

INFLUENCE OF VEGETATION, TOPOGRAPHY, AND ROADS ON COUGAR MOVEMENT IN SOUTHERN CALIFORNIA

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Abstract: Models of individual movement can help conserve wide-ranging carnivores on increasingly human-altered landscapes, and cannot be constructed solely by analyzing the daytime resting locations typically collected in carnivore studies. We examined the movements of 10 female and 7 male cougars (*Puma concolor*) at 15-min intervals during 44 nocturnal or diel periods of hunting or traveling in the Santa Ana Mountain Range of southern California, USA, between 1988 and 1992. Cougars tended to move in a meandering path (mean turning angle $\sim 54^\circ$), and distance moved (mean and mode ~ 300 m) was not correlated with turning angle. Cougars used a broader range of habitats for nocturnal or diel movements than for previously described daybed locations for this same population. Riparian vegetation ranked highest in a compositional analysis of vegetation types selected during movement; grassland, woodland and urbanized sites were least selected. During periods of stasis (we presume many of these were stalking locations), patterns of selection were less marked. Cougars spent a disproportionate amount of time in highly ranked vegetation types, and traveled slowest through riparian habitats and fastest through human-dominated areas. Our results suggest that travel speed may provide an efficient index of habitat selection in concert with other types of analysis. Hunting or traveling individuals consistently used travel paths that were less rugged than their general surroundings. Traveling cougars avoided 2-lane paved roads, but dirt roads may have facilitated movement. Maintenance and restoration of corridors between large wildlands is essential to conserving cougars in southern California. Our results indicate that riparian vegetation, and other vegetation types that provide horizontal cover, are desirable features in such corridors, that dirt roads should not impede cougar use of corridors, and that corridors should lie along routes with relatively gentle topography. Our results suggest that cougars do not key in on highway-crossing structures in a way that creates a prey trap. Our empirical frequency distributions of distances and turning angles, along with cougar responses to vegetation, topography, and roads can help parameterize an individually-based movement model for cougars in human-altered landscapes.

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Least-cost path analysis (Bunn et al. 2000, Paquet et al. 2001) and individual-based movement models (DeAngelis and Gross 1992, Bergman et al. 2000) for wide-ranging animals depend crucially on an understanding of how individuals move. These models, especially those built for terrestrial carnivores, can be used as tools for conservation planning and to assess, maintain, or improve habitat connectivity in human-dominated landscapes (Minta et al. 1999, Schadt et al. 2002). Animal movement probably depends on patterns of resource use relative to availability across multiple scales (Senft et al. 1987, Wiens 1989, Turchin 1998, Pace 2001), natural impediments in the landscape (With 1994), the animal's knowledge of its environment (including locations of conspecifics and primary

prey), and human-induced habitat fragmentation and loss (Crooks 2002). A first step to modeling movement behavior is to study fine-scale movements and patterns of selection exhibited by individual animals (Wiens et al. 1993). If the broad-scale distribution patterns of individuals are the aggregate of fine-scaled movement behaviors (Turchin 1991, With 1994), then these behaviors may provide a mechanistic link to many ecological processes (Wiens et al. 1993).

Despite the increased use of wide-ranging nocturnal carnivores in conservation planning, little research has described their fine-scale movement patterns or factors influencing those movements. For instance, most studies of movement patterns of western cougars have described these patterns over weeks or months, based on ≤ 1 location per day, usually during daylight hours (Hemker et al. 1984, Anderson et al. 1992, Beier 1995, Ruth et al. 1998, Sweanor et al. 2000). Beier et al. (1995) described patterns in the distances cougars moved per 15-min interval as a function of time

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of day, sex, gross behavior state (e.g., hunting, feeding on previously-killed deer, raising cubs), but did not characterize cougar movements as a function of vegetation, topography, or other features in the animal's vicinity.

Cougar aversion to paved roads has been documented previously (Van Dyke et al. 1986, Belden and Hagedorn 1993, Sweanor et al. 2000, Dickson and Beier 2002), but all of these studies analyzed diurnal locations, presumably daybed locations in most cases, and no study has compared the observed number of paved road crossings with the number of crossings expected if cougars were indifferent to crossing. There has been increasing concern that highway crossing structures such as underpasses and culverts could funnel prey into areas where predators would exploit high prey density, creating a prey trap (Norman et al. 1998, Little et al. 2002), but there are no data supporting or refuting this possibility for cougars.

We attempted to address some of these information gaps by examining a subset of data collected and previously analyzed by Beier et al. (1995). Because cougar movement depends not only on habitat type and arrangement, but also on nonhabitat factors (e.g., location of a previously killed carcass, interactions with conspecifics), we attempted to isolate habitat factors by studying cougar movements during those periods when the focal animal was apparently not feeding on deer or interacting with other cougars. We studied animals during diel or nocturnal monitoring sessions to include periods of greatest daily movement. We also chose a time scale (movement during 15-min intervals) that minimized the risk that habitats traversed differed from those intersected by a line segment between consecutive locations, and we buffered these line segments to reflect the resolution of our measurements. Finally, we speculated that travel speed in a habitat might be a useful index of habitat selection. We reasoned that cougars would travel most quickly through habitats in which they are most uncomfortable (or that they perceive as less-profitable places to spend their time). If our data confirmed this pattern, travel speed could be used as a complement to more complex approaches such as compositional analysis.

Our objectives were to: (1) describe the travel path characteristics of individual cougars monitored during nocturnal or diel periods; (2) compare the vegetation, topography, and road density on paths used by and available to cougars during individual movement sessions; (3) investi-

gate whether travel speed is correlated with habitat selection patterns; (4) identify landscape features that facilitated or inhibited cougar movements, with particular attention to cougar movements near 2-lane paved roads; and (5) describe the extent to which cougars might linger at road crossing structures to ambush prey.

