all home ranges and because TIGER files provided inaccurate and incomplete coverage of these roads). We classified the remaining paved roads as either high-speed 2-lane paved roads (posted speed limits 80 km/hr) or low-speed 2-lane paved roads (posted speed limits 56 km/hr). We classified surrounding areas into 4 zones with respect to each road speed, namely <500 m; 500–1,000 m; 1,000–1,500 m; or >1,500 m from roads of that speed. We calculated the proportion of individual radiolocations captured within each zone and compared this to the proportion of available area in that zone. For second-order selection, we included all individuals, but for third-order selection, we included only those individuals whose multiyear 85% home range contained roads of the road speed being considered. Compositional analysis was used to develop a ranking of zone preference relative to the proportional availability of area in that zone. We calculated high-speed, low-speed, and total 2-lane paved road densities on the study area and on the individual multiyear 85% home range.

RESULTS

Home-Range Sizes

The annual 85% home range averaged 93 km^2 (SD = 50) for 12 adult female and 363 km^2 (SD = 63) for 2 adult male cougars. For both wet and dry seasons, males also had home ranges more than twice as large as those of females. Wet-season 85% home ranges were significantly larger than those of the dry season (for 7 females with data for both seasons, $T = 2.37$, $P = 0.02$).

Multiyear 85% home ranges averaged 81 km^2 (SD = 38) for 13 females and 470 km^2 (SD = 81) for 2 males (Table 1). Wet-season 85% home ranges were significantly larger than those of the dry season ($T = 2.90$, $P = 0.004$; $n = 13$ individuals).

Influence of Vegetation Type on Habitat Selection

Cougars selected riparian vegetation types and avoided human-dominated areas and grasslands at the second-order scale (e.g., radiolocations within the study area) and the third-order scale (e.g., radiolocations within a home range). At the second-order, proportional use of vegetation types on the study area was significantly different from habitat composition of the study area during the dry season ($-\Lambda \ln \lambda = 56.68$, $P < 0.001$, df = 8; $n = 12$ females and 2 males), wet season ($-\Lambda \ln \lambda = 51.18$, $P < 0.001$, df = 8; $n = 11$ females and 2 males), and across seasons ($-\Lambda \ln \lambda = 61.99$, $P < 0.001$, df = 8; $n = 13$ females and 2 males; Fig. 1). Both within and across seasons, cougars consistently preferred riparian vegetation types. The rank order of vegetation types also was consistent

