

# Quantifying the influence of topographic position on cougar (*Puma concolor*) movement in southern California, USA

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## Keywords

compositional analysis; habitat selection; home range; scale; topography.

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## Abstract

Large carnivores are frequently used as focal species for landscape-level planning and conservation purposes. Information on cougars *Puma concolor*, for example, is being used to predict movement corridors and linkage areas in habitats influenced by rapid urbanization. However, animal movement through habitat terrain is a function of multiple factors, including complex topographic features. To assess the use of topographic position during movements by cougars in the Santa Ana Mountain Range of southern California, we analyzed the travel paths of 10–17 radio-tagged individuals monitored during 44 overnight sessions. We examined selection for canyon bottom, gentle slope, steep slope and ridgeline topography at the scale of the movement session and at the scale of the home range. At both scales of selection, our results suggest that traveling or hunting cougars discriminated in their use of topographic position, that canyon bottoms and gentle slopes (<6°) ranked highest in compositional analyses of selection, and that these patterns were not highly confounded by the presence of preferred vegetation types. Ridgelines were used significantly less often than other positions. Our novel method of quantifying availability and use of topographic positions permits the assessment of terrain features, such as canyon bottoms, in facilitating cougar movements. For complex landscapes, models of animal movement should consider the topographic context that motivates patterns of habitat use, and should be developed using data obtained and analyzed at the appropriate spatial and temporal scales.

## Introduction

Wide-ranging nocturnal carnivores are widely used as umbrella species in conservation planning at the scale of thousands of square kilometers (Beier, 1996; Soulé & Terborgh, 1999; Maehr *et al.*, 2002; Carroll, Noss & Paquet, 2003). In regions pressured by urbanization and habitat loss, planners require more specific information on landscape features critical to the linkage and maintenance of core areas (Beier *et al.*, 2006). Such conservation planning approaches often predict habitats suitable for linkage areas or core populations based on a knowledge of the species' response to vegetation, land use, road density and topography (e.g. Beier *et al.*, 2006). In previous work, we have analyzed how responses to these landscape features affect how cougars *Puma concolor* select daytime locations (primarily resting sites; Dickson & Beier, 2002) and nocturnal travel paths (Dickson, Jenness & Beier, 2005).

Forman (1995) argued that terrain has complex effects on animal movement and habitat use. Studies of habitat use typically address three topographic attributes, namely, elevation, slope and aspect as independent factors. For example, Dickson & Beier (2002) found no influence of these

three factors on daytime habitat use by cougars, and Dickson *et al.* (2005) noted a preference for nocturnal paths along slopes with relatively low grades. These three factors, however, do not convey information about landscape features – such as ridgelines, canyon bottoms and sloping terrain – that could influence animal movement. In this paper, we use the term 'topographic position' to refer to this class of features and address the influence of topographic position on cougar movement.

Because topography affects insolation, soil moisture, soil development, water flow and, consequently, vegetation (Forman, 1995), it can be difficult to separate the influence of topography on animal movement from that of vegetation community. For instance, in our study area we have noted that cougars prefer riparian vegetation for diurnal locations (Dickson & Beier, 2002) and nocturnal travel (Dickson *et al.*, 2005). Thus, an apparent preference for canyon bottoms could be an artifact of selection for riparian vegetation, or vice versa. Although an observational study such as ours cannot fully disentangle the relationship between topographic position and preferred vegetation, an objective analysis can report and discuss the degree of concordance among such variables.

We investigated the influence of topography on cougar movement in the Santa Ana Mountain Range (SAMR) of southern California, USA. Our objectives were to (1) characterize topographic positions available on the landscape, (2) compare the use and availability of topographic positions by traveling cougars monitored overnight, (3) investigate topographic use patterns during movement at two spatial scales of availability and (4) report the extent to which the effects of topographic position and vegetation might be confounded.

## Study area

The SAMR is situated in one of the fastest-growing, most densely populated regions in the USA (33–34°N, 117–118°W). At the time our study began, the SAMR study area encompassed *c.* 2060 km<sup>2</sup> of non-urban wildland and overlapped portions of three counties: Orange (38% of study area), Riverside (28%) and San Diego (34%). Cleveland National Forest, Camp Pendleton Marine Corps Base and Fallbrook Naval Weapons Station were the largest blocks of publicly owned cougar habitat on the study area (Beier & Barrett, 1993; Dickson *et al.*, 2005). We used major interstate highways and areas where human dwellings exceeded four residences per hectare to delineate the edges of potential habitat. Vegetation on the SAMR comprised many common California native plant communities, as well as orchards and other non-native vegetation types (Barbour & Major, 1995). Beier (1993, 1995), Beier & Barrett (1993), Dickson (2001) and Dickson *et al.* (2005) provide detailed descriptions and maps of the study area.