STUDY AREA

The Santa Ana Mountain Range (SAMR) encompassed approximately 2,060 km² of non-urban wildlands and 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). Our study area boundaries were delineated where the core of the study area met a major freeway or where human dwellings exceeded 4 residences per ha. 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) comprised most of the protected cougar habitat in the area. Beier (1993, 1995) and Dickson (2001) provide maps of the study area.

Plant communities on the study area included chaparral, oak woodlands (*Quercus engelmannii* and *Q. agrifolia*), coastal scrub, annual grasses, and coniferous forests at higher elevations (Barbour and Major 1995). Citrus and avocado orchards and other nonnative vegetation types occurred in parts of the area. Although human influence on the SAMR was widespread and included cattle grazing, agriculture, military training facilities, and public recreation areas, much of the study area remained undeveloped. Maximum average daily temperature was 24 °C and mean annual precipitation was 33 cm in lower elevations (Santa Ana Fire Station, Santa Ana, California, USA, 1948–2000), with somewhat cooler and more mesic conditions at higher elevations. Precipitation in the form of fog drip was common throughout the year 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. Although perennial streamflow was intermittent, springs, seeps, and other water sources were widely available throughout the study area (Beier and Barrett 1993).

Other carnivores common to the SAMR 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 this cougar population (Beier and Barrett 1993). Smaller prey included opossum (*Didelphis virginiana*), raccoon, and coyote (Beier and Barrett 1993).

METHODS

Radio-telemetry

Between May 1988 and December 1992, we captured, radio-collared, and monitored movements of cougars during distinct periods that ran from 1 hr before sunset until 1 hr after sunrise (nocturnal sessions) or for 24 hr (diel sessions, which always started and ended in the afternoon). During each session, we determined the location of a focal animal every 15 min using radiotelemetry. We obtained radiotelemetry locations from the ground using standard triangulation techniques (Mech 1983) conducted by a single observer using a vehicle. We attempted to track the focal animal at a distance >100 m to minimize influencing its movement and <500 m away to obtain accurate locations. To determine a single location, we took bearings within a span of 2–6 min. Because only a single observer was used and no network of precisely located receiving stations was available, we cannot compute meaningful error polygons (White and Garrott 1990). We minimized location errors by using only azimuths that differed by 60–120° and by getting close to the animal (White and Garrott 1990). We determined 85% and 96% of all locations from within 500 m and 1 km of the focal animal, respectively. We recorded these locations to the nearest 50 m of easting and northing; thus, movements ≤50 m in 15 min we typically recorded as stasis. We recorded each radiolocation as a Universal Transverse Mercator (UTM) point on a 1:24,000 U.S. Geological Survey (USGS) topographic map and then exported all points into a vector-based Geographic Information System (GIS; ArcView® 3.2a; Environmental Systems Research Institute, Redlands, California, USA).

By back-tracking movements with hounds on the day after a monitoring session to look for kills, tracks, and feces, and using other knowledge (such as vocalizations), Beier et al. (1995) classified the animal's behavior in each session into one of several categories. For this analysis, we used only sessions on adults (≥2 years old) and juveniles independent of their mother, excluding

sessions involving copulation, raising cubs, feeding on a previously killed large mammal, or killing a large mammal. We assume that the focal animal was hunting or traveling during these sessions; cougars in these sessions traveled much farther, and for a much larger fraction of the night, than cougars in other behavior categories (Beier et al. 1995). We chose sessions with this pattern because it was the most common movement pattern and because this choice minimized the risk that cougar response to vegetation, topography, and roads would be obscured by other factors (presence of a kill, cub, or mate).

Analysis of Movement and Selection

Within the GIS, we developed an ArcView® extension (CGRMVMNT) using an object-oriented programming language (AVENUE; Environmental Systems Research Institute). Using this extension, we calculated whether the animal was moving or static during each 15-min period (interval, hereafter), the straight-line distance and rate of movement between consecutive locations, proportion of a movement segment (the straight line connecting consecutive locations) intersecting each vegetation type, deviation angles for consecutive movement segments, and the maximum slope encountered during a movement segment. Additionally, we used the CGRMVMNT extension to calculate the proportion of vegetation types and the maximum slope available to an individual (see below). Our approach assumed a constant rate of movement during a movement interval, and attributed that rate to movement in each vegetation type traversed during the interval.

We use the term "habitat composition" to refer to a vector of proportions of vegetation types used by or available to an animal and where total habitat composition adds up to 100%. To account for error in assigning an individual radio-location to a single vegetation type, which can seriously bias analyses of selection (Rettie and McLoughlin 1999), we assumed that a cougar used all types within a 100-m radius of a linear movement segment or a static location in proportion to the area of that type within the buffered region (Fig. 1). We chose a 100-m radius buffer partly 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. Additionally, this buffer allows our analysis to detect the potential importance of habitat mosaics in the selection process (see Rettie and McLoughlin 1999).