Dry season

Wet season

Seasons combined
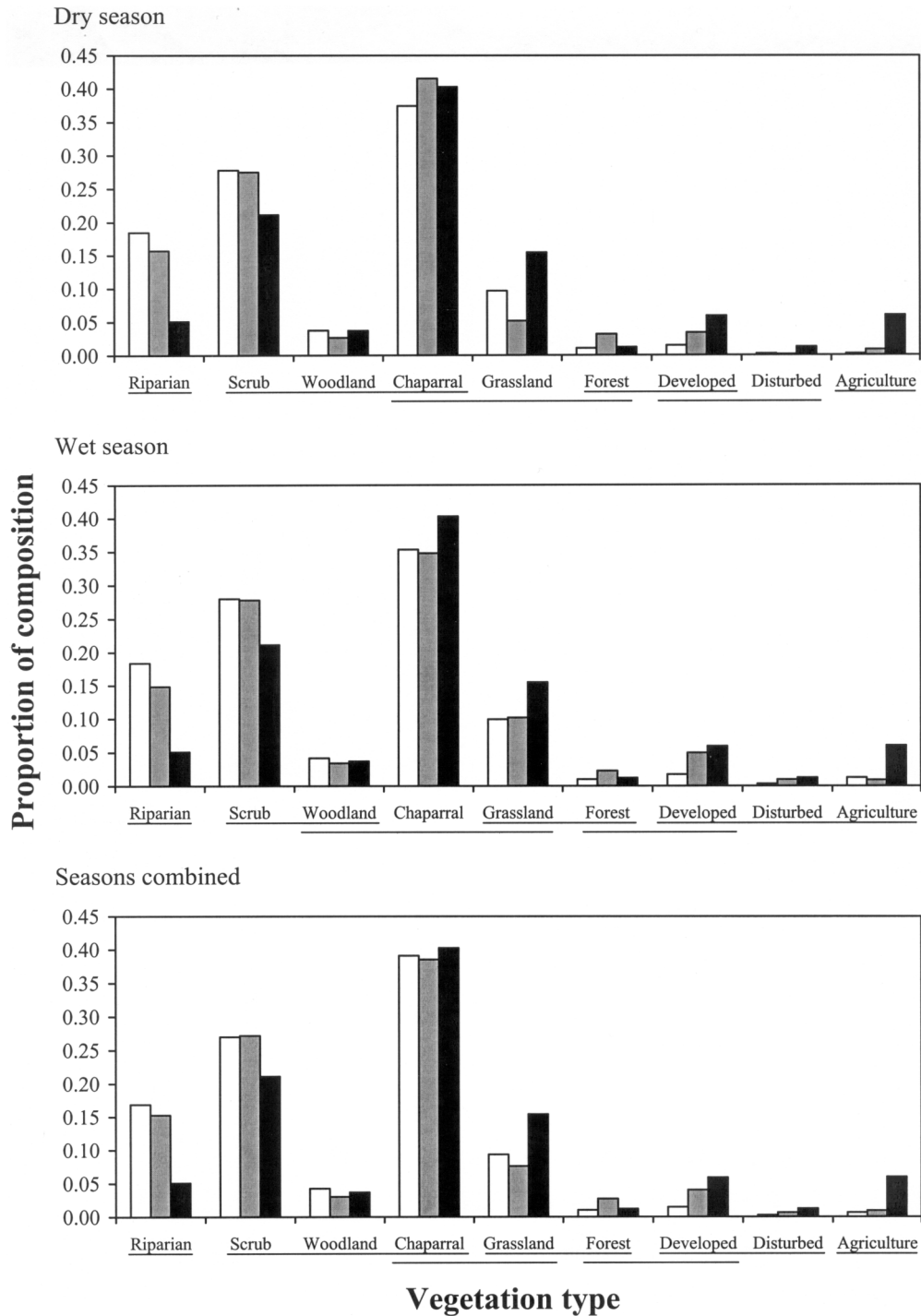
Proportion of composition

Vegetation type

Fig. 1. Second-order selection (i.e., comparing habitat composition of individual buffered radiolocations to the habitat composition of the entire study area) by cougars in the Santa Ana Mountain Range, California, USA, 1986–1992. Vegetation types are arranged from most to least preferred for dry season, wet season, and seasons combined. White bars indicate mean female proportional utilization, gray bars indicate mean male proportional utilization, and black bars indicate habitat proportional availability. Underlining under names of vegetation types on the *x*-axis indicates vegetation types for which rankings are not significantly different.
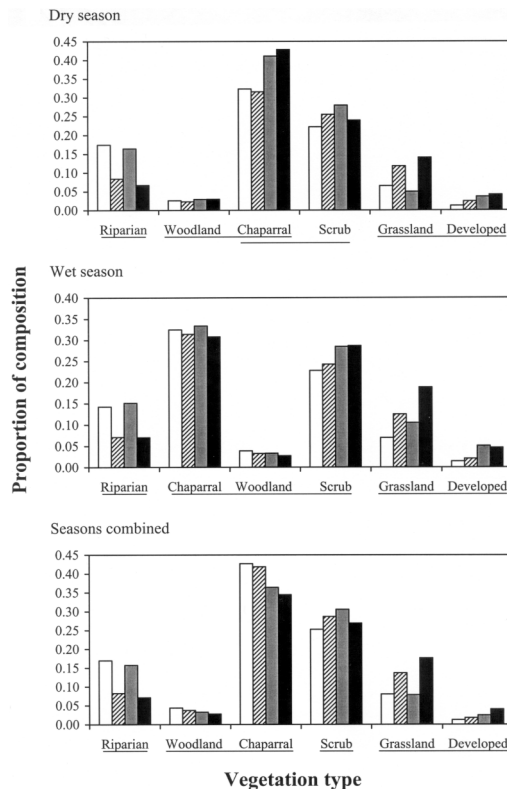
Fig. 2. Third-order selection (i.e., comparing habitat composition of individual buffered radiolocations to the habitat composition of the individual 85% home range) by cougars in the Santa Ana Mountain Range, California, USA, 1986–1992. Habitats are arranged from most to least preferred for dry season, wet season, and seasons combined. White bars indicate mean female proportional utilization, cross-hatched bars indicate mean habitat proportional availability for females, gray bars indicate mean male proportional utilization, and black bars indicate mean habitat proportional availability for males. Underlining under names of vegetation types on the *x*-axis indicates vegetation types for which rankings are not significantly different.

