

## Interfacing models of wildlife habitat and human development to predict the future distribution of puma habitat

CHRISTOPHER L. BURDETT,<sup>1,†</sup> KEVIN R. CROOKS,<sup>1</sup> DAVID M. THEOBALD,<sup>2</sup> KENNETH R. WILSON,<sup>1</sup> ERIN E. BOYDSTON,<sup>3</sup> LISA M. LYREN,<sup>4</sup> ROBERT N. FISHER,<sup>5</sup> T. WINSTON VICKERS,<sup>6</sup> SCOTT A. MORRISON,<sup>7</sup> AND WALTER M. BOYCE<sup>6</sup>

<sup>1</sup>Colorado State University, Department of Fish, Wildlife, and Conservation Biology, Fort Collins, Colorado 80523 USA

<sup>2</sup>Colorado State University, Department of Human Dimensions of Natural Resources and Natural Resources Ecology Lab, Fort Collins, Colorado 80523 USA

<sup>3</sup>U.S. Geological Survey, Western Ecological Research Center, 401 W Hillcrest Drive, Thousand Oaks, California 91360 USA

<sup>4</sup>U.S. Geological Survey, Western Ecological Research Center, 6010 Hidden Valley Road, Carlsbad, California 92011 USA

<sup>5</sup>U.S. Geological Survey, Western Ecological Research Center, 4165 Spruance Road, San Diego, California 92101 USA

<sup>6</sup>Wildlife Health Center, One Shields Avenue, University of California, Davis, California 95616 USA

<sup>7</sup>The Nature Conservancy, California Program, 201 Mission Street, Fourth Floor, San Francisco, California 94105 USA

**Abstract.** The impact of human land uses on ecological systems typically differ relative to how extensively natural conditions are modified. Exurban development is intermediate-intensity residential development that often occurs in natural landscapes. Most species-habitat models do not evaluate the effects of such intermediate levels of human development and even fewer predict how future development patterns might affect the amount and configuration of habitat. We addressed these deficiencies by interfacing a habitat model with a spatially-explicit housing-density model to study the effect of human land uses on the habitat of pumas (*Puma concolor*) in southern California. We studied the response of pumas to natural and anthropogenic features within their home ranges and how mortality risk varied across a gradient of human development. We also used our housing-density model to estimate past and future housing densities and model the distribution of puma habitat in 1970, 2000, and 2030. The natural landscape for pumas in our study area consisted of riparian areas, oak woodlands, and open, conifer forests embedded in a chaparral matrix. Pumas rarely incorporated suburban or urban development into their home ranges, which is consistent with the hypothesis that the behavioral decisions of individuals can be collectively manifested as population-limiting factors at broader spatial scales. Pumas incorporated rural and exurban development into their home ranges, apparently perceiving these areas as modified, rather than non-habitat. Overall, pumas used exurban areas less than expected and showed a neutral response to rural areas. However, individual pumas that selected for or showed a neutral response to exurban areas had a higher risk of mortality than pumas that selected against exurban habitat. Exurban areas are likely hotspots for puma-human conflict in southern California. Approximately 10% of our study area will transform from exurban, rural, or undeveloped areas to suburban or urban by 2030, and 35% of suitable puma habitat on private land in 1970 will have been lost by 2030. These land-use changes will further isolate puma populations in southern California, but the ability to visualize these changes had provided a new tool for developing proactive conservation solutions.

**Key words:** California; carnivore; exurban; generalized-linear-mixed model; habitat loss; human development; human-wildlife conflict; *Puma concolor*.

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† E-mail: cburdett@warnercnr.colostate.edu

## INTRODUCTION

A consequence of the increasing size of the human population is the large area devoted to anthropogenic land uses (Vitousek et al. 1997). However, human land uses differ in their impacts on ecological systems, typically relative to their permanence or how extensively they modify natural conditions (Marzluff and Ewing 2001, Theobald 2004). Studies that evaluate anthropogenic land uses along such an intensity gradient therefore have the potential to clarify and mitigate the negative ecological impacts of humans (McDonnell and Pickett 1990, Theobald 2004). The need for such studies has never been greater. It is widely accepted that the biodiversity crisis is driven by expanding human land uses (Jenkins 2003), and the number of declining species appears to be increasing. For example, approximately 25% of all extant mammalian species are currently threatened with extinction (Schipper et al. 2008). Effective conservation strategies now require understanding how threatened species respond to both natural and human landscapes (Sanderson et al. 2002).

Human land uses in the western United States (U.S.) have traditionally been associated with agriculture or natural-resource industries like mining and forestry, but residential development has been rapidly increasing in recent decades, particularly in natural landscapes with high amenity values due to scenery, wilderness, wildlife, and recreational opportunities (Hansen et al. 2002, Leu et al. 2008). Overall, the human population in the western U.S. is increasing three times faster than elsewhere in the U.S. (Baron et al. 2000, Travis 2007). Residential development in much of the western U.S. is actually increasing faster in rural than urban areas, and more than 60% of western counties are experiencing a “rural sprawl” known as exurban development (Theobald 2003). Exurban development has a greater housing density, approximately one housing unit per 0.7–16 ha, than the typical rural housing density of one unit on >16 ha (Theobald 2001, Travis 2007). In the conterminous U.S. exurban land-use occupies up to ten times more area than suburban and urban land uses and is increasing

at a rate of 10–15% a year (Theobald 2005). These intermediate levels of human development are rarely evaluated in species-habitat models, partly because sub-county-level spatial data on low and intermediate housing densities are unavailable for much of the U.S. (Theobald 2001).

Another limitation of most species-habitat studies is their inability to predict the future distribution of habitat. One way to add this capability would be integrating a traditional habitat model with the types of human-development models being developed within the emerging discipline of land-change science (Turner et al. 2007). Theobald (2005) recently developed a spatially-explicit model for the U.S. capable of predicting past, current, and future housing densities along a rural to exurban to urban gradient. Interfacing this model with a species-habitat model would allow the effects of intermediate-intensity human development and future-development patterns to be evaluated, therefore addressing these two common limitations of species-habitat models.

The puma (*Puma concolor*), also known as the mountain lion or cougar, was broadly distributed throughout the U.S., but persecution, deforestation, prey depletion, and urbanization led to its extirpation from nearly all of the eastern U.S. by the 20th century (Logan and Sweanor 2001). Pumas remain relatively abundant throughout the western U.S., primarily due to the region’s large amount of undeveloped or protected land. However, the number of pumas culled by management agencies has increased with the continued development of the western U.S. (Cougar Management Guidelines Working Group 2005). Most conflict between pumas and humans involves predation on domestic livestock or pets (Torres et al. 1996), but attacks on humans, although rare, may be increasing and are a major concern for land and wildlife managers (Cougar Management Guidelines Working Group 2005). Pumas avoid intensively developed suburban or urban areas (Dickson and Beier 2002), so puma-human conflict should be most prevalent in less intensively developed rural or exurban areas. The creation of proactive management and conservation plans for pumas

in rapidly developing regions of the western U.S. will require a deeper understanding of the interactions among pumas, their preferred habitat, and variable intensities of human development.

An ideal location to study the interactions between puma habitat and human land use is southern California, USA. Although nearly 20 million people live in coastal southern California, the region still contains relatively large areas of protected wild lands. Pumas occur in many of these protected areas, but are severely threatened by habitat loss and fragmentation, disappearing in habitat fragments that become too small or isolated (Beier 1993, Crooks 2002, Hunter et al. 2003). Approximately 40% of high-quality puma habitat in southern California is open to further development (Hunter et al. 2003). The charisma and large-area requirements of pumas have made them a flagship species for regional habitat connectivity initiatives (Beier et al. 2006, Morrison and Boyce 2009), so evaluating puma habitat relative to human development would not only benefit the conservation of pumas, but also enhance the broader conservation of biodiversity in southern California.

We had three main objectives in this study. First, we used movement data collected from pumas wearing global positioning system (GPS) telemetry collars and a set of a priori models in an information-theoretic approach (Burnham and Anderson 2002) to evaluate hypotheses about how natural and anthropogenic features affect the habitat use of pumas. Consequently, our models can be framed within the landscape-species concept, which discriminates between natural and human-dominated landscapes and uses their intersection to define a conservation landscape, or high-priority areas for conservation action (Sanderson et al. 2002). Second, we examined the relationship between mortality risk and how pumas responded to a gradient of development intensity in the human landscape. Given the prevalence of pumas in protected areas, we suspected the intermediate levels of development that are often adjacent to these areas could be hotspots for puma-human conflicts. Finally, in addition to mapping our habitat model relative to current (i.e., as of the 2000 U.S. Census) development levels in southern California, we also used our human-growth model

(Theobald 2005) to map puma habitat relative to forecasted housing densities for 1970 and 2030.