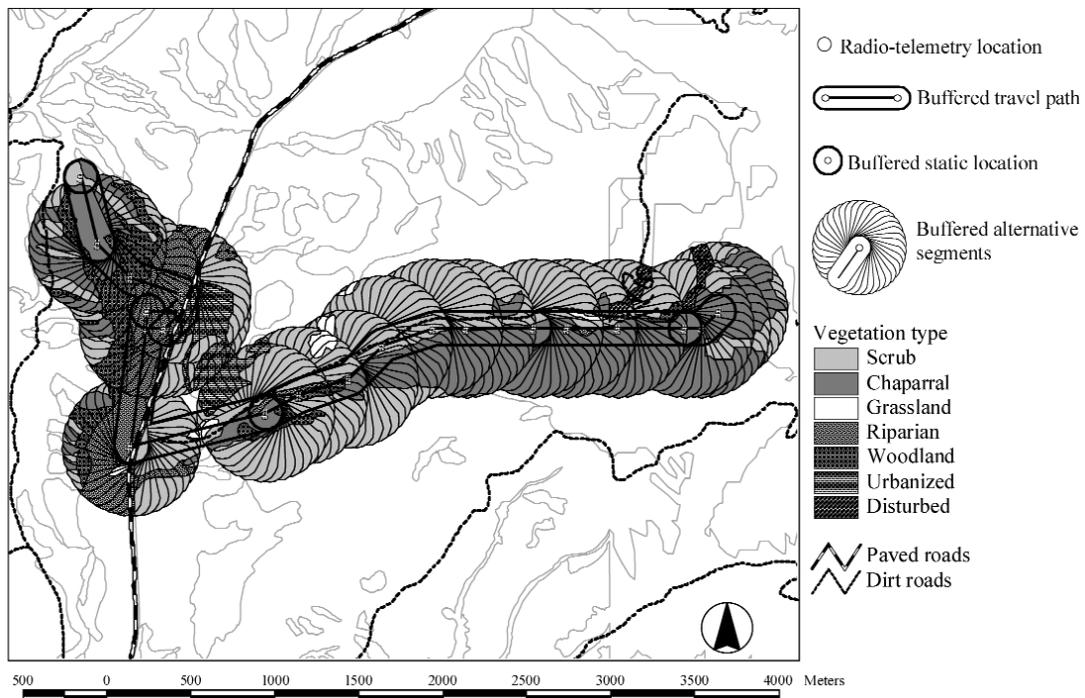


Fig. 1. Travel path through 7 vegetation types for female cougar F2 (session #100) monitored in the Santa Ana Mountain Range of southern California, USA, 1988–1992. This session began at 1800 hr, 6 Jul 1990 (eastern-most location) and ended at 0630 hr, 7 Jul 1990 (western-most location). Buffered static locations, travel path, and alternative segments generated by the CGR-MVMNT extension are shown.

To evaluate selection for all movements during an individual session, we compared the average habitat composition of the buffered movement segments (used) to the average habitat composition of systematically assigned buffered movement segments (available). To estimate availability at each movement segment, we calculated the average proportion of each vegetation type captured within 35 alternative travel path segments (also buffered at 100 m) generated at 10° increments around the starting point of each movement segment and equal in length to the mean of all movement segments during that nocturnal or diel monitoring session (Fig. 1). To evaluate selection during static intervals within a session, we compared the average habitat composition of buffered radio-locations to the average habitat compositions of buffered movement segments during that session. For an individual monitored for >1 session, we first calculated used and available habitat compositions within a session, and then averaged across sessions so that each animal contributed only 1 composition to any inferential statistical analysis.

We used compositional analysis (Aitchison 1986, Aebischer and Robertson 1992, Aebischer et al. 1993) to rank cougar selection of habitats,

with separate analyses for intervals of movement and stasis. Compositional analysis correctly uses the individual animal and not the radio-location as the sampling unit, thereby avoiding statistical problems arising from non-independence of proportions within a habitat composition (Aebischer et al. 1993). When cougar use of habitats was significantly nonrandom ($-N \ln \Lambda =$ test statistic, $\alpha < 0.05$), we used paired *t*-tests to compare mean utilization between all pairs of vegetation types ($\alpha < 0.05$). For each compositional analysis, we included only those habitat classes (e.g., vegetation types) available to all cougars, and included only those individual cougars using the same habitat classes. Because Aebischer et al. (1993) recommend a sample size ≥ 10 for compositional analyses, we pooled males and females together and did not test for sex effects on habitat selection.

For each movement session and individual cougar, we estimated the speed in each vegetation type,

$$S_v = \frac{\sum_{i=1}^n (s_i \times a_v)}{\sum_{i=1}^n a_v},$$

where n = number of movement segments during the session, s_i = the average speed (km/h) during

each 15-min interval based on the straight-line distance between locations, and a_v = area of vegetation type v within each 100-m buffered segment, i . We used the unweighted average S_v across sessions for each cougar as an estimate of that animal's speed in a particular vegetation type. To determine whether the rankings of speeds in vegetation types were correlated with the ranking of selection for each vegetation type, we used Spearman's rank order correlation coefficient (r_s = test statistic, $\alpha < 0.05$). We also used a paired t -test to test for differences between male and female mean movement rates through each vegetation type (t = test statistic, $\alpha < 0.05$).

We calculated the angular deviation from a straight line for all consecutive movement segments for all cougars. To test whether the circular distribution of deviation angles during movements ≥ 100 m was nonuniform, we performed a Rao's (1976) spacing test of uniformity (U = test statistic, $\alpha < 0.05$). To determine whether mean movement distance was correlated with turning angle, we calculated an angular-linear correlation coefficient (Fisher 1993, Zar 1999; nr_{al}^2 = test statistic, $\alpha < 0.05$).

We had an insufficient number of observations to investigate seasonal differences in patterns of selection during movements. Similarly, we had too few observations of daytime movement to compare nocturnal and daytime movements: we monitored all 17 individuals overnight, but only 5 cougars during diel sessions that included daylight hours.