across seasons, although the statistical significance of pairwise contrasts varied slightly between seasons. Developed, disturbed, and agricultural vegetation types were consistently avoided.

In assessing third-order selection, we dropped forested, agricultural, and disturbed vegetation types from the compositional analysis because they were available to only a few individuals. Use of vegetation types on multiyear 85% home ranges was significantly different from availability during the dry season ($-$Λnλ = 24.70, P < 0.001, df = 5; n = 10 females and 2 males), wet season ($-$Λnλ = 24.60, P < 0.001, df = 5; n = 10 females and 2 males), and across seasons ($-$Λnλ = 23.95,

P < 0.001, df = 5; n = 12 females and 2 males; Fig. 2). In all cases, riparian vegetation types were preferred, although significance of differences varied by season. When grassland and developed vegetation types occurred within a cougar's home range, they generally were used in lower proportion than their availability on that home range.

Influence of Topography on Habitat Selection

During both wet and dry seasons and at both second- and third-orders of selection, cougar locations tended to be lower in elevation and on gentler slopes than the average within the study area or home range, but differences were small and not statistically significant. Across years and seasons, locations of 13 female and 2 male cougars averaged about 275 m (SD = 146) in elevation and 12° (SD = 3) slope compared to an average elevation of 415 m (SD = 286) and 13° (SD = 9) slope on the entire study area (second-order z = $-$1.79, P = 0.07 for elevation and z = $-$0.48, P = 0.63 for slope) and an average elevation of 310 m (SD = 154) and 13° (SD = 3) slope within home ranges (third-order z = $-$0.98, P = 0.32 for elevation and z = $-$1.50, P = 0.13 for slope). These trends were similar for females and males. These small differences are consistent with selection for riparian areas (invariably slightly lower in elevation and gradient than the adjacent slopes). Cougars did not select habitats based on aspect at either the second- or third-order of selection.

Influence of Paved Roads on Habitat Selection

At the second-order scale, cougars used areas in zones that were farther from both high-speed and low-speed paved roads than would be typical of the study area ($-$Λnλ = 8.90, P < 0.05, df = 3; n = 13 females and 2 males; Fig. 3). In general, use of areas increased with distance from paved roads.

These preferences were not evident at third-order selection. Although cougar locations were nonrandomly distributed with respect to high-speed paved roads ($-$Λnλ = 11.88, P < 0.01, df = 3; n = 8 females and 2 males), preference patterns were inconsistent, with cougars apparently preferring areas 500 to 1,000 m from high-speed roads to all other zones. Furthermore, cougar use of areas was random with respect to low-speed paved roads within their home range ($-$Λnλ = 3.10, P > 0.05, df = 3; n = 8 females and 2 males). Thus, although cougars tended to locate their home ranges away from paved roads, once they established a home range they did not avoid using areas close to those roads.