## METHODS

### Study area

We defined the boundaries of our study area by placing a minimum convex polygon (MCP) around all locations of pumas wearing GPS telemetry collars. The resulting 14,520-km<sup>2</sup> study area was within the Peninsular Mountain Range of southern California (116° 4' 23" - 117° 45' 28" W, 32° 36' 36" - 33° 52' 39" N) (Fig. 1). Major public-land holdings within our study area included the Cleveland National Forest, Anza Borrego Desert State Park, and Cuyamaca Rancho State Park.

The natural vegetation in our study area is a mosaic of chaparral, sage scrub, oak woodlands, open-conifer forests, and grasslands (Barbour et al. 2007). Sage scrub dominated by California sagebrush (*Artemisia californica*) occurs at low elevations near the coast, while chaparral communities of chamise (*Adenostoma fasciculatum*), scrub oak (*Quercus dumosa*), and ceanothus (*Ceanothus* spp.), savannah-like open oak (*Q. agrifolia* and *Q. engelmannii*) woodlands with grass and low-shrub understories, and grasslands occur at intermediate elevations. The highest elevations are mostly open-canopy coniferous forests of ponderosa pine (*Pinus ponderosa*), Jeffrey pine (*P. jeffreyi*), and Coulter pine (*P. coulteri*), with closed-canopy white fir (*Abies concolor*) forests present at the highest elevations. The eastern portion of our study area borders the Sonoran and Mojave Deserts where desert-scrub species like creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) are common. Although much of our study area is undeveloped, urbanization and agriculture, primarily citrus and avocado orchards, are also present. Extensive urban development occurs to the west and north of our study area.

The mountains of the Peninsular Range are relatively narrow with gentle western slopes and steeper eastern slopes (Norris and Webb 1990). Elevations range from below sea level in the desert east of the Santa Rosa Mountains to over 3200 m at San Jacinto Peak in the San Jacinto Mountains. However, elevations in the Peninsular Range are generally moderate with most

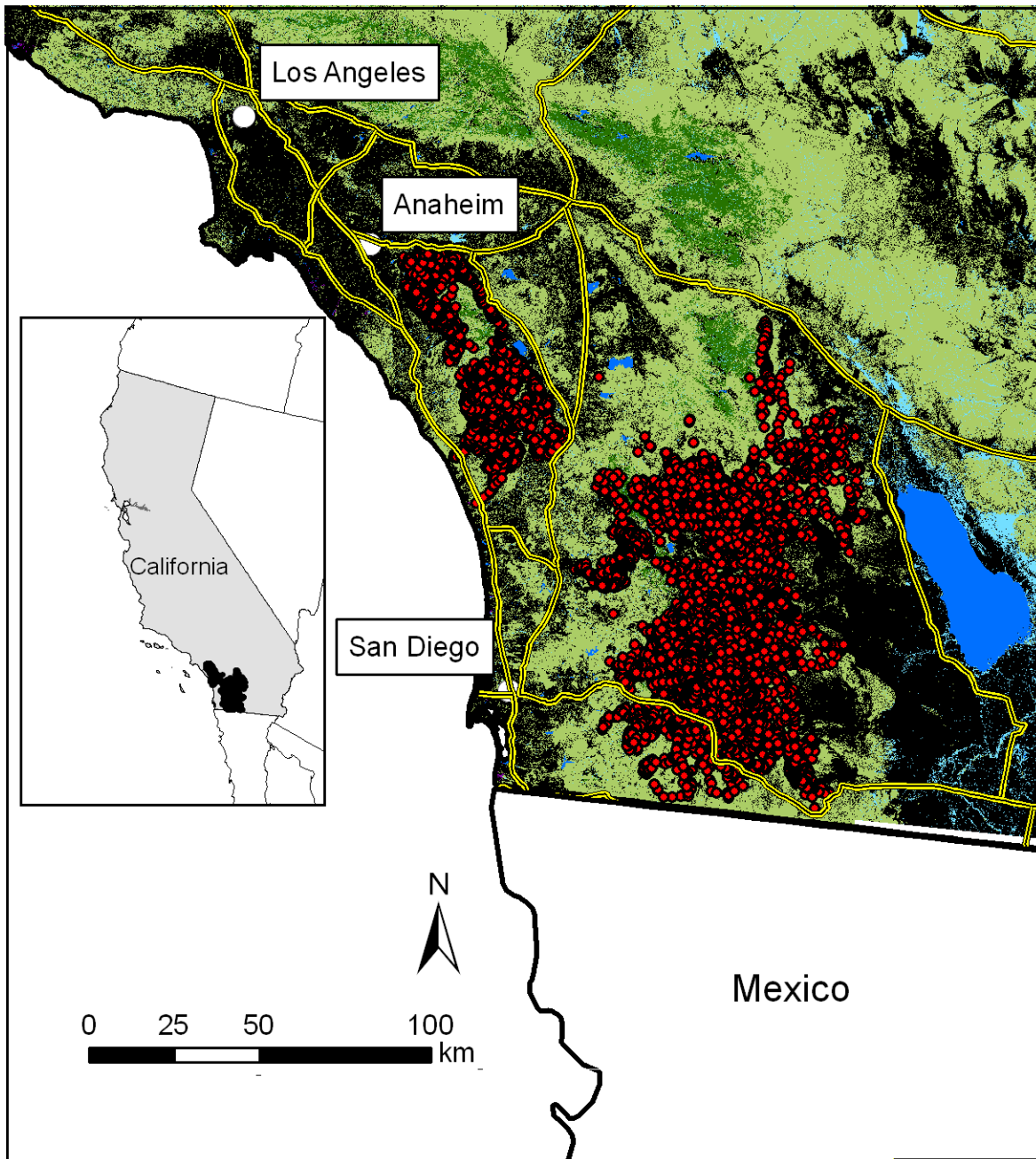


Fig. 1. The telemetry locations ( $n = 61,611$ ) of 37 pumas (red circles) depicted relative to major cities (labeled), major highways (yellow/black lines), human development and sparsely-vegetated, non-forested, open areas (black areas), and the natural landscape (green) in our southwestern California study area. The inset shows the telemetry locations (black area) relative to the rest of California.

peaks < 1800 m.

Southern California experiences a mediterranean climate characterized by mild, wet winters and hot, dry summers. Rainfall in the Peninsular

Ranges varies from 250–900 mm annually so many streams are intermittent (Norris and Webb 1990).

### *Puma capture and telemetry*

Pumas were captured from 2001–2007 with foot-hold snares, baited cage traps, or treed with hounds. Captured pumas were anesthetized with ketamine hydrochloride (HCl), Telazol (tileamine HCl and zolazepam HCl), or Capture-All-5 (ketamine HCl and xylazine HCl), sexed and measured, ear-tagged and ear-tattooed, and fitted with one of four models of GPS collar (TGW3580, Telonics, Inc., Mesa, Arizona, USA; Simplex P-1D, Televilt, Lindesberg, Sweden; 3300S or 4400S, Lotek Wireless, Inc., Newmarket, Ontario, Canada). The minimum sampling intensity across all collar models was four location attempts per day (included diurnal, nocturnal, and crepuscular periods). Data were remotely downloaded from these collars once per month, screened for inaccurate or questionable locations, and entered into the ArcGIS 9.2 geographic information system (GIS) (ESRI 2006). We did not correct for how location acquisition varied among vegetation classes, which could increase the probability of type II errors in our models (Frair et al. 2004). However, locations were more frequently missed during diurnal periods, which is when pumas in southern California are typically resting in dense cover (Beier et al. 1995). Therefore our models may better represent the use of foraging habitat than resting habitat. We calculated annual 95% fixed-kernel home ranges for pumas monitored for at least three months, defining bandwidth with least-squares cross validation (LSCV). To obtain a suitable level of smoothing, we used one randomly selected location from each day that a puma was monitored because kernel bandwidths estimated with LSCV often fail to converge for large datasets (Hemson et al. 2005, Burdett et al. 2007). Mortalities were detected by aerial and ground monitoring of telemetry collars or when project personnel were contacted about a dead puma. The capture and handling protocol used in this study followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and was approved by the Animal Care and Use Committee at the University of California, Davis.

We included telemetry data from 37 (22 female, 15 male) of the 40 pumas captured during this study; the remaining three pumas were not included because they were monitored for less than 30 days. The mean ( $\pm$  SE)

monitoring period for our annual home-range estimates was  $256 \pm 16$  days (range = 87–365 days) with four pumas monitored for two consecutive years. We used the annual home range from the second year of monitoring for these four pumas because the location of their home ranges changed little, and all were smaller in the second year, possibly reflecting greater territorial familiarity. The total number of puma locations available for analysis was 61,611 with a mean number of locations per puma of  $1502 \pm 143$  (range = 318–3492 locations).

### *Habitat data and covariates*

We incorporated variables from the natural (vegetation types and topographic features) and human (protection status and the intensity of human development, which we depicted as a gradient of housing densities) landscapes into our models (Table 1). We evaluated these variables within the home ranges of pumas, which represents the third order of habitat selection using the hierarchical scheme proposed by Johnson (1980).