The SAMR is one of the northernmost parts of the Peninsular Mountain Complex, which extends 1450 km from the Los Angeles Basin in the north to the southern tip of Baja California (Norris & Webb, 1990). The range is characterized by a steep eastern face and more gentle western slopes (Norris & Webb, 1990). The complex topography of the SAMR study area included numerous undulating canyons and ridgelines and large basins at the outlet of many Pacific slope drainages. The southern SAMR was characterized by lower elevations and the broad mesas of the Santa Rosa plateau. Elevations within the SAMR ranged from sea level at the coast to 1717 m on Santiago Peak (mean elevation = 415 m ± 285 SD). The maximum average daily temperature was 24 °C and the mean annual precipitation was 33 cm at lower elevations (1948–2000; Santa Ana Fire Station, Santa Ana, CA, 41-m elevation), with slightly cooler and drier conditions at higher elevations.

## Methods

### Radio-telemetry

Between May 1988 and December 1992, 32 cougars were captured in cable snares set out at dusk and checked at dawn and immobilized with ketamine hydrochloride and xylazine hydrochloride in a concentrated 5:1 mixture. Except for mild abrasions and temporary swelling of the forefoot by

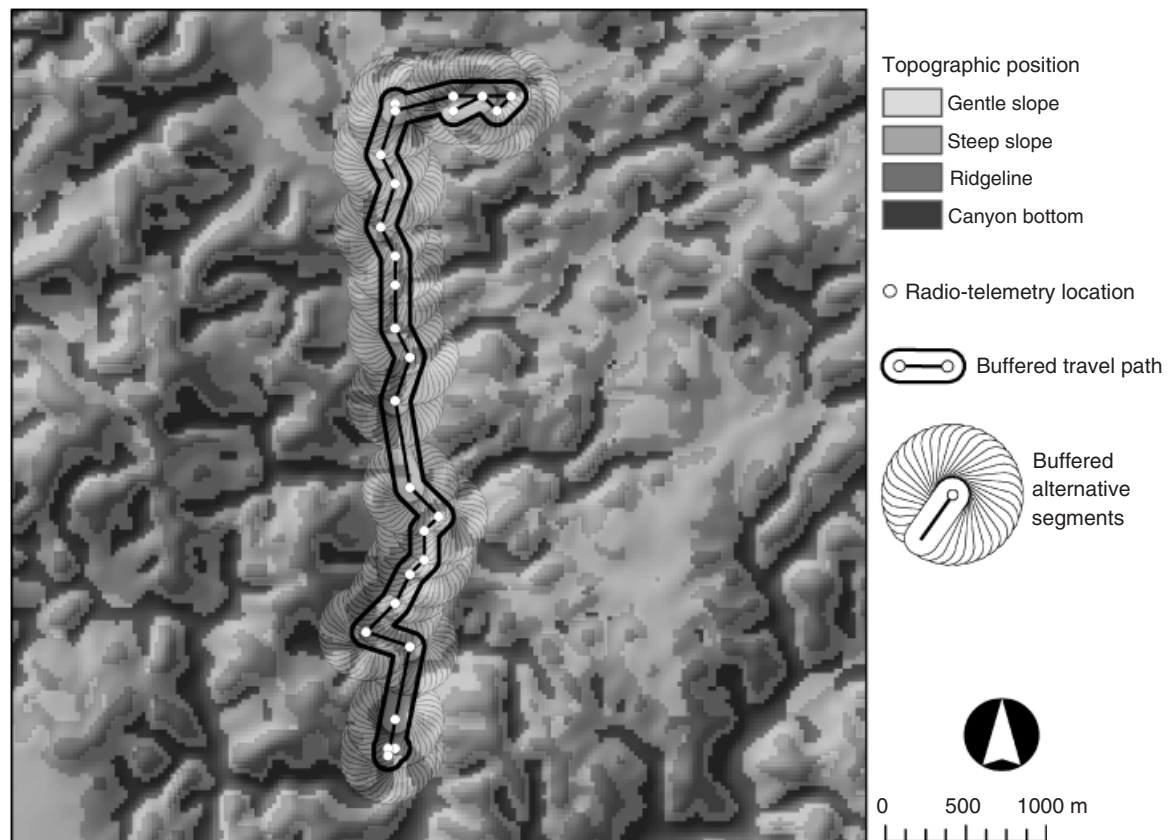
the cable snare, no animals were injured. Antibacterial dressing was applied to these abrasions and any pre-capture wounds, ophthalmic salve was applied to prevent drug-induced corneal dehydration, and temperature and respirations were monitored. Yohimbine was administered to most cougars to speed up recovery from the drugs and each animal was observed until it was able to walk, typically within 1 h of capture. Each captured cougar was fitted with a radio-transmitter collar, weighing about 650 g (model 500, Telonics Inc., Mesa, AZ, USA). Collars were not removed at the end of the study. The field study operated under Protocol R139-0394 issued by the Animal Care and Use Committee at the University of California at Berkeley, USA.