Vegetation Types

Digital coverages of available vegetation types were acquired from Orange, Riverside, and San Diego counties. Vegetation polygons were identified by county personnel during 1990, 1992, 1993, and 1995 using LANDSAT Thematic Mapper and SPOT 2 satellite imagery, aerial photo interpretation, and field vegetation mapping surveys (ground-based and aerial). Although these data are nearly contemporaneous with our cougar locations, we checked all polygons classed as urban, disturbed, or agriculture in the vicinity of a session against field maps and notes, and made appropriate adjustments. We digitized and georeferenced all polygons using terrain-corrected satellite data and then digitally coded and projected these data as UTM coordinates (zone 11, North American Datum of 1927). These methods achieved a mean spatial accuracy of approximately 25 m and a minimum mapping unit between 0.2 and 2.0 ha. When possible, we more

precisely delineated narrow riparian areas using the near infrared band of a SPOT image to 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. Preliminary Descriptions of the Terrestrial Natural Communities of California. California Department of Fish and Game, Non-game Heritage Program, Sacramento, California, USA, unpublished report). By consolidating infrequent vegetation types with similar types, our analyses used 9 general vegetation types: scrub, chaparral, grassland, riparian, forest, woodland, agriculture, urbanized (residential, industrial, or commercial developments), and disturbed (see Dickson 2001). We classified lakes, rivers, wetlands, vernal pools, beaches, and man-made watercourses (0.70% of the study area) within the riparian vegetation type. Cliff and rock habitats (0.04%) were most often adjacent to chaparral vegetation types, and so we reclassified these as such. Because coastal dunes (0.01%) were usually associated with scrub vegetation, we grouped these types together.

Topography

We merged 26 USGS 1:24,000 digital elevation models (DEMs) to describe elevation and slope of the study area. We derived the slope (in degrees) of a cell location from the DEM using the ArcView[®] Spatial Analyst extension (Environmental Systems Research Institute, Redlands, California, USA). On the scale of individual movements, we considered maximum slope to be the most appropriate measure of topographic roughness encountered by an individual cougar. To calculate the maximum slope encountered (used) by an individual during a movement segment, we generated 100 alternative segments (of length equal to the original and terminating at a randomly located point within 50 m of the start and end point of the original) within a movement segment buffer and intersected these alternative segments with the DEM to derive an average value of maximum slope. We assumed that the maximum slope available to an individual was the average maximum slope value for the 35 alternative segments intersected with the DEM. We used a paired t -test to assess topographic selection for slope during all movement sessions for all individuals ($\alpha < 0.05$). For each individual monitored for >1 session, we calculated the mean maximum slope encountered during each ses-

sion, and then averaged across sessions so that each animal contributed only 1 value to the statistical analysis.

Roads

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 maps based on paper maps on which field crews had indicated accurate road location and condition (paved, dirt, absent) of mapped roads. To assess if roads affected cougar movements, we calculated total paved and dirt road densities (m/km^2) for all buffered movement (used) and alternative (available) paths. For each session, we calculated road densities at each used and available segment. To determine available densities, we averaged across the 35 alternative segments. We used a paired *t*-test to determine whether mean road densities for each session differed ($\alpha < 0.05$) between movements and alternative paths.

We analyzed road crossings by comparing the minimum number of crossings of 2-lane paved roads during a diel session to the number of crossings that would have occurred if the focal animal were indifferent to paved roads. We excluded freeway crossings from our analyses because 5 years of study documented only a single non-fatal freeway crossing (except via underpasses). To avoid having simulated paths cross paved driveways and residential roads, we restricted all simulations to a study area that was clipped to exclude residential areas within or abutting potential cougar habitat.

We inferred a single crossing for any movement segment that crossed a paved road. To estimate the expected number of crossings, we constructed a simple individual-based movement model, and generated 50 simulated paths for each session, each with the same number of movement segments as the actual travel path. Each simulation started using the initial bearing of the actual movement path, giving each simulation a tendency to move in the direction that the focal animal moved. Each subsequent movement segment in the simulations used a circular deviation angle and displacement selected at random, with replacement, from the observed distributions (Fig. 2). If a simulated travel path encountered a study area boundary or residential area, we forced the contacting segment to reflect back into the study area at a random deviation angle. We used a paired *t*-test to determine if the mean

number of actual road crossings was less ($\alpha < 0.05$) than expected. For individuals monitored for >1 session, we calculated a mean for each session, and then averaged across sessions so that each animal contributed only 1 value to the statistical analysis.

To examine whether cougars might exploit road crossing structures, such as underpasses or culverts, to trap prey, we examined the locations of all 5,562 daybed locations, 855 nocturnal static locations, and 145 cougar-killed prey carcasses in this study area during 1986–1992 (Beier and Barrett 1993, Beier 1995, Beier et al. 1995, Dickson and Beier 2002). We tallied the number of locations by type (daybed, static, carcass) that occurred within 300 m of a crossing structure under major roads (>2 lanes in each direction).

RESULTS

We analyzed 44 tracking sessions (29 nocturnal, 15 diel), including 22 sessions on 10 female cougars, and 22 sessions on 7 male cougars (Table 1). Although most cougars were monitored for 3 or more sessions, 5 individuals were monitored for only 1 nocturnal or diel session. The behavior of these 5 animals was thus measured with relatively low precision. Imprecision in measurements decreases the power of statistical tests but does not increase risk of Type I error (because these errors are subsumed in the residual sum of squares). Such risk is even lower for compositional analysis, which forced us to drop some of these animals from analyses when, for example, the individual did not use all vegetation types.

Movement Statistics

Total number of movement segments ≥ 50 m and static locations was 1,647 and 356, respectively. Following Beier et al. (1995) we assume that cougars were hunting during these sessions, and that many static locations represented sites where cougars slowly stalked and attempted to ambush prey. Other static locations probably represented rest sites.