*Vegetation covariates.*—We defined vegetation types with the Landscape Fire and Resource Management Planning Tools Project (LANDFIRE), a national geospatial dataset developed to support wildland fire management and planning (Rollins and Frame 2006). Vegetation in LANDFIRE was mapped at a 30-m resolution using Landsat satellite imagery obtained in 2001. The existing vegetation-type data from LANDFIRE were too fine-grained for our analyses so we reclassified it into ten vegetation classes similar to those used in a nearby puma study (Dickson and Beier 2002) (Table 1).

*Topographic covariates.*—We obtained topographic data for elevation, slope, and aspect from the National Elevation Dataset (Gesch et al. 2002). We subsequently calculated topographic ruggedness from elevation using the vector-ruggedness measure (VRM) (Sappington et al. 2007).

*Protection-status covariates.*—We defined protection status with an updated version of the Protected Areas Database (DellaSala et al. 2001) and other publically-available land-ownership datasets. Protection status was classified into four categories: (1) private, unprotected, (2) private, protected, (3) public, protected, and (4)

Table 1. Habitat variables evaluated in puma-habitat models for southern California.

Variable	Abbrev.†	Description
Vegetation classes‡		
Agriculture	AGR	Pasture, cropland, orchards
Barren	BAR	Open areas lacking vegetation
Conifer forest	CFO	Pine/fir forests
Chaparral	CHP	Chamise-dominated areas
Coastal scrub	CSC	Coastal sage dominated areas
Desert scrub	DSC	Sagebrush/creosotebush-bursage-dominated areas
Grassland	GRS	Graminoid-dominated areas
Oak woodland	OAK	Oak-dominated open canopy woodlands
Riparian	RIP	Mixed coniferous/deciduous forests
Sparse	SPS	Sparsely-vegetated areas
Topographic features		
Elevation	Elev	Meters above sea level
Slope	Slp	Degrees of slope
Aspect	Asp	Direction of slope
Ruggedness	VRM	Ruggedness metric
Protection status‡		
Private, unprotected	PrUnp	Private land with no protection status
Private, protected	PrPro	Private land not open to development
Public, protected	PbPro	Public land not open to development
Tribal	Tribal	Land in Native American ownership
Human development‡		
Private, undeveloped	PrUnd	Privately-owned land with no housing units
Rural	Rural	Housing density > 16.18 ha/unit
Exurban	Exurb	Housing density 0.68–16.18 ha/unit
Suburban/Urban	SubUrb	Housing density < 0.68 ha/unit

† Abbrev. = codes used to abbreviate each variable.

‡ Measured as the proportional area of this category within 30 meters of a location.

tribal land in Native American ownership.

*Housing-density covariates.*—We defined housing densities with an updated version of the Spatially Explicit Regional Growth Model (SERGoM) (Theobald 2005). We used SERGoM to classify private land in southern California into four development categories: (1) private, undeveloped, (2) rural (>16.18 ha per unit), (3) exurban (0.68–16.18 ha per unit), and (4) suburban/urban (<0.68 ha per unit) (Theobald 2005). We mapped these development categories at a 100 m resolution.

In addition to current (2000) housing densities, SERGoM can also estimate historical (1970–1990) and future (2000–2030) housing densities. The historical and current housing densities were developed with datasets from the 2000 U.S. Census. Historical data in SERGoM is based on block-groups, which contain about 250–550 housing units, and current (2000) data from blocks, which are subdivisions of block-groups that range in size from 1–2 ha in urban areas to 100–1000 ha in rural areas (Theobald 2005). Models similar to SERGoM often assume homogeneity or modifications based on land-cover within their primary analytical unit (i.e., blocks

for SERGoM), but these assumptions are inadequate for modeling housing densities (Theobald 2003, Theobald 2005). Instead, SERGoM assumes the spatial distribution of the housing units within a block will be spatially correlated with the densities of roads and ground-water wells (Theobald 2003, Theobald 2005). These steps produce current housing densities, whereas historical housing densities can be generated using the “Year Housing Built” question from the U.S. Census.

Forecasts of future housing-density patterns are created in SERGoM with a supply-demand-allocation approach that forces the number of new housing units (i.e., supply) to meet county-level forecasts of human population growth (i.e., demand) (Theobald 2005). The spatially-explicit allocation of new housing units is then based upon the assumption that development will progressively expand outward from an urban core, defined as a >100-ha patch of urban land use, and areas closer to the urban core will be developed earliest. This assumption is depicted in SERGoM using travel time along local major roads and highways, rather than a more simplistic metric such as straight-line distance. Accessi-

bility and the distribution of housing units are reevaluated each decade because of the ongoing creation of new urban cores. Validation analyses indicate SERGoM is 91.2 – 99.0% accurate in predicting urban, exurban and rural land uses over a ten-year period and 79.4 – 99.1% accurate in predicting those land uses over a 20-year period (Theobald 2005).

### *Sampling design*

We evaluated habitat use with a Design III use-availability sampling design (Manly et al. 2002). We defined each puma's habitat use with its GPS-collar locations and defined habitat availability by generating the same number of random locations within each puma's 95% fixed-kernel home range. We measured the vegetation, protection-status, and housing-density covariates at each use or availability location as continuous variables, using the proportion of each of these classes occurring within 30 m of the location. This 30-m radius accounted for any spatial error in the GPS telemetry locations or habitat variables. While our VRM variable quantified ruggedness within approximately 100m of each location, the other topographic variables of elevation, slope, and aspect were measured at the locations without buffering.

We chose a use-availability sampling design because it has been widely used to evaluate habitat-selection patterns (Johnson 1980, Manly et al. 2002, Johnson et al. 2006). Use-availability sampling designs utilize selection, or the disproportionality between use and availability, as the response variable (Aarts et al. 2008). A limitation of using selection as a response variable is that the results become strongly dependent on the researcher's definition of habitat availability. We avoided an arbitrary definition of availability by analyzing habitat selection within the 95% home range, which has been the standard metric of space use in territorial mammals for decades (Burt 1943). Nonetheless, sampling designs employing intensity of use as the response variable may provide a more straightforward metric for relating animal behavior to habitat requirements (Marzluff et al. 2004).

Lastly, to relate the habitat use of pumas within their home ranges to the composition of the broader southern California landscape, we

calculated a use vector (mean  $\pm$  95% CI) for all covariates within the home ranges and compared this to composition of our study area. Our study area excluded extensively urbanized areas to the west and north that presumably once supported pumas, and desert areas that limit puma movements to the east (Ernest et al. 2003), so we also calculated the composition of a broader regional-scale (34,790 km<sup>2</sup>) landscape that we defined by placing a 50-km buffer around our study-area MCP.

### *Habitat modeling*

We developed a set of candidate models that represented hypotheses about how features in natural and human landscapes affect the habitat selection of pumas. Our candidate models were based on two fundamental beliefs about the habitat selection of pumas in southern California: (1) puma habitat selection is primarily dependent upon the ecological factors associated with prey-rich areas, but (2) anthropogenic factors can modify the ecological basis for puma habitat suitability. Our candidate models therefore evaluated the explanatory power of two components of the natural landscape, vegetation (partitioned into selected, avoided, and all vegetation categories) and topography, and two components of the human landscape, protection status and housing density. Our set of candidate models examined the effects of these four components separately and in various combinations designed to reflect the complex social-ecological landscape of southern California (Table 2). We used an information-theoretic approach based on the small sample correction of Akaike's Information Criterion (AIC<sub>c</sub>) to select the most appropriate models from our candidate set based on our data (Burnham and Anderson 2002). We reported AIC<sub>c</sub> differences (AIC<sub>c</sub> $\Delta_i$ , the relative difference in AIC<sub>c</sub> model scores) and AIC<sub>c</sub> weights (AIC<sub>c</sub> $w_i$ , the relative likelihood of a model as a value between zero and one) to compare model rankings, and used the Hosmer and Lemeshow goodness-of-fit statistic ( $G_{ILL}^2$ ) (Hosmer and Lemeshow 2000) to assess overall model fit.

*Preliminary analyses of predictor variables.*— Before developing our candidate models, we evaluated each predictor variable with a simple logistic regression, assessing coefficient significance with a Wald  $\chi^2$  test. We used a cluster-

Table 2. Set of candidate models used to evaluate the habitat use of pumas in southern California.