We monitored cougar movements during periods that ran from 1 h before sunset until 1 h after sunrise (nocturnal sessions) or for 24 h (diel sessions, which always started and ended in the afternoon). We recorded the location of the focal animal every quarter-hour using standard radio-telemetry triangulation techniques (Mech, 1983) conducted by a single observer who attempted to stay > 100 m from a focal animal to avoid influencing its movement, and used a motor vehicle to obtain two to three bearings within a 5-min period to estimate each animal location. About 85% of bearings were taken from within 500 m, and 96% from within 1000 m. We minimized location errors by getting close to the animal and by using only those azimuths that differed by 60–120° (White & Garrott, 1990; Dickson *et al.*, 2005). Locations were plotted on 1:24 000 US Geological Survey (USGS) topographic maps and recorded to the nearest 50 m of east and north. We exported each radio-location into a geographic information system (GIS; ArcGIS® 8.3; Environmental Systems Research Institute, Redlands, CA, USA) for analysis.

### Topographic surface classification

We created a topographic surface for the study area by merging 26 USGS 1:24 000 Level-1 digital elevation models (DEMs). These DEMs are digital representations of cartographic information in a raster form (regular grid with 30-m spacing of cells) produced from scanned National Aerial Photography Program photographs with a vertical accuracy between 7 and 15 m (USGS 1993. US GeoData digital elevation model factsheet, Reston, VA, USA). Our final composite DEM consisted of over 2.2 million 30 × 30-m grid cells. From this composite surface, we derived the elevation (in meters) and slope (in degrees) of each cell location using algorithms implemented in the Spatial Analyst extension (Environmental Systems Research Institute) to ArcGIS®.

We developed a grid-based algorithm to classify the topography of the SAMR into four classes or positions: canyon bottom, gentle slope, steep slope and ridgeline. The algorithm generated a circular moving window with a radius of 180 m (six grid cells, encompassing an area of about 10.1 ha) around a focal cell and subtracted the mean elevation for all cells within the circular window from the



**Figure 1** Travel path through four topographic positions for female cougar *Puma concolor* F10 (session #105) monitored in the Santa Ana Mountain Range of southern California, USA. This session began at 18:30 h, 10 August 1990 (southern end) and ended at 07:15 h, 11 August 1990 (northern end). Radio-telemetry locations, buffered travel path and buffered alternative segments generated by the CGRMVMNT extension are shown.

elevation value at the focal cell. For example, a resultant negative difference indicated a cell lower in elevation than the mean of its circular neighborhood. We defined cells with difference values  $\leq -8$  m as canyon bottoms, cells with difference values  $\geq 8$  m as ridgelines, and cells with difference values between  $-8$  and  $+8$  m as gentle slopes (slope  $< 6^\circ$ ) or steep slopes (slope  $\geq 6^\circ$ ). We buffered the study area at 300 m to avoid the influence of edges on our algorithm.

We could have devised a larger number of slope classes, and there is no 'correct' method or criteria to select the radius of the circular window, threshold difference in elevation or threshold slope value. The values we chose produced a map that corresponded to how a human observer familiar with our landscape perceives topographic position in our study area and may approximate the topographic perception of other medium-sized terrestrial mammals, such as cougars (see Fig. 1). We chose to recognize only four positions to increase statistical power and to minimize the risk of over-interpreting DEMs beyond their accuracy and precision (Shortridge, 2001). Before our analysis of movement and selection, we converted our grid-based classification to vector format.

### Analysis of movement and topographic selection

We used the CGRMVMNT extension (Dickson *et al.*, 2005) to the ArcView<sup>®</sup> GIS (Environmental Systems Research Institute) to calculate whether an animal was moving during each 15-min period (*interval* hereafter), the straight-line distance between consecutive locations and the proportion of topographic positions used by and available to an individual (see below). We investigated selection at two spatial scales, by comparing used settings with those available at the scale of the movement session and at the scale of the home range.