The mean number of movement segments per session was 36.4 (SD = 6.3) for females and 37.7 (SD = 7.7) for males. On average, tracking sessions lasted 19.9 hrs (SD = 5.1) for females and 17.3 hrs (SD = 1.9) for males. Total duration of movements during a session averaged 9.1 hrs (SD = 1.6) for females and 9.4 hrs (SD = 1.9) for males. During a session, female cougars traveled an average of 10.7 km (SD = 4.5) and males traveled 10.0 km (SD = 3.0). Average time in static

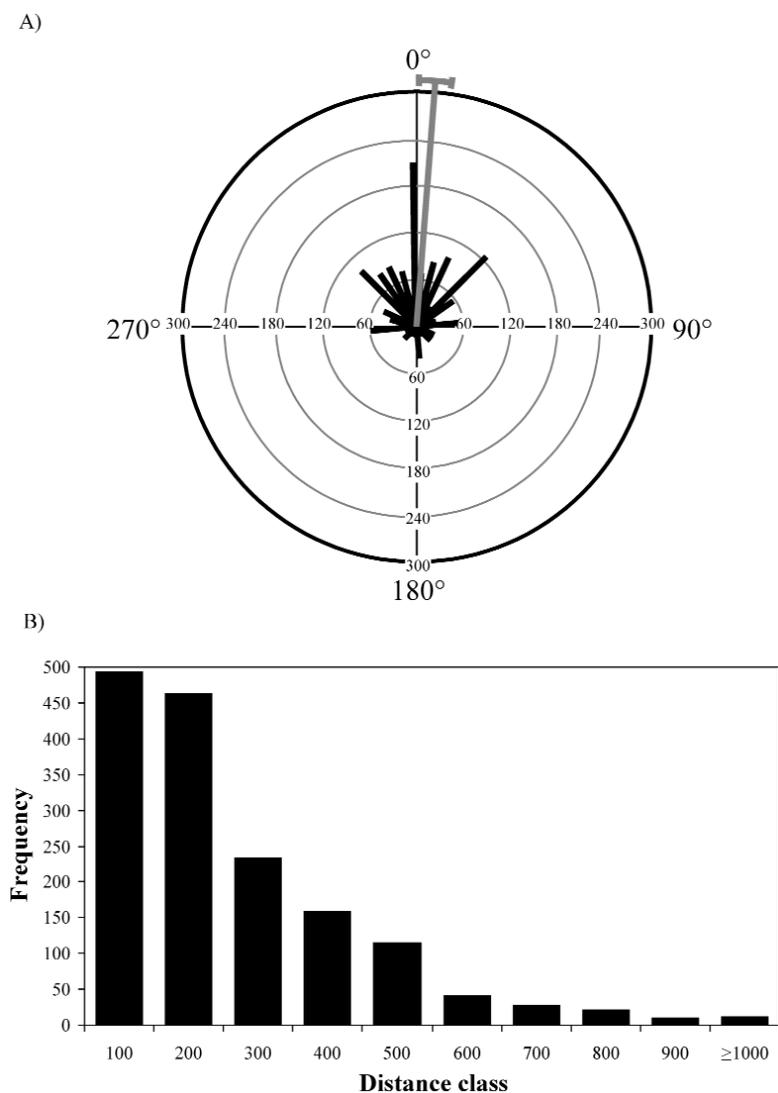


Fig. 2. (A) Frequency distribution of circular deviation angles for movements ≥ 100 m ($n = 1,536$) for 10 female and 7 male cougars during 44 radio-tracking sessions in southern California, USA, 1988–1992. An angle of 0° indicates an animal did not deviate from a straight line. Mean deviation angle and $\pm 95\%$ confidence intervals are shown. (B) Frequency distribution of distance moved per 15 min; abscissa is lower bound of each 100-m distance class ($n = 1,572$).

positions during a session was 10.8 hrs ($SD = 5.1$) for females and 7.9 hrs ($SD = 3.5$) for males, excluding the static intervals (of unknown duration) that occurred at the start and end of each session.

Movement segments between 50 and 100 m probably approached the resolution of triangulation. Because these short segments comprised only 0.4% of all movement segments, including these segments introduces little if any error to our analyses.

For 1,536 movement segments ≥ 100 m, cougars tended to move in a straight-line; the mean circular angle was $4.4^\circ \pm 3.8$ (95%CI; Fig. 2A) and the circular distribution of deviation angles was not uniform ($U = 351.8$, $P < 0.001$). During consecutive 15-min movement intervals, cougars often turned to the right or left; the average deviation angle during a session was 52.8° ($SD = 47.8$, $n = 1,536$). Distance traveled per 15 min (Fig. 2B) averaged 288 m ($SD = 192$, range = 100 – 2,059 m, $n = 1,572$), with 61% of movements < 300 m. The distance moved was not correlated with turning angle ($n r^2_{al} = 4.13$, $r = 0.34$, $P > 0.10$, $n = 36$ angle classes of 10° each).

Influence of Vegetation Type

The habitat composition of travel paths used by cougars differed from the habitat composition of alternative segments ($-N \ln \Lambda = 15.00$, $P < 0.025$, $df = 5$, $n = 9$ females and 7 males; Fig. 3). Because forested, agricultural, and disturbed vegetation types were not available to

some individuals, these types were dropped from all compositional analyses. Although riparian types ranked highest in the compositional analysis of habitat use during movements, use was statistically significant only in contrast with urbanized types. Chaparral and scrub types also were ranked above urbanized types. However, other contrasts were more ambiguous and difficult to interpret.

During intervals of stasis, cougar use of vegetation types was not statistically different from the habitat composition through which they traveled

during movement intervals ($-M\ln\Lambda = 4.76$, $P > 0.25$, $df = 4$, $n = 8$ females and 7 males with ≥ 7 static locations). Urbanized vegetation types were available to only a few individuals and were excluded from this analysis. Although neither the omnibus test nor pairwise contrasts were significant ($P > 0.05$), chaparral (10%) and riparian vegetation types (27%) ranked higher than scrub, grassland, and woodland types during periods of stasis, and were used as stopping points more often than they were encountered on travel paths.

Cougars moved slowest through riparian vegetation (grand mean = 1.07 km/hr), which was the type ranked highest in the compositional analysis of movements, and fastest through urbanized types (1.49 km/hr), the lowest ranking type (Table 1; Fig. 4A). In all vegetation types, females moved faster than males ($t = 5.52$, $P < 0.001$, $n = 9$). There was a significant negative correlation between ranks for travel speed and selection for a vegetation type ($r_s = -0.89$, $P < 0.05$, $n = 6$; Fig. 4B).