Model number	Model name	Model structure†
1	Selected vegetation model	OAK + RIP
2	Avoided vegetation model	BAR + CSC + DSC + GRS
3	All vegetation model	BAR + CSC + DSC + GRS + RIP + OAK
4	Protection status models‡	PrUnp/PbPro
5	Housing density model	Exurb + SubUrb
6	Topography model	Elev + VRM
7	Selected vegetation/protection status models‡	RIP + OAK + PrUnp/PbPro
8	Avoided vegetation/protection status models‡	BAR + CSC + DSC + GRS + PrUnp/PbPro
9	All vegetation/protection status models‡	BAR + CSC + DSC + GRS + RIP + OAK + PrUnp/PbPro
10	Selected vegetation/housing density model	RIP + OAK + Exurb + SubUrb
11	Avoided vegetation/housing density model	BAR + CSC + DSC + GRS + Exurb + SubUrb
12	All vegetation/housing density model	BAR + CSC + DSC + GRS + RIP + OAK + Exurb + SubUrb
13	Selected vegetation/topography model	RIP + OAK + Elev + VRM
14	Avoided vegetation/topography model	BAR + CSC + DSC + GRS + Elev + VRM
15	All vegetation/topography model	BAR + CSC + DSC + GRS + RIP + OAK + Elev + VRM

† Abbreviations as in Table 1. The variables incorporated into these models were restricted to those found to be statistically significant in the preliminary simple logistic-regression models (Table 3).

‡ Due to strong negative correlation between PrUnp and PbPro, we evaluated two models, one with each protection-status covariate.

correlated form of the Huber-White-sandwich estimator to calculate robust standard errors for these preliminary analyses because this estimator corrected the variance for intra-puma correlation and spatial autocorrelation in the GPS-telemetry locations (Clark and Stevens 2008). Given the large number of locations in our GPS-telemetry dataset, we excluded variables with  $P > 0.10$  from our models. We also calculated a correlation matrix of predictor variables using Spearman rank coefficients to avoid including correlated variables ( $|r| > 0.6$ ) in the same candidate model.

*Statistical analysis.*—We used generalized-linear-mixed models (GLMMs) to evaluate the fine-scale habitat selection of pumas within their home ranges. Also known as random-effects models, GLMMs are well-suited for telemetry-based habitat-selection analyses because they estimate population-level effects while also incorporating variation in habitat-selection patterns occurring among individual animals (Gillies et al. 2006). Random effects in GLMMs occur as random intercepts and random coefficients (Gelman and Hill 2007). In our analyses, we used random intercepts because they correctly adjusted our parameter estimates for individual pumas by accounting for spatial autocorrelation and unbalanced sampling among pumas (Gillies et al. 2006, McLoughlin et al. 2010).

Our two-level GLMM evaluated the fine-scale habitat selection of pumas at the population-level by nesting locations  $i = 1, \dots, n$  within individual

pumas  $j = 1, \dots, m$ . Our dependent variable was binomially distributed as zero (availability locations) or one (use locations), so probability of use,  $w^*(x)$ , was modeled as

$$w^*(x) = \frac{\exp(\beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \dots + \beta_n x_{nij} + \gamma_{0j})}{1 + \exp(\beta_0 + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \dots + \beta_n x_{nij} + \gamma_{0j})}$$

where  $\beta_0$  is the mean intercept,  $\beta_n$  are the fixed-effect coefficients for covariates  $x_n$ , and  $\gamma_{0j}$  is the random intercept. Although we used Akaike differences and weights to rank these models, AIC scores for GLMMs are approximate because the maximum-likelihood estimate of a GLLM is actually a marginal likelihood that must be estimated with integration (Burnham and Anderson 2002).

*Model evaluation.*—We used  $k$ -fold cross-validation interfaced with a GIS to evaluate the predictive success of our best model (Boyce et al. 2002, Johnson et al. 2006). We split the dataset into five partitions, using four of them (80% of the data) to create a training dataset and the remaining partition (20% of the data) as a testing dataset. We repeated the cross-validation procedure five times until each partition served as a testing dataset. Using the variables from our best model, we created a new GLMM habitat model for each of the five training partitions, mapped it in a GIS, and classified the resulting habitat-suitability scores into ten equal-interval bins. We determined the area-adjusted expected counts in



each bin for the testing datasets, and compared these to the observed counts from the testing dataset. A good model would show a close relationship between the area-adjusted expected and observed habitat-suitability scores (Johnson et al. 2006), indicating the ability to accurately predict the probability of use by pumas. We therefore assessed predictive performance with Spearman rank correlations and linear regressions between the expected and observed bin counts (Boyce et al. 2002, Johnson et al. 2006).

*Spatial depiction of habitat models.*—We created spatially-explicit maps of puma habitat to examine the implications of including exurban development in a puma-habitat model, and evaluate the past and future distribution of puma habitat in southern California. The large number of locations we obtained from GPS telemetry allowed us to map habitat with a global model that included all uncorrelated covariates from our preliminary analyses. Although this global model was clearly the best model ( $AIC_c w > 0.999$ ; see Results), note we did not evaluate global models in our candidate-model set because we wanted to compare the relative influences of the covariates from the natural and human landscapes on puma movement and behavior; this global model simply allowed us to more accurately map the distribution of puma habitat. The probability of use,  $w^*(x)$ , from our global GLMM model represented a greater predicted probability of the area being used by pumas as  $w^*(x)$  approached one. We defined suitable puma habitat as  $w^*(x) \geq 0.5$ .

We created several maps using the global model to depict the current distribution of puma habitat in southern California. First, we estimated the effect of not incorporating the response of pumas to intermediate housing densities, which was done by excluding these covariates from the global model. Second, we estimated how continuing development would affect the future distribution of suitable puma habitat in southern California by mapping our global model using housing-density covariates output from a SERGoM simulation for 2030. We also obtained a historical perspective on how land-use changes have affected the distribution of puma habitat in southern California by mapping the global model with housing-density covariates from a SERGoM simulation for 1970. Finally, to examine

changing habitat conditions at a broader scale, we also mapped the 1970, 2000, and 2030 habitat maps for our larger regional landscape.

#### *Puma mortality in the human landscape*

We used the best model emerging from our model-selection analysis and modeled habitat selection separately for individual pumas to examine the relationship between mortality and an individual puma's selection for exurban development. We used these individual models to classify each puma as showing positive, negative, or neutral selection for exurban development based on whether the 95% confidence interval of the exurban coefficient was above, below, or overlapped zero. We used logistic regression to determine if pumas that selected against exurban areas had a lower risk of mortality. We then repeated these analyses to examine the relationship between mortality and an individual puma's selection for rural development. All statistical analyses were conducted with Stata 9.0 (StataCorp 2005).

## RESULTS

### *Habitat modeling*

*Preliminary analyses.*—Pumas showed significant ( $P \leq 0.10$ ) responses to several of our habitat variables (Table 3). In the natural landscape, pumas used oak woodlands, riparian areas, higher elevations, and more rugged terrain to a greater extent than expected based on our definition of availability. They used barren areas, grasslands, and scrublands less than we expected. Pumas showed use equal to availability for chaparral, which was the most common vegetation-class in their home ranges, and for all aspects. Based on their availability in the human landscape, pumas used public protected land more than expected and unprotected private land, exurban development, and suburban/urban development less than expected. Pumas responded neutrally to rural development.

There was a strong negative correlation ( $r = -0.76$ ) between private, unprotected land and public, protected land. The covariate for private, protected land had more model support ( $AIC_c \Delta_i = 158$ ) so we included this covariate in our candidate models

*Statistical analyses.*—Including random inter-

Table 3. Results of simple logistic regressions examining the probability of puma use at two spatial scales.

Variable†	Coefficient ± SE‡	P
AGR	-0.47 ± 0.34	0.175
BAR	-0.87 ± 0.31	0.005
CHP	0.04 ± 0.08	0.632
CSC	-0.25 ± 0.07	<0.001
DSC	-0.32 ± 0.18	0.075
CFC	0.36 ± 0.23	0.125
CFO	0.14 ± 0.09	0.140
GRS	-0.97 ± 0.16	<0.001
RIP	1.90 ± 0.19	<0.001
OAK	0.65 ± 0.12	<0.001
SPS	0.51 ± 0.38	0.180
PrUnp	-0.25 ± 0.10	0.014
PrPro	0.04 ± 0.16	0.816
PubPro	0.15 ± 0.09	0.088
Tribal	0.12 ± 0.19	0.523
PrUnd	-0.03 ± 0.09	0.709
Rural	0.00 ± 0.08	0.982
Exurb	-0.40 ± 0.13	0.002
SubUrb	-0.80 ± 0.39	0.039
Elev	12.11 ± 5.69 ( $\times 10^{-5}$ )	0.033
Slp	-4.63 ± 3.45 ( $\times 10^{-3}$ )	0.180
VRM	13.88 ± 1.76	<0.001
Asp	-0.08 - 0.07	0.125 - 0.951

† Abbreviations as in Table 1.

‡ Standard errors obtained from the Huber-White-sandwich variance estimator.

cepts typically improved the model by >100 AIC points over the fixed-effects logistic-regression version of the model (Table 4). Our best model ( $AIC_c w_i > 0.999$ ) included all important vegetation (i.e., those emerging from the preliminary

analysis) and housing-density covariates and was clearly superior to the next best candidate model that included the vegetation and protection-status covariates ( $AIC_c \Delta_i = 131$ , Table 4). When vegetation was partitioned into selected and avoided classes, all of the selected-vegetation models were superior to the avoided-vegetation models (Table 4).