We calculated a 'topographic composition' used by or available to an animal based on a vector of proportions of topographic positions; for each individual movement or home range, the topographic composition sums to 1.00. To account for triangulation error and errors inherent in the digital coverages, we assumed that a cougar used all of the topographic positions within a 100-m radius of a linear movement segment in proportion to the area of that position within this buffered movement segment (Rettie & McLoughlin, 1999; Dickson *et al.*, 2005). This approach

**Table 1** Movement and home range statistics for 17 cougars *Puma concolor* in the Santa Ana Mountain Range, CA, USA, 1988–1992

Animal ID	Movements			Home range		
	Total no. of sessions monitored	Total no. of movement segments	Total distance moved (km)	Total no. of years monitored	Total no. of locations on separate days	Home range size <sup>a</sup> (km <sup>2</sup> )
F1	4	164	13.3	3	433	79.7
F2	4	142	10.2	4	718	52.3
F3	4	146	9.1	2	590	42.5
F4	2	68	6.6	3	537	37.5
F8	1	34	8.6	1	37	–
F10	1	28	6.6	3	380	85.2
F11	1	27	7.1	5	357	75.1
F17	2	87	11.5	1	53	–
F18	1	47	21.3	2	70	147.5
F19	2	74	13.1	1	130	114.0
M2	5	154	10.7	2	290	412.0
M5	1	26	6.0	1	164	–
M6	3	126	9.5	1	190	–
M9	2	97	15.1	2	129	527.2
M10	4	140	6.7	1	162	–
M12	3	116	10.9	1	77	–
M13	4	171	10.7	1	110	–
Mean (± 1SD)	2.6 (1.4)	96.9 (52.0)	10.4 (3.8)	2.0 (1.2)	260.4 (208.0)	157.3 (170.0)

Multi-year home ranges were calculated only for individual adult cougars that yielded >50 total locations across ≥1 year of monitoring. '–' indicates that home range size was not estimated for this dispersing juvenile because it did not have a stable home range during the session(s) it was monitored.

<sup>a</sup>Multi-year 85% fixed-kernel home range estimated by Dickson & Beier (2002).

also allowed us to detect patterns of selection for topographic habitat mosaics (Rettie & McLoughlin, 1999).

At the scale of the movement session, we evaluated selection during an individual session by comparing the average topographic composition of all buffered movement segments ('used') to the average topographic composition of systematically assigned and buffered alternative segments ('available'). We estimated availability at each movement segment by calculating the average topographic composition within 35 alternative travel path segments generated at 10° increments around the starting point of each movement segment and buffered at 100 m. These alternative segments were each equal in length to the mean of all movement segments during that nocturnal or diel monitoring session (Fig. 1). For each cougar monitored for >1 session, we calculated used and available topographic compositions within a session and then averaged across all sessions for that individual so that each individual contributed only one composition to any inferential statistical analysis. We excluded a movement session if the focal animal was >1 km from the observer for >2 h or did not move during the session, or if we failed to obtain locations for >1 h, or if we later determined that the animal's movement had probably been influenced by a vehicle collision. All other animals and movement sessions were used in the analyses.

At the scale of the individual home range, we compared the average topographic composition used by an individual with the available topographic composition within the individual's multi-year 85% fixed-kernel home range

(Dickson & Beier, 2002). At the scale of the home range, we considered only 10 individuals in the analysis, excluding several juvenile dispersers that did not have a stable home range during the monitoring sessions (Table 1).

At both scales, we used compositional analysis (Aitchison, 1986; Aebischer & Robertson, 1992; Aebischer, Robertson & Kenward, 1993) to test whether cougar use of topographic positions was significantly non-random and to rank cougar selection for topographic position. Aebischer *et al.* (1993) and Dickson & Beier (2002) provide detailed descriptions of compositional analysis and the derivation of the statistical models we used. When our test statistic ( $-N \ln \Lambda$ ,  $\alpha = 0.05$ ) indicated non-random use of topographic positions, we used paired *t*-tests to compare mean utilization between all pairs of topographic positions (test statistic = *t*,  $\alpha = 0.05$ ). Because compositional analyses can be sensitive to small sample size (generally <10; Aebischer *et al.*, 1993), we pooled males and females and did not test for sex effects on selection.

For our analyses we used the 44 tracking sessions previously examined by Dickson *et al.* (2005) and identified by Beier, Choate & Barrett (1995) as those for hunting or traveling individuals. We included sessions on adults (≥2 years old) and juveniles independent of their mother and excluded sessions in which the focal animal was copulating, rearing cubs <7 weeks old, or feeding on or killing a large mammal. These data included 1647 movement segments ≥50 m distributed among 22 sessions on 10 female cougars and 22 sessions on seven male cougars (Table 1). We

had insufficient observations to investigate seasonal differences in patterns of selection during movements, or to compare nocturnal and daytime movements.