Influence of Topography

During monitored intervals of movement, all cougars used maximum slopes that were more gentle than those available ($t = 7.38$, $P < 0.001$, $n = 17$). For indi-

Table 1. Mean travel speeds in 9 vegetation types for 10 female and 7 male cougars in the Santa Ana Mountain Range, California, USA, 1988–1992. “—” indicates vegetation type was not encountered on travel path.

Animal ID	Total # of sessions monitored	Total # of movement segments	Travel speed (km/hr)									Mean travel speed (+/- 1SD)
			Scrub	Chaparral	Grassland	Riparian	Woodland	Forest	Agriculture	Urbanized	Disturbed	
F1	4	164	1.17	1.33	1.30	1.22	1.29	2.42	1.30	1.43	1.85	1.48 (0.41)
F2	4	142	1.22	1.06	1.42	1.11	1.30	—	1.19	1.23	1.29	1.23 (0.12)
F3	4	146	1.05	1.04	0.98	0.92	1.04	1.10	—	3.50	1.60	1.40 (0.87)
F4	2	68	0.84	0.87	0.79	0.77	0.48	0.90	—	0.60	0.74	0.75 (0.14)
F8	1	34	1.23	0.98	1.86	0.72	2.58	2.01	—	—	—	1.56 (0.70)
F10	1	28	0.78	0.99	—	0.98	1.03	—	0.63	1.16	—	0.93 (0.19)
F11	1	27	1.55	0.71	1.33	1.38	0.83	—	—	—	—	1.16 (0.37)
F17	2	87	1.05	0.98	1.02	1.10	1.09	1.16	1.74	1.05	1.09	1.14 (0.23)
F18	1	47	1.47	1.67	2.04	1.19	2.12	—	1.67	1.79	—	1.71 (0.32)
F19	2	74	1.54	1.64	1.28	1.50	1.48	1.03	—	1.40	—	1.41 (0.20)
Female mean (+/- 1SD)	2	82	1.19 (0.27)	1.13 (0.32)	1.34 (0.40)	1.09 (0.25)	1.32 (0.62)	1.44 (0.63)	1.31 (0.45)	1.52 (0.87)	1.32 (0.43)	1.29 (0.14)
M2	5	154	1.29	1.45	1.25	1.14	1.20	2.54	2.13	1.83	1.44	1.59 (0.48)
M5	1	26	0.81	0.73	1.12	1.13	0.83	—	—	—	—	0.93 (0.17)
M6	3	126	0.87	0.96	1.09	1.02	0.79	—	0.80	1.34	0.75	0.95 (0.20)
M9	2	97	1.33	1.22	1.25	1.17	1.54	1.02	—	1.56	2.22	1.41 (0.37)
M10	4	140	0.77	0.90	0.79	0.64	0.44	0.44	0.50	0.58	0.40	0.61 (0.18)
M12	3	116	1.05	1.01	1.42	1.21	1.09	0.85	0.56	0.85	0.99	1.00 (0.24)
M13	4	171	0.96	0.94	0.99	1.01	1.18	1.17	—	2.47	1.28	1.25 (0.51)
Male mean (+/- 1SD)	3	119	1.01 (0.22)	1.03 (0.24)	1.13 (0.20)	1.04 (0.19)	1.01 (0.36)	1.20 (0.79)	1.00 (0.77)	1.44 (0.68)	1.15 (0.58)	1.11 (0.14)
Grand mean (+/- 1SD)	3	97	1.11 (0.26)	1.09 (0.28)	1.25 (0.45)	1.07 (0.22)	1.19 (0.53)	1.33 (0.68)	1.17 (0.59)	1.49 (0.77)	1.22 (0.51)	1.21 (0.31)

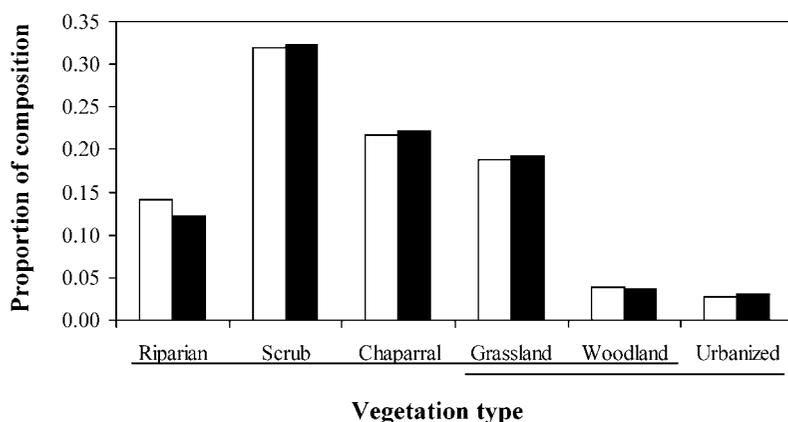


Fig. 3. Cougars ($n = 9$ females, 7 males) in the Santa Ana Mountain Range, California, USA, 1988–1992, tended to avoid human-dominated vegetation types and areas lacking understory woody plants during 15-min intervals when the animal moved ≥ 50 m. White bars indicate mean proportional utilization and black bars indicate mean proportional availability. Vegetation types are arranged from highest to lowest rank; underlining under names of vegetation types on the x-axis indicates vegetation types for which rankings are not significantly ($P > 0.05$) different.

vidual cougars, the mean available maximum slopes exceeded the used slopes by 0.71° to 3.54° (mean difference = 1.49° , SD = 0.81).