The vector depicting puma use of model covariates within their home ranges differed from the composition of our study area and broader regional landscape (Table 5). Relative to their availability in these broader areas, pumas showed more use of open-conifer forests, chaparral, oak woodlands, riparian areas, and public land, and less use of agriculture, barren land, desert scrub, grassland, sparsely-vegetated areas, private lands, rural areas, exurban areas, and suburban/urban areas. Pumas also occupied higher elevations, and steeper and more rugged areas relative to the mean values of these topographic covariates in our study area and regional landscape.

*Model evaluation.*—The mean Spearman rank correlation between expected and observed counts of the habitat-suitability scores for each training/testing partition ( $n = 5$ ) was  $\rho = 0.78 \pm 0.03$ , and the mean  $R^2$  was  $0.60 \pm 0.08$ , indicating good agreement between the expected and

Table 4. The complete model-selection results, ranked by differences in Akaike's information criterion corrected for small sample size ( $AIC_c \Delta_i$ ) for candidate models depicting habitat selection within the home ranges of pumas in southern California.

Model†	k	$AIC_c$	$AIC_c \Delta_i$	$AIC_c w_i$	$G_{HL}^2$
Global-vegetation/housing-density model	11	167063	0	>0.999	90.2
Global-vegetation/unprotected-land model	10	167194	131	<0.001	338.0
Global-vegetation/topography model	11	167214	151	<0.001	54.3
Global-vegetation model	9	167459	396	<0.001	12.4
Selected-vegetation/topography model	7	168163	1100	<0.001	509.8
Selected-vegetation/housing-density model	7	168229	1166	<0.001	49.8
Selected-vegetation/unprotected-land model	6	168294	1231	<0.001	57.3
Selected-vegetation model	5	168676	1614	<0.001	50.0
Avoided-vegetation/housing-density model	9	168782	1719	<0.001	37.0
Avoided-vegetation/topography model	9	168805	1742	<0.001	40.9
Avoided-vegetation/unprotected-land model	8	168938	1876	<0.001	298.9
Avoided-vegetation model	7	169135	2073	<0.001	40.3
Topography model	5	170252	3189	<0.001	249.1
Housing-density model	5	170411	3348	<0.001	-
Unprotected-land model	4	170538	3475	<0.001	9.6

Note: The  $AIC_c$  model weights,  $AIC_c w_i$  are the likelihood of a model given the data (a value between zero and one), and  $G_{HL}^2$  is the Hosmer and Lemeshow statistic for goodness-of-fit. Because robust overall goodness-of-fit statistics for generalized-linear-mixed models are currently unavailable, the  $G_{HL}^2$  for our home-range-scale models is based on the fixed-effect version of the model that did not include a random intercept. The random-intercept models typically had  $AIC_c$  values approximately 100 lower than their fixed-effect versions.

† The model structure (i.e., variables) is provided in Table 2.

Table 5. The percent use and 95% confidence interval (CI) for 21 habitat features measured within the home ranges of pumas ( $n = 37$ ) in southern California contrasted with the percent composition of the study area (14 520 km<sup>2</sup>) and regional landscape (34 790 km<sup>2</sup>).

Covariate	Study area	Regional landscape	Habitat use (mean)	Habitat use (95% CI)
Vegetation†, ‡				
AGR	2.0	3.5	0.6	0.4–0.8
BAR	6.8	7.3	2.1	0.3–3.8
CFO	7.4	6.1	23.6	16.4–30.8
CHP	35.8	20.8	41.6	35.8–47.3
CSC	13.3	9.7	7.4	2.2–12.6
DSC	9.6	15.5	5.1	2.3–8.0
GRS	12.4	8.6	4.2	2.8–5.7
OAK	4.2	2.6	8.9	6.0–11.9
RIP	1.4	2.9	4.9	4.0–5.8
SPS	1.2	5.4	0.6	0.2–1.0
Topography†				
Elev (m)	744	609	1062	938–1186
Slp (°)	12.3	9.9	14.3	13.3–15.4
VRM§	$4.5 \times 10^{-3}$	$4.5 \times 10^{-3}$	$6.9 \times 10^{-3}$	$5.9\text{--}7.9 \times 10^{-3}$
Protection status†, ‡				
PrUnp	40.6	45.0	19.2	14.4–23.9
PrPro	1.6	1.3	5.4	0.4–10.4
PubPro	53.2	51.1	69.7	62.5–76.9
Tribal	4.6	2.6	5.8	1.6–9.9
Housing density†, ‡				
PrUnd	9.5	20.1	9.3	6.7–11.8
Rural	14.4	18.3	10.7	6.7–14.6
Exurb	15.7	20.3	5.8	3.4–8.1
SubUrb	5.4	27.1	0.6	0.3–0.9

† Abbreviations as in Table 1.

‡ Values are the percentage that these habitat features comprise in the study area or regional landscape, and the mean percentage that these features comprise within 37 puma home ranges.

§ Value for ruggedness reflects the relative ruggedness (no units) on a scale of 0–1 using the vector-ruggedness measure (VRM) index (Sappington et al. 2007).

observed counts and good predictive capacity. All linear regressions had a slope different than 0 (indicative of the presence of selection), and all but one of our  $k$ -fold partitions had a slope not different from one (indicative of the model being proportional to the expected probability of use) (Johnson et al. 2006). All intercepts of the linear regression were near zero, also indicating that the model was generally proportional to the expected probability of use.

*Spatial depiction of habitat models.*—A global model that included all of the significant, uncorrelated covariates from the preliminary analyses was a better model ( $AIC_c\Delta_i = 257$ ) than the best model from our candidate set. We therefore mapped puma habitat with the global model

$$\text{logit}(w^*(x)) = -0.06 + (-0.88*\text{BAR}) + (-0.24*\text{CSC}) + (-0.35*\text{DSC}) + (-0.86*\text{GRS}) + (1.73*\text{RIP}) + (0.60*\text{OAK}) + (-0.28*\text{Exurb}) + (-0.62*\text{SubUrb}) + (8.11 \times 10^{-5}*\text{Elev}) + (9.23*\text{VRM}) + (-0.14*\text{PrUnpro}) + 0.14$$

where the mean intercept ( $\beta_0$ ) =  $-0.06$  and random intercept ( $\gamma_{0j}$ ) =  $0.14$ .

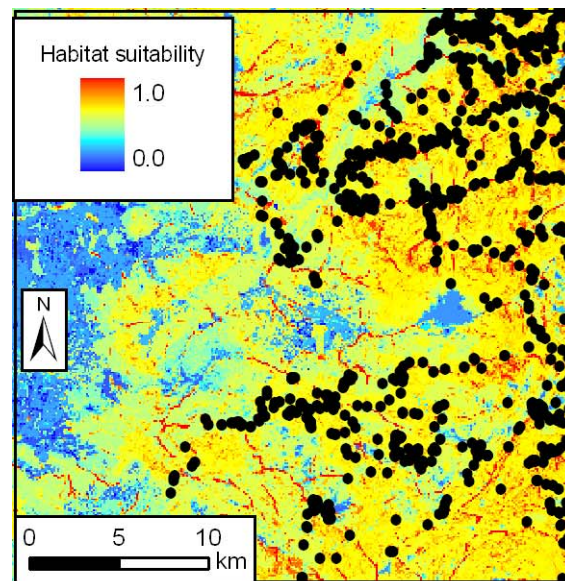
Not evaluating the response of pumas to exurban development overestimated the amount of suitable puma habitat in our 14,520 km<sup>2</sup> study area (Fig. 1) by approximately 9%, because there was 7108 km<sup>2</sup> (49% of study area) of suitable habitat in a model that did not include the exurban covariate, and 6527 km<sup>2</sup> (45%) of suitable habitat in the correct model that included the exurban covariate (Fig. 2). In 2000, there was 2284 km<sup>2</sup> (16%) of exurban development and 781 km<sup>2</sup> (5%) of suburban/urban development in this study area. By 2030, SERGoM predicts exurban development will slightly decrease to 2047 km<sup>2</sup> (14% of study area), whereas suburban/urban development will increase markedly to 2233 km<sup>2</sup> (15%). Most of this additional suburban and urban development projected for 2030 will come from areas that were classified as undeveloped or rural in 2000, but 2% of the current exurban area will be converted to suburban/urban.