### Concordance between topographic position and vegetation

To identify whether the topographic position of cougars was confounded with vegetation type, we calculated the total proportional overlap, or concordance between each topographic position and each of the nine major vegetation types identified by Dickson (2001) for all grid cells used by cougars during monitoring sessions. We were especially interested in whether the expected preference for canyon bottoms might reflect a high degree of concordance between canyon bottoms and riparian vegetation.

## Results

### Movement and topographic selection

For the four topographic positions characterized on the SAMR landscape, 16% of the total area was classified as canyon bottom, 21% as gentle slope, 45% as steep slope and 18% as ridgeline (Table 2). All individual cougars in all sessions used each of the four topographic positions during monitored periods of movement and all four positions were available at the movement session or home-range scale of selection.

The topographic composition of travel paths used by cougars on the SAMR differed from the composition of alternative segments ( $-N \ln \Lambda = 23.30$ ,  $P < 0.001$ , d.f. = 3,  $n = 17$ ; Fig. 2). The canyon bottom position ranked highest in the compositional analysis of selection and the ridgeline position ranked lowest. Compared with all other topographic positions, canyon bottoms received disproportionately high use and ridgelines received disproportionately low use (Table 3). The difference between use of the gentle and steep slopes, however, was not statistically significant.

The topographic composition of travel paths used by cougars also differed from the composition of the multi-year 85% fixed-kernel home range ( $-N \ln \Lambda = 10.92$ ,  $P < 0.025$ , d.f. = 3,  $n = 10$ ; Fig. 3). The gentle slope position ranked first, followed by canyon bottoms and steep slopes, with ridgelines ranked last. Although ridgelines were used

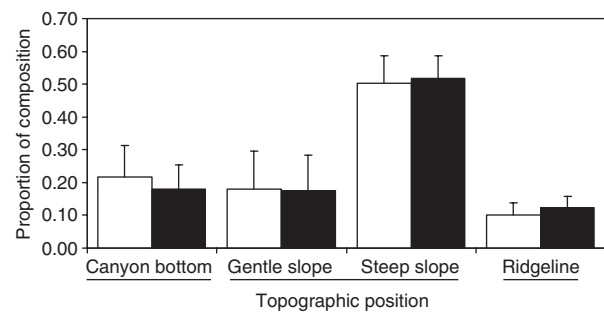
significantly less often than all other positions, no other pairwise comparisons were statistically significant (Table 3).

### Confounding between topographic position and vegetation

In areas used by cougars at both scales of selection, concordance between topographic position and vegetation type was not high (Tables 2 and 4). Although areas with riparian vegetation often coincided with gentle slopes and canyon bottoms, over 75% of canyon bottoms and gentle slopes supported non-riparian vegetation and cougar use of these topographic positions did not appear to be highly influenced by the presence of riparian areas.

## Discussion

On the SAMR study area, our results suggest that traveling or hunting cougars discriminated in their use of topographic positions. Our method of characterizing availability and use of topographic positions permits the assessment of complex landscape features, such as canyon bottoms, in facilitating cougar movements. If, as suggested by Forman (1995), vegetation mosaics facilitate horizontal animal movements



**Figure 2** When topographic positions used during movements are compared with topographic positions available at each 15-min interval, cougars *Puma concolor* ( $n = 17$ ) in the Santa Ana Mountain Range, CA, USA, 1988–1992, used canyon topography significantly more often than ridgelines during 15-min intervals when they moved  $\geq 50$  m. White bars indicate mean (+1sd) proportional utilization and black bars indicate mean (+1sd) proportional availability. Topographic positions are arranged from most to least preferred; underlining on the x-axis labels indicates positions for which rankings are not significantly different.

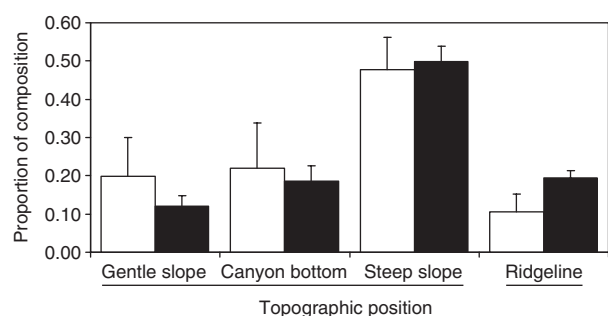
**Table 2** Total proportion of each vegetation type coinciding with each topographic position for all grid cells used by 17 cougars *Puma concolor* during monitoring sessions in the Santa Ana Mountain Range (SAMR), CA, USA, 1988–1992