High-speed
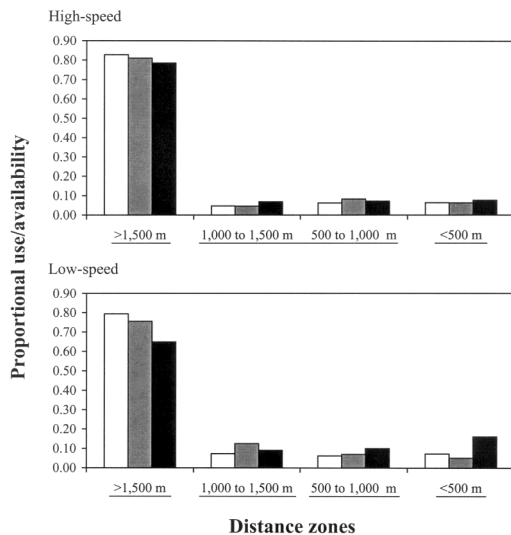

Low-speed

Distance zones

Fig. 3. Cougar use of areas at various distances from high- and low-speed 2-lane paved roads, compared to the proportion of area available in each zone on the study area, in the Santa Ana Mountain Range, California, USA, 1986–1992. Zones are arranged from most to least preferred. White bars indicate mean female proportional utilization, gray bars indicate mean male proportional utilization, and black bars indicate proportional availability. Underlining under names of zones on the *x*-axis indicates zones for which rankings are not significantly different.

A general avoidance of paved roads also was evidenced by the fact that density of low-speed paved (0.11 km/km^2, SD = 0.16 for females and 0.22 km/km^2, SD = 0.02 for males) and total paved roads (0.18 km/km^2, SD = 0.20 for females and 0.29 km/km^2, SD = 0.01 for males) in cougar home ranges was far lower than the density in the study area (0.40 km/km^2 for low-speed paved roads and 0.46 km/km^2 for total paved roads). Only 2 animals (F12, F15) had paved road densities in their home ranges that approached the densities for the study area.

DISCUSSION

Home-Range Size

Cougar home-range sizes reported in the literature are quite variable (see reviews in Anderson 1983 and Anderson et al. 1992), primarily due to both differences in estimation techniques and environments. Annual 85% home ranges for females in the SAMR were about 10% larger than those reported in the Diablo Range of northern California (Hopkins 1989; MCP estimator). Multiyear 85% home ranges for female cougars in the SAMR were about 38% smaller than those report-

ed by Hopkins (1989; MCP estimator) for comparable periods, and about 54% larger than those reported on the central coast of California by Sitton and Wallen (1976; MCP estimator) in a study area similar to the SAMR. Annual 85% home ranges and multiyear 85% home ranges for male cougars in the SAMR were larger than those reported by Hopkins (1989) and Sitton and Wallen (1976). Female multiyear 85% home ranges in the SAMR were smaller than those reported in the Sierra Nevada Mountain Range by Neal et al. (1987) and Pierce et al. (1999), although male multiyear 85% home ranges were larger.

All previous studies in the West also have reported that home-range sizes of male cougars were larger than those of females (see reviews in Anderson 1983, Anderson et al. 1992, Logan et al. 1996, and Pittman et al. 2000). Males M2 and M9 probably were the only adult male residents in the southern half of the study area, and the large size of their home ranges may reflect limited competition from other males. These males covered 875 km^2 (42%) of the study area with their combined multiyear 85% home ranges (compared with 51% for 13 females), and each consorted with a number of females on the study area (Beier and Barrett 1993).

As did Hopkins (1989), we documented a decrease in most of the adult 85% home ranges during the dry season, perhaps because both cougars and prey concentrate near water sources during the dry season. Cover density and water sources were characteristics of areas heavily used by cougars in southern Utah (Laing 1988).