Although the SERGoM simulation predicts only 2% of the suitable puma habitat in our 14,520 km<sup>2</sup> study area will be lost due to residential growth from 2000–2030, 55% of our study area is protected land, meaning all of this habitat loss will occur in the remaining 45% of our study area open to development. Further, 73% of this developable land was already classified as unsuitable puma habitat in 2000. By limiting our calculations to suitable puma habitat on developable land, we found 19% of the remaining suitable habitat will be lost from 2000–2030. This is in addition to a 20% loss from 1970–2000, or a total loss of 35% of the remaining suitable habitat on developable land from 1970–2030 (Fig. 3). Quantifying spatially-explicit changes in the past and future distribution of protected areas was beyond the scope of this project, so we assumed the current proportion of protected to developable land remained constant when making the calculations for 1970 and 2030. We believe any changes occurring during this time period would not substantially alter our results due to the large areas over which we quantified these proportional changes in puma habitat.

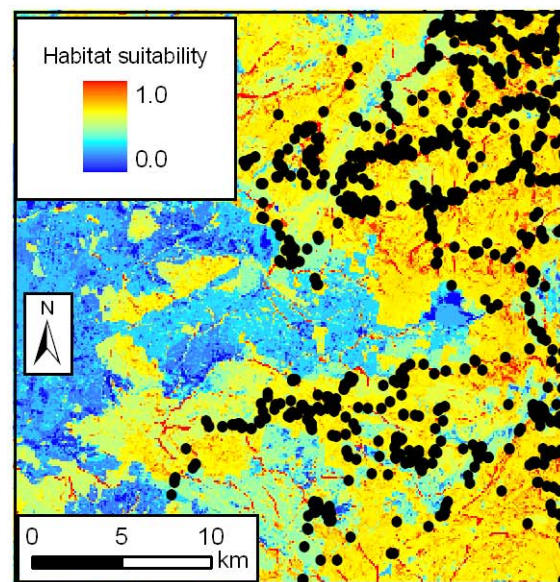
We also used the housing-density projections from SERGoM for 1970, 2000, and 2030 to map the global model in our broader (34,790 km<sup>2</sup>) regional landscape. The non-random use of riparian habitat by pumas may have slightly overestimated the amount of suitable puma habitat in this regional landscape, because riparian areas near the Salton Sea were classified as suitable habitat despite the poor habitat suitability provided by the prevailing land-cover conditions (Ernest et al. 2003). There were 12,777 km<sup>2</sup> (37% of regional scale) of suitable puma habitat in 1970, 12,166 km<sup>2</sup> (35%) in 2000, and 11,626 km<sup>2</sup> (33%) in 2030. Using similar summary statistics as those calculated within our study area, we found 19% of the privately-owned land containing suitable puma habitat in 2000 will be lost by 2030, and 32% of suitable, privately-owned puma habitat will have been lost from 1970–2030. This lost puma habitat often occurred on the periphery of protected areas (Fig. 4).

#### *Puma mortality in the human landscape*

Overall, pumas showed a negative response to exurban development (Table 3). But individual



A



B

Fig. 2. A comparison of the distribution telemetry locations (black points) relative to habitat suitability for pumas (scaled from 0.0–1.0) in a reduced model (A) that only included vegetation and urban/suburban development, and the correct model (B) that included exurban areas as well as vegetation and urban/suburban development. The consequence of not including exurban development in our habitat model was a 9% overestimate of the amount of suitable habitat in our study area.

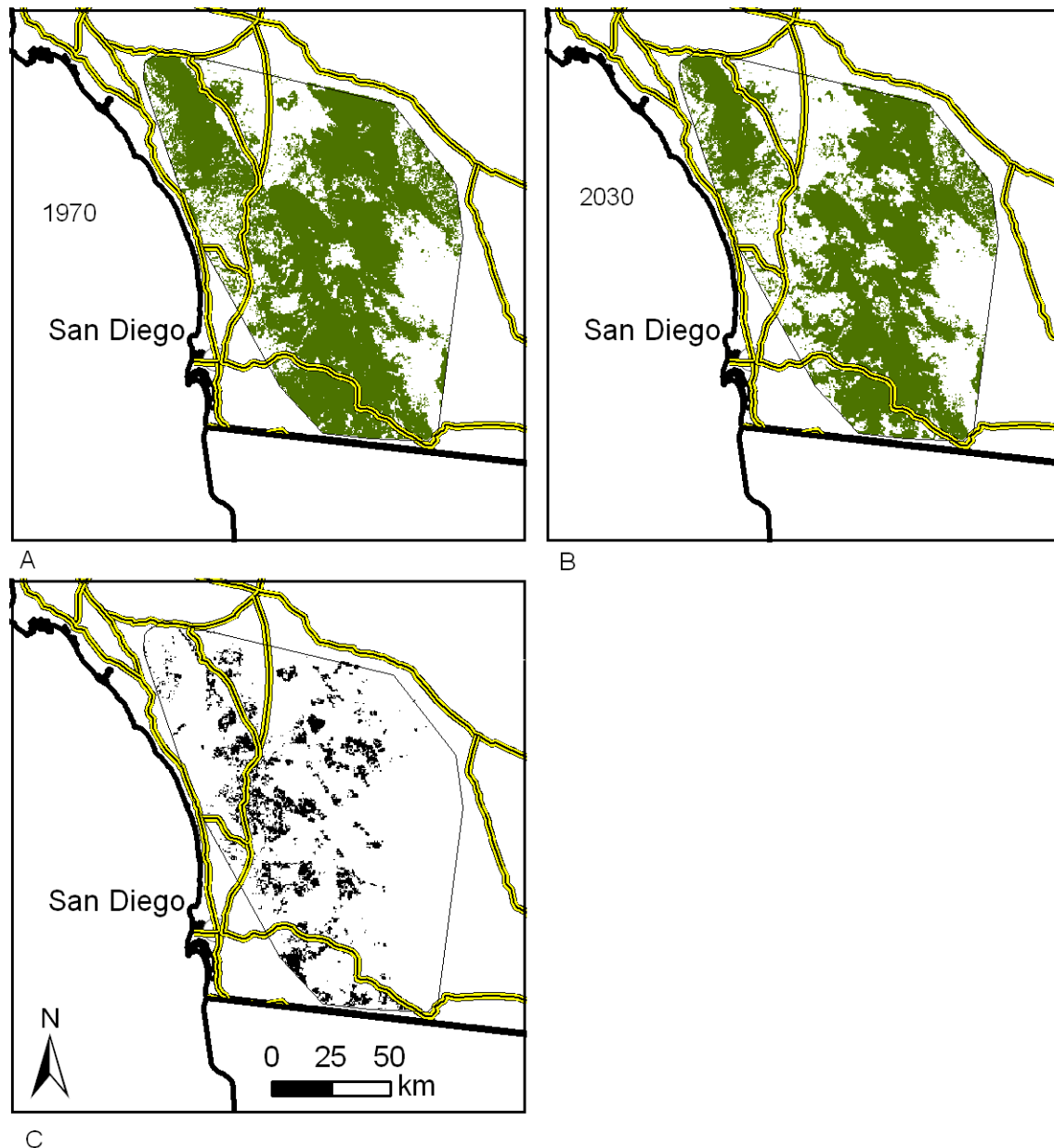


Fig. 3. The predicted distribution of suitable puma habitat (green areas) is shown for our southern California study area in (A) 1970, and (B) 2030. The suitable habitat lost between 1970–2030 (black areas) is shown in (C). These predictions of suitable habitat are contained within the minimum-convex polygon that surrounded the locations of all pumas monitored during this study. The past and future estimates of housing densities were obtained from SERGoM (Theobald 2005).

animal responses were variable: four of 36 (11%) used exurban development more than expected, 12 of 36 (33%) showed random use, 20 of 36 (56%) used exurban development less than expected, and one puma was never detected

using exurban areas. All four of the pumas selecting for exurban areas died during the monitoring period (causes of death were two depredation permits, one road kill, and one unknown). Seven of the 12 pumas (58%) showing

neutral use of exurban areas died (causes of death were one intraspecific strife, one depredation permit, one capture-related mortality, one road kill, and three unknown mortalities), and five of the 20 pumas (25%) that selected against exurban areas died (causes of death were two road kills and three unknown mortalities). Pumas that selected against exurban development had a lower risk of mortality than pumas that selected for or showed a neutral response to exurban development ( $\beta \pm SE = 1.89 \pm 0.75$ ,  $z = 2.53$ ,  $P < 0.01$ ).

Pumas displayed a neutral response to rural development (Table 3). Again, individual use was variable: nine of 37 (22%) used rural development more than expected, 15 of 37 (40%) used it as expected, and 14 of 37 (38%) used rural development less than expected. Three of the nine pumas (33%) selecting for rural development died during the monitoring period, while nine of the 15 (60%) showing a neutral response, and four of the 14 (29%) avoiding rural development, died during monitoring. Pumas that selected against rural development did not have a lower risk of mortality than pumas that selected for or showed a neutral response to rural development ( $\beta \pm SE = 1.00 \pm 0.72$ ,  $z = 1.39$ ,  $P = 0.17$ ).