Topographic position	Vegetation type									Area of used	Area of SAMR
	Riparian	Scrub	Woodland	Chaparral	Grassland	Forest	Developed	Disturbed	Agriculture		
Canyon bottom	0.304	0.180	0.126	0.262	0.111	0.224	0.120	0.135	0.054	0.187	0.163
Gentle slope	0.336	0.111	0.326	0.059	0.242	0.016	0.213	0.310	0.363	0.184	0.212
Steep slope	0.344	0.560	0.484	0.537	0.562	0.624	0.524	0.468	0.512	0.521	0.450
Ridgeline	0.016	0.149	0.064	0.142	0.085	0.136	0.143	0.087	0.071	0.108	0.175

Each column sums to 1.00. Vegetation types are arranged from most to least preferred (after Dickson & Beier, 2002).

**Table 3** Statistics for pairwise comparisons of topographic positions at the movement session and home range scales for 17 cougars *Puma concolor* in the Santa Ana Mountain Range, CA, USA, 1988–1992

	Gentle slope		Steep slope		Ridgeline		
	d.f.	t	P	t	P	t	P
<i>Movement</i>							
Canyon bottom	16	5.078	<0.001	5.833	<0.001	6.043	<0.001
Gentle slope	16			1.089	0.292	3.978	0.001
Steep slope	16					3.970	0.001
<i>Home range</i>							
Canyon bottom	9	-0.623	0.549	0.683	0.512	3.574	0.006
Gentle slope	9			1.370	0.204	2.485	0.035
Steep slope	9					3.665	0.005



**Figure 3** When topographic positions used during movements are compared with topographic positions available in the individual's home range, cougars *Puma concolor* ( $n=10$ ) in the Santa Ana Mountain Range, CA, USA, 1988–1992, rarely used ridgelines during 15-min intervals when they moved  $\geq 50$  m. Other trends were not statistically significant. White bars indicate mean (+1sd) proportional utilization and black bars indicate mean (+1sd) proportional availability. Topographic positions are arranged from most to least preferred; underlining on the x-axis labels indicates positions for which rankings are not significantly different.

**Table 4** Total proportion of each topographic position coinciding with each vegetation type for all grid cells used by 17 cougars *Puma concolor* during monitoring sessions in the Santa Ana Mountain Range (SAMR), CA, USA, 1988–1992

Vegetation type	Topographic position				Area used	Area of SAMR
	Canyon bottom	Gentle slope	Steep slope	Ridgeline		
Riparian	0.217	0.245	0.088	0.020	0.134	0.050
Scrub	0.334	0.210	0.373	0.475	0.347	0.210
Woodland	0.027	0.072	0.038	0.024	0.040	0.037
Chaparral	0.239	0.055	0.176	0.224	0.171	0.406
Grassland	0.119	0.264	0.217	0.157	0.201	0.154
Forest	0.022	0.002	0.021	0.022	0.018	0.012
Developed	0.015	0.028	0.024	0.032	0.024	0.059
Disturbed	0.014	0.034	0.018	0.016	0.020	0.012
Agriculture	0.013	0.090	0.045	0.030	0.045	0.060

Each column sums to 1.00. Vegetation types are arranged from most to least preferred (after Dickson & Beier, 2002).

in rugged terrain and valleys permit vertical movements, then our results, combined with the results of Dickson *et al.* (2005), capture many of the habitat-level cues associated with cougar movement.

Across the two scales of selection for topographic position that we examined, cougars tended to use canyon bottom and slope positions gentler than their surroundings. These results are consistent with the results of Dickson *et al.* (2005), who identified cougar use of travel paths on the SAMR with maximum slopes that were more gentle than those available on alternative paths. In contrast to our results, previous studies using information from diurnal locations suggested that cougars select high-elevation, steep habitats. For example, Logan & Irwin (1985) reported that cougar locations were on more rugged and steeper terrain than random points in their north central Wyoming study area. This difference may in part be due to differences in the analytical approach. To the extent that cougar home ranges were steeper and more rugged than the study area as a whole, the analysis of Logan & Irwin (1985) could reflect selection of home ranges within a landscape that may differ from selection at the third-order scale (*sensu* Johnson, 1980) that we studied. In southern Utah, Laing (1988) reported selection for higher elevations and steeper slopes but did not specifically characterize topographic availability on his study area. These apparent selection patterns for higher elevations and steeper slopes may have been driven by the migratory movements of prey and availability of water. Perhaps most important, these previous studies examined individual locations acquired at intervals  $\geq 3$  days and did not address terrain feature selection during periods of movement.