Vegetation Types

The strong concordance between rank orders for vegetation types at second- and third-order selection suggests that our results are not an artifact of factors operating at 1 scale (e.g., avoidance of conspecifics) distorting selection at another scale. At both scales of selection, and during both wet and dry seasons, riparian vegetation types were preferred to all other vegetation types. Previous studies have not documented selection for this vegetation type. Logan and Irwin (1985) reported statistically nonsignificant preference for riparian zones relative to their availability (3.6% vs. 1.3%) in north-central Wyoming. Without reporting riparian use, Laing (1988) stated that cougars used riparian zones proportional to their availability (8.9%) in southern Utah. Williams et al. (1995) reported the use (3.3%) of river and marsh habitats less than their

availability (5.1%) in northern Montana. Some of these differences could be accounted for by methodological differences. For instance, Williams et al. (1995) documented selection for closed conifer vegetation, which included an unquantified amount of riparian areas. Riparian areas in the Santa Ana (and in much of the western United States) are narrow polygons relative to the average radiolocation error (White and Garrott 1990), so treating radiolocations as discrete points is likely to underestimate the importance of riparian areas. Thus, Logan and Irwin (1985) and Laing (1988), by treating locations as point data, may have had reduced ability to detect preference for riparian habitats. Poor representation of riparian areas on vegetation maps also could have skewed our results to indicate preference (if riparian areas are overmapped) or avoidance (if undermapped). An accuracy assessment (San Diego State University. 1993. Accuracy Assessment of MSCP GIS Vegetation Layer, San Diego, California, USA, unpublished report) on a 2,357-km^2 portion of the San Diego County vegetation map south of our study area suggests that such risks were low in our study, with riparian vegetation types correctly mapped 86% ± 4.6 (95% CI) of the time.

Logan and Irwin (1985), Laing (1988), Koehler and Hornocker (1991), and Williams et al. (1995) each emphasized the importance of cover characteristic of selected habitat types for stalking and feeding. Undoubtedly, riparian areas provide important stalking and feeding cover for the SAMR cougar population, as kill sites and caches were most often associated with this vegetation type (Beier et al. 1995). In northern California, Hopkins (1989) found 73% of all deer kill caches in creek bottoms. Preference for riparian habitats by nonmigratory mule deer in the West has been documented previously (Swenson et al. 1983, Carson and Peek 1987). Bowyer (1986) found that the seasonal distribution of mule deer does and fawns in San Diego County was regulated by proximity to water sources and succulent vegetation.

Logan and Irwin (1985) and Laing (1988) suggested that cougars use selected habitats adjacent to grassland habitats to stalk and kill prey. On the SAMR, riparian habitat patch perimeters did not often abut grassland patches (20% of total perimeter length) and were more often adjacent to chaparral and scrub vegetation types (36% and 27%, respectively). Environmental Science Associates (1992. Eastern Transportation Corridor Deer Telemetry Study, San Francisco, California, USA, unpublished report) noted that scrub habitats were preferred by mule deer in the Santa Ana Mountains. These scrub habitats provide little stalking cover (vegetation height typically <0.5 m), and adjacent riparian areas are thus likely ambush sites. Finally, riparian areas in major drainages provided important movement corridors for cougars on the study area and were often associated with travel paths (Beier and Barrett 1993, Beier 1995).

Across both scales of selection, grasslands were the only natural vegetation type that cougars avoided as strongly as they avoided developed areas. Our results support findings by Logan and Irwin (1985), Laing (1988), and Williams et al. (1995) that avoidance of grassland vegetation types by cougars is due to a lack of sufficient cover. Additionally, Laing (1988) reported an avoidance of agricultural/pasture lands by cougars in southern Utah due to a lack of adequate cover, and this is consistent with our findings. On the second-order scale, agricultural areas were consistently the most avoided vegetation type on the SAMR. Although the aversion to disturbed and developed habitat types is not surprising, this study is the first to document such avoidance.