## DISCUSSION

The ongoing biodiversity crisis is primarily driven by the loss and fragmentation of natural habitats (Jenkins 2003, Schipper et al. 2008). However, it has long been noted that habitat loss resulting from the conversion of natural landscapes to intensive human land uses like agriculture or urban development is often preceded by gradual processes of habitat modification and degradation (McDonnell and Pickett 1990, Marzluff and Ewing 2001, Theobald 2004). Partially degraded natural landscapes containing low- and intermediate-intensity human development are already common and certain to expand in coming decades, making it imperative to devise studies that can both quantify how species are affected by less intensive levels of development and forecast how future patterns of development may affect species persistence. While our study focused on a large carnivore, species that are usually among the first to be

extirpated from developing landscapes, the approach we developed here facilitates understanding how species respond to developing landscapes and could be applied to nearly any taxa threatened by human development.

Several studies have investigated how human development affects habitat suitability for carnivores (Mace et al. 1999, Schadt et al. 2002, Naves et al. 2003), but our study highlights the value of interfacing wildlife-habitat models with spatially-explicit, predictive housing-density models like SERGoM. One advantage of using SERGoM was the ability to quantify the habitat selection and mortality of pumas across a gradient of development intensities without using tax-parcel records, which, if available, can be expensive and time-consuming to compile. However, clearly the greatest advantage of interfacing a wildlife-habitat model with SERGoM was the ability to predict the spatial distribution of puma habitat in future decades. The greatest threat facing the puma population in southern California is the continuing loss, degradation, and fragmentation of habitat (Beier 1993, Crooks 2002, Morrison and Boyce 2009). Unlike the static predictions of most wildlife-habitat models that address only the conditions occurring when data were collected, our approach allowed dynamic spatially-explicit predictions of habitat loss through time. A dynamic model like ours can facilitate more proactive management and conservation of pumas and other wildlife in areas facing complex land-use decisions like southern California (Beier et al. 2006, Morrison and Boyce 2009).

### *Puma response to the natural landscape*

Our analyses indicated pumas were primarily selecting for vegetation types in the natural landscape that provided high-quality habitat. Models containing these vegetation covariates consistently had lower AIC<sub>c</sub> scores than comparable models where the natural landscape was represented with topographic features. Further, models for vegetation types that pumas selected for were usually better models than those depicting the vegetation communities that pumas selected against. However, the AIC<sub>c</sub> scores clearly indicated the best models incorporated features from both the natural and human landscapes. This showed that, while the habitat use and selection of individual pumas was most

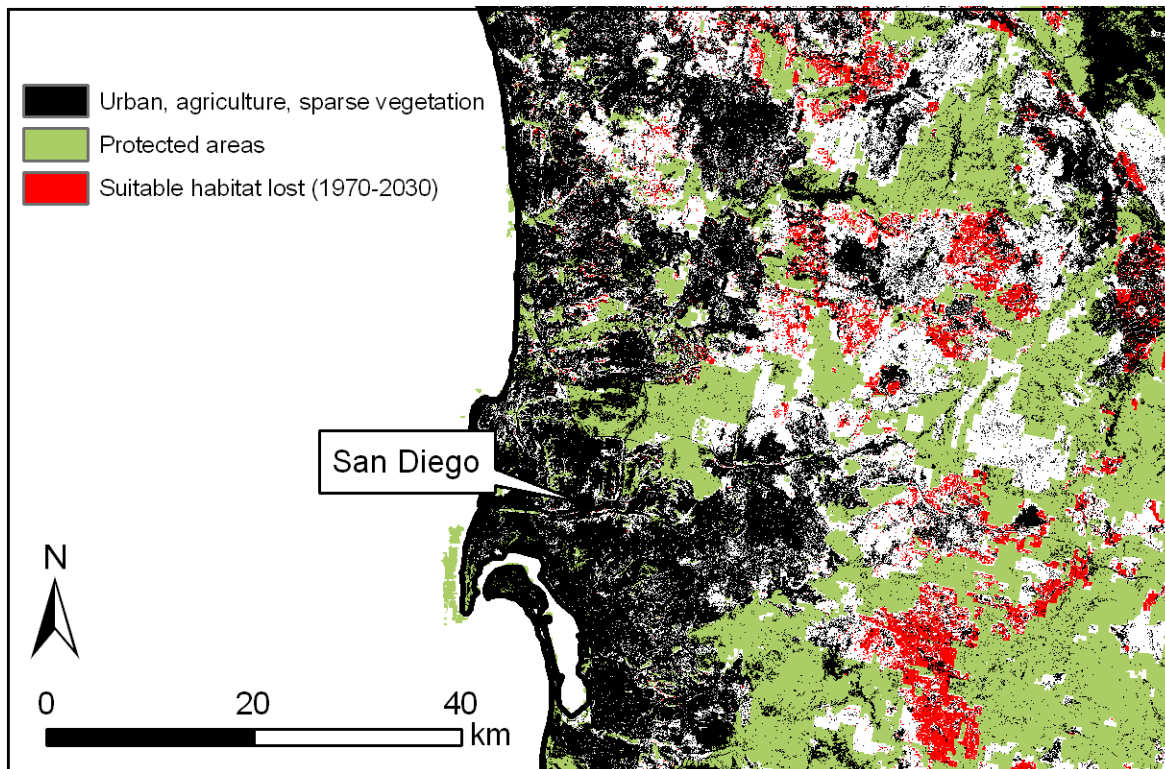


Fig. 4. The predicted distribution of suitable puma habitat that will be lost during 1970–2030 shown relative to protected areas in southwestern California. Black areas represent urbanization, agriculture and sparsely-vegetated, non-forested open areas, green areas are protected land, red areas represent suitable puma habitat that has or will be lost from 1970–2030, and white areas represent unprotected land that is largely still in a natural condition. With the exception of habitat that has already been lost from 1970–2000, the red and white areas collectively represent the current conservation landscape.

strongly associated with the vegetation types that supported sufficient prey for survival and reproduction (Bowyer 1986, Nicholson et al. 1997), pumas concurrently attempted to avoid human-dominated areas.

Predators aggregate in areas with abundant prey (Sih 1984). However, this aggregation deteriorates at finer spatial scales because the opposing evolutionary forces of prey searching and predator avoidance create negative spatial correlation between predators and prey (Sih 1984, Hobbs 2003). Pumas primarily consume mule deer (*Odocoileus hemionus*) in southern California, although mountain sheep (*Ovis canadensis*) are also taken in the eastern portion of our study area where they are sympatric with mule deer (Schaffer et al. 2000). The responses of pumas to the vegetation communities and

topographic features comprising our natural landscape generally reflect the habitat-selection patterns of mule deer in southern California, which select for a mosaic of oak woodlands, pine forests, riparian areas, and grasslands (Bowyer 1986, Nicholson et al. 1997). This trend was particularly apparent when comparing the habitat use of pumas within their home ranges to composition of the surrounding landscape. However, the responses we found for some habitat categories relative to their availability in the surrounding landscape may reflect how the aggregation of pumas and their prey can be influenced by top-down constraints imposed by the regional social-ecological system, or bottom-up mechanistic processes operating at finer-spatial scales.

For example, while puma home ranges con-

tained more chaparral than was available in our study area or regional landscape, pumas showed no selection for chaparral within their home ranges. If habitat-selection patterns measured at broad scales better indicate the critical factors limiting population growth (Rettie and Messier 2000), puma occupancy of chaparral-dominated areas would enhance survival and reproduction or minimize mortality. Since chaparral was the most abundant vegetation type in the natural landscape of our study area, we suspect the greater amount of chaparral in home ranges primarily reflects that pumas are largely restricted to protected areas in southern California, and these natural areas contain sufficient prey to support puma populations. However, despite the aggregation of pumas and their prey in a chaparral-dominated natural landscape, our models indicated pumas showed a neutral response to chaparral within their home ranges. Because the density of mature chaparral inhibits the movement of mule deer and pumas (Bowyer 1986, Beier 1995), we hypothesize that prey is often less abundant or more difficult for pumas to access in such stands. African lions (*Panthera leo*) similarly base their broad-scale habitat selection upon prey abundance, but then adjust their fine-scale habitat selection toward mechanistic processes promoting accessibility, or catchability, of prey (Hopcraft et al. 2005). Factors we did not evaluate, such as prey migrations and fire history, may further explain this scale-dependent response to chaparral (Nicholson et al. 1997, Loft et al. 1998). While pumas also showed a similar scale-dependent response to conifer forests, we suspect this response is mostly due to social-ecological constraints (i.e., the clustering of human development at lower elevations and protected areas at higher elevations) rather than fine-scale, mechanistic processes like prey accessibility.

Puma responses to the other features of the natural landscape also appear consistent with the distribution of their prey. Pumas were positively associated with riparian areas and oak woodlands, which are vegetation communities frequently used by mule deer for bedding and escape cover (Bowyer 1986). Similarly, pumas were negatively associated with vegetation like grasslands, desert scrub, and barren or sparsely vegetated areas that lacked cover for hunting.