At both scales of selection, our results suggest that cougars avoided ridgelines during periods of movement. Studying the SAMR population, Beier (1995) claimed (without quantitative support) that 'the most frequently used travel routes ... were ... stream channels, followed by ridgeline routes.' This claim for preferential use of ridges was based on Beier's impression from personal radio-tracking experience, but is not supported by our quantitative analysis.

We speculate that cougars selectively use canyons for two reasons. First, populations of non-migratory mule deer *Odocoileus hemionus*, the most important prey species for cougars on the SAMR (Beier & Barrett, 1993), frequently used canyons [Environmental Science Associates, 1992 (unpubl. report), Eastern Transportation Corridor Deer Telemetry Study, San Francisco, CA, USA], and cougar kills and cache sites were most often associated with canyons or riparian vegetation (Beier *et al.*, 1995). Although quantitative information on the spatial distribution of mule deer on our study area was unavailable, how cougars use terrain features on the SAMR is likely correlated with where and when their primary prey are also using these features. Second, hunting or traveling cougars probably minimize energetic expense by using canyon bottoms and gentle slopes (Dickson *et al.*, 2005). Apps (1999) similarly concluded that Canadian lynx *Lynx canadensis* avoided higher

elevations and steeper slopes in south-eastern British Columbia in part due to the energetic cost of accessing suitable habitats in these areas.

Animal movements are influenced by the major spatial attributes of a habitat mosaic, including terrain features (Forman, 1995). Elevation, slope and aspect are the variables most commonly used to describe terrain, but they are incomplete descriptors of the topographic context that motivates patterns of selection. Herein we demonstrate that topographic position can be calculated from widely available digital elevation data and that cougars exhibit patterns of selection for certain topographic positions that are at least partially independent of preferences for vegetation types. We could have defined more than four topographic positions and we acknowledge the arbitrary nature of some of our decision rules (e.g. size of neighborhood, class thresholds for elevation differences between a focal cell and its neighborhood). We urge others using our approach to develop rules appropriate to the focal species and landscape.

Increasingly, GIS-based models are used to predict not only habitat use but also areas important for animal movement. Such approaches include least-cost path analysis (Bani *et al.*, 2002; Schadt *et al.*, 2002; Adriaensen *et al.*, 2003), least-cost corridor analysis (Quinby *et al.*, 2000; Miller *et al.*, 2003; Beier *et al.*, 2006) and similar types of permeability analysis (Singleton, Gaines & Lehmkuhl, 2002; Theobald, 2006). In developing their least-cost corridor models for 20 focal species in southern California, Beier *et al.* (2006) were initially unable to take advantage of reported associations between animals and topographic features. Our approach remedies this shortcoming and may improve the realism of quantitative models developed for delineating and conserving movement corridors for cougars and other sensitive taxa.

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## References

Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H. & Matthysen, E. (2003). The

application of 'least-cost' modeling as a functional landscape model. *Landscape Urban Plann.* **64**, 233–247.

- Aebischer, N.J. & Robertson, P.A. (1992). Practical aspects of compositional analysis as applied to pheasant habitat utilization. In *Wildlife telemetry: remote monitoring and tracking of animals*: 285–293. Priede, I.G. & Swift, S.M. (Eds). Chichester: Ellis Horwood.
- Aebischer, N.J., Robertson, P.A. & Kenward, R.E. (1993). Compositional analysis of habitat use from animal radio-tracking data. *Ecology* **74**, 1313–1325.
- Aitchison, J. (1986). *The statistical analysis of compositional data*. London: Chapman & Hall.
- Apps, C.D. (1999). Space-use, diet, demographics, and topographic associations of lynx in the southern Canadian Rocky Mountains: a study. In *Ecology and conservation of lynx in the United States*: 351–371. Ruggiero, L.F., Aubry, K.B., Buskirk, S.W., Koehler, G.M., Krebs, C.J., McKelvey, K.S. & Squires, J.R. (Eds). Boulder: University Press of Colorado.
- Bani, L., Baietto, M., Bottoni, L. & Massa, R. (2002). The use of focal species in designing a habitat network for a lowland area of Lombardy, Italy. *Conserv. Biol.* **16**, 826–831.
- Barbour, M.G. & Major, J. (1995). *Terrestrial vegetation of California*. Davis: California Native Plant Society.
- Beier, P. (1993). Determining minimum habitat areas and habitat corridors for cougars. *Conserv. Biol.* **7**, 94–108.
- Beier, P. (1995). Dispersal of juvenile cougars in fragmented habitat. *J. Wildl. Mgmt.* **59**, 228–237.
- Beier, P. (1996). Metapopulation modeling, tenacious tracking, and cougar conservation. In *Metapopulations and wildlife management*: 293–323. McCullough, D.R. (Ed.). Washington, DC: Island Press.
- Beier, P. & Barrett, R.H. (1993). *The cougar in the Santa Ana Mountain Range, California*. Final report, Orange County Cooperative Mountain Lion Study, Department of Forestry and Resource Management, University of California, Berkeley.
- Beier, P., Choate, D. & Barrett, R.H. (1995). Movement patterns of mountain lions during different behaviors. *J. Mammal.* **76**, 1056–1070.
- Beier, P., Penrod, K., Luke, C., Spencer, W. & Cabañero, C. (2006). South Coast missing linkages: restoring connectivity to wildlands in the largest metropolitan area in the United States. In *Connectivity and conservation*: 555–586. Crooks, K.R. & Sanjayan, M.A. (Eds). London: Cambridge University Press.
- Carroll, C., Noss, R.F. & Paquet, P. (2003). Carnivores as focal species for conservation planning in the Rocky Mountain Region. *Ecol. Appl.* **11**, 961–980.
- Dickson, B.G. (2001). *Home range and habitat selection by adult cougars in the Santa Ana Mountain Range of southern California*. MS thesis, Northern Arizona University, Flagstaff, USA.
- Dickson, B.G. & Beier, P. (2002). Home range and habitat selection by adult cougars in southern California. *J. Wildl. Mgmt.* **66**, 1235–1245.

