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Featured Article

Big Cats in the Big City: Spatial Ecology of Mountain Lions in Greater Los Angeles

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ABSTRACT Large carnivores can represent the ultimate challenge for conservation in developed landscapes because of their large area requirements and potential for conflict with humans. Some large carnivores such as mountain lions (*Puma concolor*) can use a wide range of biomes and vegetation types, and in southern California, USA, they persist in metropolitan Los Angeles, a megacity of 18 million people. Understanding how large carnivores use highly altered landscapes is important for their conservation and management. We estimated home range size, landscape use, and landscape selection for mountain lions in the Santa Monica Mountains and surrounding areas for 29 subadult and adult animals from 2002 to 2016, using 128,133 locations from global positioning system (GPS)-collars. Home range size was similar to that reported by other researchers; home ranges averaged 372 km^2 for adult males and 134 km^2 for adult females, except for 2 adult males in isolated habitat fragments that maintained 2 of the smallest adult male home ranges ever recorded (24 km^2 and 54 km^2). Mountain lions very rarely entered developed areas, consistently avoided altered open areas such as golf courses, cemeteries, or other landscaped spaces, and showed a positive relationship between home range size and amount of development, all indicating that developed areas have reduced value for mountain lions. Mountain lions from all sex and age classes selected areas closer to development than expected by chance, which could be related to the presence of mule deer (*Odocoileus hemionus*) or other prey in or adjacent to urbanization. For 2 adult males that occupied home ranges within the most urban portions of our study area, their response to urban development differed strongly across diurnal periods, ranging from avoidance during the day to selection at night. Shrub vegetation types, especially chaparral, were important in terms of habitat use and resource selection, highlighting their importance for conservation of the species in southern California. North America's largest felid can thrive in shrublands and persist even in one of the world's largest cities, although they only very rarely venture into developed areas within that city.

KEY WORDS chaparral, habitat use, large carnivore, megacity, mountain lion, resource selection, urbanization.

Understanding how animals use and select resources is fundamental to ecology and conservation biology. Landscapes, however, are becoming increasingly modified by human activities (Newbold et al. 2015), which presents challenges and opportunities for wildlife species occupying anthropogenic landscapes, including cities (McKinney 2002, Gehrt et al. 2010, Guetté et al. 2017). More than half of the world's population now lives in cities, and as the human population grows, the number and areal expanse of cities continues to grow (Grimm et al. 2008, Seto et al. 2012). Urbanization removes natural areas entirely, fragments remaining natural areas into smaller patches, and results in a myriad of edge effects such that the city and its human population can severely affect the urban-wildland border and adjacent natural areas (McKinney 2002, Mcdonald et al. 2009). Perhaps most important are the conservation questions of how habitat loss, fragmentation, and alteration affect wildlife populations and communities (McKinney 2008, Gagné and Fahrig 2010, Delaney et al. 2021), and specifically which species survive in urban landscapes and can be expected to over the long-term (i.e., for which species are urban landscapes not sinks).

Mammalian carnivores are of particular interest to ecologists and managers in urban landscapes because they are likely to be strongly affected by habitat loss and fragmentation (Sunquist and Sunquist 2001) and are often unable to maintain viable populations in cities because of their

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extensive area requirements (Beier 1993, Cypher et al. 2010, Benson et al. 2016*a*). The potential for real or perceived conflict with domestic animals such as pets or livestock, or even with humans, can also make urban carnivores an important and challenging management concern (Curtis and Hadidian 2010). Both of these issues are even more pronounced for large carnivores such as wolves (*Canis lupus*), bears (*Ursus* spp.), or large cats, which have greater energetic requirements and roam over far greater areas even than medium-sized carnivores such as coyotes (*Canis latrans*), raccoons (*Procyon lotor*), or bobcats (*Lynx rufus*), and pose a greater risk of conflict. Large felids are obligate carnivores and do not take advantage of anthropogenic resources (e.g., trash or ornamental fruit), in contrast to coyotes (Larson et al. 2020) and black bears (*Ursus americanus*; Baruch-Mordo et al. 2014); therefore, large felids face perhaps some of the greatest challenges for wildlife in metropolitan areas because they require sufficient densities of large herbivore prey. Consequently, there are few populations of large carnivores, and even fewer of large felids, in cities (Bhatia et al. 2013, Riley et al. 2014).

As of 2009, there were essentially only 2 studies that had investigated the ecology of large felids in urban areas, both of mountain lions (*Puma concolor*) in southern California, USA (Beier et al. 2010). More recently, the response of mountain lions to development of varying intensities, up to and including urban development, has been studied in a number of places across the West including the Front Range of the Rocky Mountains in Colorado (Moss et al. 2016, Blecha et al. 2018, Alldredge et al. 2019), in Washington west of Seattle (Kertson et al. 2011, 2013, Robins et al. 2019), around 3 cities in Arizona, including Tucson (Nicholson et al. 2014), in the Santa Cruz Mountains of central California (Wilmers et al. 2013, Smith et al. 2015, Wang et al. 2017), and in Orange and San Diego counties south of Los Angeles (Burdett et al. 2010, Jennings et al. 2016, Zeller et al. 2017) building on the seminal work of Beier (1993, 1995). These studies have reported on the ecology and behavior of mountain lions relative to humans and residential development. In these studies, the intensity of development that the mountain lion population was exposed to was generally suburban or exurban, significantly less dense than that typically associated with urbanization.