Except for grasslands, mule deer rarely use these areas (Bowyer 1986, Loft et al. 1998). Pumas also selected for higher elevation and more rugged terrain. While home ranges were established in steeper areas of the study area, pumas showed a neutral response to slope within their home ranges. The ruggedness index captures the local heterogeneity of the terrain better than slope or elevation (Sappington et al. 2007), and probably better depicts how topography enhances hunting cover for pumas (Logan and Irwin 1985). However, we caution pumas are probably not biologically constrained to inhabit steep and rugged areas, but may have instead showed greater use of these areas due to the clustering of suburban and urban development in flatter terrain, particularly the coastal areas of southern California.

#### *Puma response to the human landscape*

Pumas appear to ameliorate the high risk of mortality and lack of prey in suburban/urban development by rarely incorporating these areas into their home ranges. This broad-scale avoidance of suburban/urban development also supports the hypothesis that habitat choices made at broad scales reflect critical population limiting factors (Rettie and Messier 2000). Although pumas will take smaller prey, including pets, near human development (Torres et al. 1996), less ungulate prey and a high risk of mortality mean that suburban/urban development effectively represents non-habitat to pumas. Pumas also selected against exurban development but, unlike suburban and urban areas, pumas appear to consider exurban development to be modified habitat rather than non-habitat. Although exurban areas were a smaller proportion of puma home ranges relative to the composition of the surrounding landscape, pumas showed some use (5.8%) of exurban areas within their home ranges. Given the relatively small amount of human development pumas incorporated into their home ranges, alternative sampling designs, statistical models, or sampling scales may provide additional insights into the behavioral response of pumas to human development at finer spatial scales (Marzluff et al. 2004, Gillies et al. 2006, McLoughlin et al. 2010).

Large carnivores consistently experience higher mortality in human landscapes (Woodroffe



and Ginsberg 1998, Mace et al. 1999, Naves et al. 2003). Our access to spatially-explicit housing-density data allowed us to refine this pattern and use the results from our habitat analysis to evaluate how puma mortality varied relative to the intensity of human development. We found no increased mortality risk associated with selection, neutrality, or avoidance of rural areas and could not even evaluate mortality in suburban/urban areas because pumas had already so strongly selected against these areas at broader spatial scales. However, pumas that selected against exurban areas had a lower mortality risk than those that showed a neutral response or positive selection for exurban areas. The implications of this finding are that exurban areas are likely to be hotspots for puma-human conflicts and potentially even population sinks.

Exurban land-use covers about 25% of the conterminous U.S., which is 5–10 times larger than the combined area of urban and suburban land uses, and is increasing at a rate of 10–15% per year (Theobald 2005). In addition to the overall amount of exurban development, additional problems can result from its location. Exurban land use in southern California tended to occur at higher elevations than suburban and urban land use; this association of exurban development with mountain landscapes is common throughout the western U.S. (Theobald 2001, Hansen et al. 2002, Travis 2007). These rugged, high elevation areas also are often good puma habitat (Logan and Irwin 1985, Logan and Sweaner 2001, Hunter et al. 2003), thus increasing the probability of puma-human conflict associated with exurban development.

#### *Potential applications*

The intersection of the natural and human landscapes defines the conservation landscape, or priority areas for conservation action (Sanderson et al. 2002). The conservation landscape in our study area consisted of protected land (private and public) and privately-owned, unprotected land (undeveloped, rural, or exurban) occurring in a mid- to high-elevation chaparral matrix. Areas with similar protection status and housing densities in the adjacent, lower-elevation coastal region should also be considered part of the regional conservation landscape (Dickson and Beier 2002). Within this generalized conser-

vation landscape, additional priority should be given to areas that preserve connectivity between the remaining large blocks of suitable puma habitat (Morrison and Boyce 2009). Habitat fragmentation has strong effects on the carnivore community of southern California (Crooks 2002), and in our study area the isolation of pumas in the Santa Ana Mountains from the larger population occurring in the Palomar Mountains has long been recognized as a critical conservation issue (Beier 1993, Morrison and Boyce 2009). Some of the most important potential applications for our model will therefore include applied, empirical, or theoretical studies examining the consequences of further fragmenting the remaining puma habitat.

The effects of habitat loss and habitat fragmentation can become independent and synergistic in intensively modified landscapes (Bascompte and Solé 1996, Fahrig 2002). Many theoretical models of spatially-structured populations indicate extinction occurs before all suitable habitat is destroyed, and that habitat fragmentation can enhance nonlinear extinction thresholds in situations where much habitat has already been lost (Hanski 1999). These non-linear responses also can be affected by the nature of the matrix, with extinction occurring earlier (i.e., with more suitable habitat remaining) when the matrix consists of highly unsuitable habitat (Bascompte and Solé 1996, Fahrig 2002). These theoretical relationships provide critical insights for using the results of this study to inform conservation planning and guide future research.

The amount of habitat loss we forecasted from 1970–2030 in our study area should therefore be viewed from multiple perspectives. If we calculate the percentage of habitat loss from the entire 14,520 km<sup>2</sup> study area and ignore protection status, approximately 6%, or approximately 800 km<sup>2</sup>, of suitable puma habitat has been or will be lost from southern California from 1970–2030. This amount of habitat loss does not seem overly problematic, especially to ecologists conditioned to hearing about high rates of habitat destruction in developing areas. But this 6% can be a misleading percentage because it masks that only 55% of our study area is protected land and development is still proceeding relatively rapidly on the remaining 45% of our study area open to development. Our model forecasted

about 35% of the remaining suitable puma habitat open to development in the conservation landscape has been or will be lost from 1970–2030. In addition, we caution that our forecasts cover a time period in which southern California was already one of the most urbanized regions in the world. These results collectively suggest land-use changes in southern California have progressed past the initial period of rapid habitat loss and the effect of increased development on pumas may now primarily involve the emergent effects of habitat fragmentation and the concurrent isolation of puma populations (Fig. 3).

We found pumas were strongly associated with protected areas because these areas comprise most of southern California's remaining natural landscape. Recently, the isolation of protected areas by development has emerged as a global conservation problem for carnivores and other large mammals (Hansen and DeFries 2007, Wittemyer et al. 2008) since adjacent development can create population sinks in the outermost portion of protected areas (Woodroffe and Ginsberg 1998). For example, the effective size of game reserves for leopards in South Africa is less than their actual size because the risk of human mortality extends inside the reserve boundaries (Balme et al. 2010). Similarly, our finding that mortality risk increased with increased selection for exurban areas suggests that even moderate intensity development near protected areas could reduce the effective size of southern California's protected areas for pumas. While development on the periphery of protected areas often reduces habitat connectivity, the negative demographic consequences of such development on carnivores could still occur in areas where connectivity has been preserved or restored. In addition to any negative demographic consequences for pumas living on the periphery of protected land, most conflicts between humans and large cats occur in developed areas adjacent to wild lands (Jackson and Nowell 1996). The losses of suitable puma habitat our model projected from 1970–2030 often occurred near protected areas supporting our puma population (Fig. 4), which both corroborates recent increases in puma-human conflict in southern California (Torres et al. 1996) and suggests these conflicts may continue to increase. While the conservation of pumas in southern California is clearly a formidable and

complex challenge, our model provides spatially-explicit forecasts of the conservation landscape in future decades and provides a playing field on which to try to ameliorate the effects of habitat loss, habitat fragmentation, and puma-human conflict. The spatially-explicit nature of our model will facilitate additional empirical and theoretical research that will be needed to craft more effective solutions to these conservation challenges.

The International Union for the Conservation of Nature (IUCN) classifies the puma as an unthreatened species, but one with declining populations (Caso et al. 2008). Although the wide distribution of pumas reflects their ecological flexibility and resilience, the development accompanying a regional human population of approximately 20 million has severely threatened the puma population of southern California. While our study will most directly benefit conservation planning for pumas in southern California, the potential for exurban development to reduce and fragment puma habitat warrants attention throughout the western U.S. The opportunity still exists to address the effect of exurban development on puma populations in the western U.S. in a relatively proactive and cost-effective fashion. In contrast, the minimum estimated cost of the current recovery plan for the highly endangered Florida panther exceeds \$3.5 million per year, a figure that does not include funds for the acquisition or protection of land (United States Fish and Wildlife Service 2006). The cost of land acquisition to protect a substantial number of threatened species in Florida will cost over \$5.7 billion (Mann 1995). Coupled with concern for human livelihood and safety, species conservation linked with wildlife-human conflicts will continue to require increased resources for managers (Woodroffe et al. 2005). Models like ours that interface wildlife-habitat models with spatially-explicit, predictive human-development models will help wildlife and land-use managers create more efficient, effective, and preferably proactive solutions to conserve and manage carnivore populations in an increasingly human-dominated world.

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