Other researchers have documented differences in the seasonal selection patterns of cougars in winter versus nonwinter (Logan and Irwin 1985, Laing 1988, Williams et al. 1995), each noting that these differences likely were due to the seasonal shifts of mule deer herds. The relatively mild climate of our study area, as well as a nonmigratory prey base, did not produce seasonal habitat shifts.

Because compositional analysis requires a minimum sample size of 6 animals (Aebischer et al. 1993), we were unable to test for sex effects on habitat selection. Laing (1988) detected minimal to no difference between the habitat selection patterns of male and female cougars in southern Utah.

Although 88% of all radiolocations used in these analyses were obtained during the daylight hours, patterns of selection could differ during crepuscular and nocturnal hours when SAMR cougars exhibit peaks in movement activity (Beier et al. 1995).

Roads

We found that cougars avoided paved roads in placing a home range within the SAMR (second-order) but did not avoid zones nearest to paved roads within their home ranges (third-order). Similarly, cougar home ranges in northern Arizona and southern Utah contained road densities lower than those found on the respective study areas (Van Dyke et al. 1986) and cougars translo-

cated into northern Florida established home ranges that contained road densities roughly 50% the density on that study area (Belden and Hagedorn 1993). Maehr and Cox (1995) assessed the influence of road-related variables on the distribution of cougars in Florida and suggested a pattern of second-order avoidance toward major highways. Hard-surface road densities on the SAMR study area were greater than in northern Florida (0.18 km/km^2; Belden and Hagedorn 1993), and greater than on 2 study areas in Arizona (0.02 km/km^2 and 0.04 km/km^2; Van Dyke et al. 1986). Van Dyke et al. (1986) reported an apparent pattern of third-order avoidance of hard-surfaced roads on 1 of 2 study areas in Arizona. The southeastern portion of the SAMR study area had the highest density of low-speed paved roads, which probably rendered it unsuitable for regular use as part of cougar home ranges.

Cougars did not avoid high-speed paved roads within their home ranges. These roads often were in highly preferred riparian areas. For example, of all cougars in this study, F15 showed the strongest apparent preference for areas close to high-speed paved roads. This almost certainly reflected the fact that such a road ran alongside the Santa Margarita River, which comprised the bulk of the riparian habitat in her home range. Where paved roads were not associated with riparian areas, cougars exhibited neither aversion nor avoidance of high-speed paved roads. Vehicle mortality on high-speed paved roads was the main source of mortality in this population (Beier and Barrett 1993). The combination of avoidance of paved roads in locating a home range and indifference toward paved roads within a home range means that roads have potentially severe impacts on both habitat suitability and mortality of cougars. Roads also have a third negative impact on cougars in that construction of a road into wild areas is often followed by a shift toward disturbed areas typically avoided by cougars.

MANAGEMENT IMPLICATIONS

California has lost over 95% of the riparian vegetation present prior to European settlement (Smith 1977, Katibah 1984). Habitat mosaics, including riparian areas, provide the survival and movement requisites of cougars. Protection of riparian areas from development, road building, and habitat alteration is crucially important to this population. Moreover, it is not sufficient to simply preserve riparian habitats alone. If these habitats are important because they offer ambush

cover and cache sites adjacent to other habitats used by prey, it is important to maintain the relationships between riparian and other natural habitat types that support native prey.

Collisions with vehicles are the leading cause of mortality for this population, resulting in 10 (32%) deaths of radiotagged cougars and their offspring between 1988 and 1993 (Beier and Barrett 1993). Because cougars do not avoid paved roads within their home range, new paved roads should be located away from preferred cougar habitats such as riparian areas. Approximately 61 km (48%) of the total length of high-speed paved roads on the study area are within 200 m of riparian areas, and land within 200 m of a high-speed road encompasses 10% of the riparian vegetation types on the study area. Future transportation projects in the region must consider not only habitats directly lost to road building but also effects of roads on adjacent habitats.

ACKNOWLEDGMENTS

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