Influence of Roads

Total paved road density was about 21% lower on cougar travel paths (4.20 m/km^2 , = $0.10 \pm 0.20 \text{ m/km}^2$ [SD]) compared to available paths (5.30 m/km^2 , = $0.12 \pm 0.22 \text{ m/km}^2$; $t = -2.16$, $P = 0.04$, $n = 44$). Density of dirt roads was slightly higher on paths used by cougars (62.50 m/km^2 , = $1.42 \pm 1.04 \text{ m/km}^2$) compared to available paths (59.17 m/km^2 , = $1.34 \pm 0.78 \text{ m/km}^2$; $t = 1.48$, $P = 0.15$, $n = 44$). Buffered movement segments intersected dirt roads in all but 2 sessions, during which no dirt roads were available. All tracked individuals encountered or used dirt roads (368 occasions during 41 sessions).

Focal animals crossed 2-lane paved roads a total of 19 times; crossings involved 9 individual cougars, and occurred during 11 of the 44 sessions, with a mean of 0.45 crossings per cougar per session (SD = 0.67, $n = 17$ individuals). In contrast, simulated paths had a mean of 1.29 crossings per cougar per session (SD = 1.37), a difference that was statistically significant ($t = -2.50$, $P = 0.012$). The simulated travel paths of all individuals crossed paved roads. Only 3 individuals (F2, F10, M10) crossed paved roads more often (1 crossing each) than expected (0.37, 0.12, 0.87, respectively), based on simulated paths.

Three of 5,562 daybed locations, 0 of 855 nocturnal static locations, 0 of 85 deer killed by

cougars, and 2 of 60 small mammal kills (opossum, raccoon in these cases) were within 300 m of a crossing structure under a major highway. All 5 of these locations reflected the activities of a single female (F2) during the last days before her death, when she was apparently keying in on garbage-eating animals near a housing development, not on animals using the crossing structure. These numbers are lower than the 42 documented crossings via such structures (Beier

and Barrett 1993, Beier 1995). Because we required cougar tracks or unambiguous radio signals to confirm a crossing, these 42 crossings underestimate the true frequency of these events.

DISCUSSION

Based on our observations, traveling cougars tended to continue moving in a consistent direction, but often turned $\sim 54^\circ$ right or left, with few retrograde movements; movements averaged 288 m per 15-min interval and were not correlated with turning angle (Fig. 2). Our analysis of frequency of road crossings illustrates how these data can generate a null (random walk) model for hypothesis testing. These distributional data also can form the basis of more-sophisticated individually based movement models. Our results suggest that these advanced cougar movement models should reflect an aversion to paved roads and human-modified vegetation types, little differentiation among natural vegetation types, no aversion to dirt roads, and selection for gentle grades.

Our results support the assertion (Doak et al. 1992, Andren 1994, Dickson and Beier 2002) that habitat pattern has multi-scale impacts on the movement and distribution of animals. On the SAMR, Dickson and Beier (2002) identified strong patterns of selection by adult cougars for riparian areas at 2 spatial scales (based mostly on 1 static, diurnal location per animal per day). During the movement periods we analyzed here, riparian vegetation again ranked first, but several other natural vegetation types were statistically as

preferred as riparian vegetation. Additionally, grasslands ranked below riparian, scrub, and chaparral vegetation types for cougar movements—but not with the statistical significance Dickson and Beier (2002) observed for diurnal locations. Thus, traveling cougars monitored over nocturnal or diel periods used a broader range of habitats than used for diurnal locations alone (typically daybed sites; Beier et al. 1995). Our findings support the argument of Comiskey et al. (2002) that analysis of diurnal locations provides limited information about cougar patterns of selection during the times they are most active. We conclude that habitat use of cougars (and other nocturnal carnivores) estimated solely by analysis of diurnal locations may not accurately reflect habitat preferences of hunting and traveling animals. Movement studies of nocturnal carnivores should include data collected during those periods when the animal is most active.

Although previous research using diurnal locations suggested that cougars avoided grasslands due to lack of cover (Logan and Irwin 1985, Laing 1988, Williams et al. 1995, Dickson and Beier 2002), grasslands may play a more important role during cougar movement. Grassland vegetation constituted 19% of the composition of used movement segments. Perhaps grasslands provide cougars with the means to more readily permeate areas already known to them or to stalk and pursue prey. Grassland vegetation types were also a common (19%) characteristic of habitat mosaics used during intervals of stasis, which in some cases probably represented stalking or attempts to ambush prey (Beier et al. 1995).