- Dickson, B.G., Jenness, J.S. & Beier, P. (2005). Influence of vegetation, topography, and roads on cougar movement in southern California. *J. Wildl. Mgmt.* **69**, 264–276.
- Forman, R.T.T. (1995). *Land mosaics: the ecology of landscapes and regions*. Cambridge: Cambridge University Press.
- Johnson, D.H. (1980). The comparison of usage and availability measurements for evaluation of resource preference. *Ecology* **61**, 65–71.
- Laing, S.P. (1988). *Cougar habitat selection and spatial use patterns in southern Utah*. MS thesis, University of Wyoming, Laramie, USA.
- Logan, K.A. & Irwin, L.L. (1985). Mountain lion habitats in the Big Horn Mountains, Wyoming. *Wildl. Soc. Bull.* **13**, 257–262.
- Maehr, D.S., Land, E.D., Shindle, D.B., Bass, O.L. & Hctor, T.S. (2002). Florida panther dispersal and conservation. *Biol. Conserv.* **106**, 187–197.
- Mech, L.D. (1983). *Handbook of animal radio-tracking*. Minneapolis: University of Minnesota.
- Miller, B., Foreman, D., Fink, M., Shinneman, D., Smith, J., DeMarco, M., Soulé, M. & Howard, R. (2003). *Southern rockies wildlands network vision*. Boulder: Colorado Mountain Club Press.
- Norris, R.M. & Webb, R.W. (1990). *Geology of California*. New York: John Wiley and Sons.
- Quinby, P., Trombulak, S., Lee, T., Long, R., MacKay, P., Lane, J. & Henry, M. (2000). Opportunities for wildlife habitat connectivity between Algonquin Provincial Park and the Adirondack Park. *Wild Earth* **10**, 75–80.
- Rettie, J.W. & McLoughlin, P.D. (1999). Overcoming radiotelemetry bias in habitat-selection studies. *Can. J. Zool.* **77**, 1175–1184.
- Schadt, S., Knauer, F., Kaczensky, P., Revilla, E., Wiegand, T. & Trepl, L. (2002). Rule-based assessment of suitable habitat and patch connectivity for the Eurasian lynx. *Ecol. Appl.* **12**, 1469–1483.
- Shortridge, A. (2001). Characterizing uncertainty in digital elevation models. In *Spatial uncertainty in ecology: implications for remote sensing and GIS applications*: 238–257. Hunsaker, C.T., Goodchild, M.F., Friedl, M.A. & Case, T.J. (Eds). New York: Springer.
- Singleton, P.H., Gaines, W.L. & Lehmkuhl, J.F. (2002). *Landscape permeability for large carnivores in Washington: a geographic information system weighted-distance and least-cost corridor assessment*. Research paper PNW-RP-549, USDA Pacific Northwest Research Station.
- Soulé, M.E. & Terborgh, J. (1999). *Continental conservation*. Covelo: Island Press.
- Theobald, D.M. (2006). Landscape networks: modeling functional connectivity using least-cost path analysis and graph theory. In *Connectivity and conservation*: 416–443. Crooks, K.R. & Sanjayan, M.A. (Eds). London: Cambridge University Press.
- White, G.C. & Garrott, R.A. (1990). *Analysis of wildlife radio-tracking data*. San Diego: Academic Press.