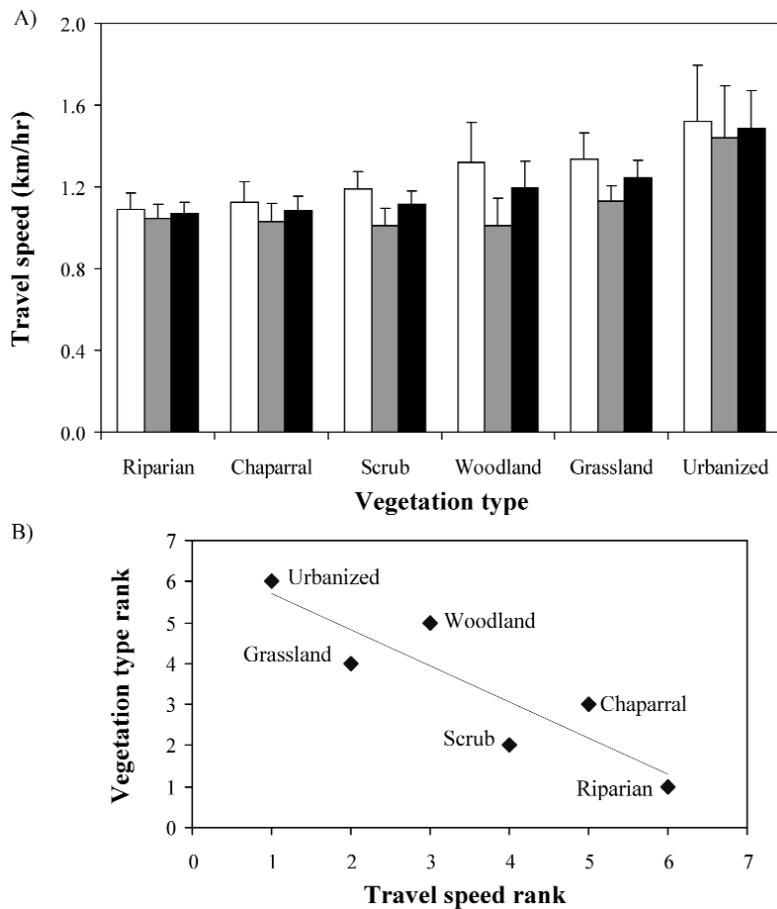


Fig. 4. Cougars in the Santa Ana Mountain Range tended to move more slowly through highly ranked vegetation types and more quickly through human-dominated types. (A) White bars indicate mean travel speed for females, gray bars indicate mean speed for males, and black bars indicate mean speed for the sexes combined. Error bars indicate +1 SE. Vegetation types are arranged from slowest to fastest based on the mean travel speed for the sexes combined. (B) The correlation between ranks for travel speed and vegetation type was statistically significant ($P < 0.05$).

If animals tend to move more rapidly through environments that make them uncomfortable or that offer few resources, our results on travel speed through various vegetation types is consistent with the rankings based on compositional analysis. An analysis of habitat selection based on travel speed, unlike other analyses of habitat use, does not require an estimate of habitat availability. Estimating habitat availability invariably requires making arbitrary assumptions. For instance, we made the reasonable assumption that habitat availability could be estimated by the average habitat composition in 35 buffered vectors with length equal to the average distance moved during a session. It would have been equally reasonable to estimate availability by buffered vectors with length equal to the actual distance moved in

a particular interval, or the average for all study animals. Our diligent search of the literature suggests that our study is the first attempt to make inferences about habitat use from travel speed for any terrestrial vertebrate, and we believe travel speed may offer an efficient tool for study of habitat selection patterns.

We found travel speed to be a useful complement to compositional analysis and other traditional methods of analyzing habitat selection. However, our single illustration of the method does not constitute a full exploration of its strengths and weaknesses. One important limitation of the travel speed method is that it cannot assess habitats the animal does not use at all. Similarly, travel speed cannot be used to assess animal response to fine-scale features such as paved roads.

Cougars consistently used travel paths that were less rugged than their general surroundings. This suggests that individuals consider the energetic cost of alternative paths, and that they probably have a mental map of their surroundings. This is consistent with Beier's (1995) description of canyon bottoms and ridgelines as common travel routes for dispersing cougars. Hunting or traveling individuals minimize energetic expense by frequenting landscape features that cost the least.

The effectiveness of habitats to support cougars is reduced by human disturbance, particularly roads (Murphy et al. 1999). Our results indicate that 2-lane paved roads constrain cougar movement significantly, but do not prevent movement. Indeed, vehicle collisions are the leading cause of mortality in this population, comprising 32% of all deaths of radiotagged cougars and their offspring (Beier and Barrett 1993). The problem is exacerbated by the placement of paved roads in preferred riparian habitats on the SAMR (Dickson and Beier 2002). Underpasses and other structures can facilitate cougar movements across paved roads (Beier 1993, Beier 1995, Foster and Humphrey 1995, Gloyne and Clevenger 2001), and we encourage efforts to construct or enhance crossing structures in preferred habitats.

Our data suggest that such structures are not exploited by predators in a way that creates a prey trap, supporting the conclusion of a recent review (Little et al. 2002). However, most crossings on our study area occurred where major roads crossed narrow, degraded habitat corridors, where cougars and their prey may not wish to linger. Cougars may behave differently where such crossing structures occur along roads passing through large blocks of intact habitat.

All individuals tracked during this study encountered or used dirt roads and dirt road density was 8% higher on cougar travel paths than on available travel segments, suggesting that dirt roads do not inhibit, and may even promote, cougar movement. Back-tracking with hounds after our monitoring sessions confirmed that individuals frequently used dirt roads or trails to travel up to 2 km, especially in areas of dense scrub or chaparral (Beier 1995). In northern Florida, translocated cougars tended to cross light duty roads and trails in favor of all other road types (Belden and Hagedorn 1993). On study areas in northern Arizona and southern Utah, Van Dyke et al. (1986) reported that most cougars crossed most of the unimproved dirt roads within their home ranges. In addition to providing a path through dense scrub, dirt roads and trails may facilitate predator access to prey (James and Stuart-Smith 2000, Kinley and Apps 2001, Kerley et al. 2002). We believe that retaining or creating a dirt road or trail along the midline of a planned movement corridor would facilitate its use by cougars and minimize straying into adjacent human-dominated landscapes.

MANAGEMENT IMPLICATIONS

Our results suggest that riparian vegetation, and other vegetation types that provide horizontal cover, are desirable features in movement corridors, that dirt roads should not impede cougar use of corridors, that corridors should lie along routes with relatively gentle topography, and that cougars do not use road crossing structures to create prey traps. Managers and land-use planners are using these findings to design corridors to facilitate cougar movement in the South Coast ecoregion of California (Beier et al. 2005).

Because cougars will become extinct in even the largest core areas of this ecoregion if connectivity is severed (Beier 1996), cougars are an appropriate focal species for corridor design. However, because a corridor that serves cougars will not serve all species, we urge planners to consider a broad suite of focal species in designing landscape linkages (Beier et al. 2005).

Our frequency distributions of movement lengths and turning angles, in conjunction with the habitat preferences documented herein, are also being used to construct sophisticated individual-based movement models (in collaboration with J. Tracey and K. Crooks, Colorado State University). We hope these approaches can help quantify the influence of landscape features on

other, large carnivores used as umbrella species for conservation planning.

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