We know of just 1 other megacity in the world where there is a population of large felids: Mumbai, India where there are resident leopards (*Panthera pardus*; Braczkowski et al. 2018). The fact that there are still mountain lions in Los Angeles supports the importance of significant natural open space in and around the city, in the San Gabriel Mountains and Santa Susana Mountains to the north and in the Santa Monica Mountains to the west. The long-term persistence of the species in Los Angeles, however, is far from certain. In the Santa Monica Mountains population, movement of mountain lions is significantly restricted by major freeways and development. This restriction has led to very low genetic diversity and potentially increased incidence of social interactions such as intraspecific killing and inbreeding between close relatives (Riley et al. 2014). Benson et al. (2016*a*, 2019) modeled the viability of the population using demographic and genetic information and estimated that there was a 20% probability of extirpation over the next 50 years due purely to demographic processes. If inbreeding depression increases mortality as in another isolated, inbred population of mountain lions (Florida panthers [*P. c. coryi*]; Johnson et al. 2010), the modeling of Benson et al. (2016*a*, 2019) predicted that rapid extinction of the Santa Monica Mountains population would be almost certain in the following 50 years. Individuals in this population face significant mortality risk from humans from vehicle collisions and exposure to anticoagulant rodenticides (Riley et al. 2007, Benson et al. 2020). Thus, a better understanding of their space use and resource selection within this human-dominated landscape is essential for management of this population and of the species more broadly. For example, California is currently considering listing mountain lions in coastal California, including in this population, as threatened under the state Endangered Species Act, and improved understanding of mountain lion spatial ecology in relevant areas would benefit both the listing evaluation and subsequent protection actions.

Mountain lions persisting in one of the largest metropolitan areas in the world present a rare opportunity to increase our understanding of how large carnivores navigate heterogeneous and fragmented urban landscapes. We studied the behavior of mountain lions in and around the City of Los Angeles, a metropolitan area of >18.5 million people (U.S. Census Bureau 2015), the second largest in the United States, and 1 of just 3 megacities (>10 million inhabitants) in North America. Our work provides a detailed evaluation of the spatial ecology of mountain lions from the most urban landscape in North America occupied by mountain lions, thus providing valuable information to managers of mountain lions and potentially other top predators in and around urban centers.

Overall, we hypothesized that development and other anthropogenic modification of natural landscape features decrease the value of these areas for mountain lions in human-affected ecosystems. We addressed this general hypothesis by testing a number of specific predictions about space and habitat use relative to human disturbance. First, we investigated the relationship between home range size and the degree of development, predicting that the size of home ranges would increase with the proportion of development within them, except in extreme cases where home ranges were constrained to small fragments of natural areas surrounded by freeways and urbanization. Second, we evaluated how mountain lions used the landscape, both in terms of natural vegetation types and in terms of human land use, including intensely developed areas such as residential, commercial, or industrial areas, and altered open areas such as golf courses, cemeteries, or other managed areas of vegetation. Based on previous results with other local carnivores such as bobcats (Riley et al. 2003), we predicted that mountain lions would rarely be in developed areas but would potentially more often be in altered open areas. Third, in a resource selection context, we evaluated whether mountain lions selected or avoided these modified areas. Similar to our predictions for habitat use, we predicted that mountain lions would avoid developed areas and perhaps somewhat less so altered open areas, and on an individual level, that mountain lions in the most urban areas would respond most strongly during the day, when people are more active. We also evaluated the use and selection of natural vegetation types, and predicted that mountain lions would most strongly select riparian and oak (*Quercus* spp.) woodlands, based on previous studies in the region. Finally, we determined mountain lion selection of recently burned areas, predicting that they would select them in the first few years after fire.

STUDY AREA

We conducted research in and adjacent to the city of Los Angeles in Los Angeles and Ventura counties, California (Fig. 1) from 2002 through 2016. The study was focused on Santa Monica Mountains National Recreation Area, a unit of the National Park System, and surrounding areas. The park boundary encompassed approximately 600 km^2 and included an assemblage of federal, state, and privately owned lands largely in the Santa Monica Mountains. The Santa Monica Mountains were bordered by the Pacific Ocean to the south; by United States Highway 101, an 8–10 lane freeway, and various urban and suburban communities to the north; by the highly urbanized Los Angeles basin to the east; and by agricultural and developed areas in Ventura County to the west. Additionally, we studied mountain lions in areas north and east of the Santa Monica Mountains in the Simi Hills, the Santa Susana Mountains, Griffith Park, and the Verdugo Mountains (Fig. 1). Griffith Park was a municipal park lying within the City of Los Angeles in the eastern portion of the Santa Monica Mountain Range and was completely surrounded by freeways (134, 5, and 101) and intense development in Burbank, Glendale, and Hollywood (Fig. 1). The Verdugo Mountains were a small, rugged mountain range spanning several cities, including Los Angeles, which were surrounded by intense development in Burbank and Glendale to the south and east and by the 210 Freeway to the north (Fig. 1). All patches of natural land cover in the study area were bordered by major freeways, urbanization, or agricultural development. The study area was characterized by a Mediterranean climate, with cool, wet winters (Nov–Apr) and hot, dry summers (May–Oct). There were multiple land uses throughout the area including federal, state, and local parklands, urban and suburban areas with commercial and residential (both high and low density) development, and agricultural areas. Elevation ranged from sea level (0 m) to 948 m, and the topography ranged from steep, rugged canyons to rolling hills and valleys. Natural vegetation consisted of mixed chaparral, coastal sage scrub, oak

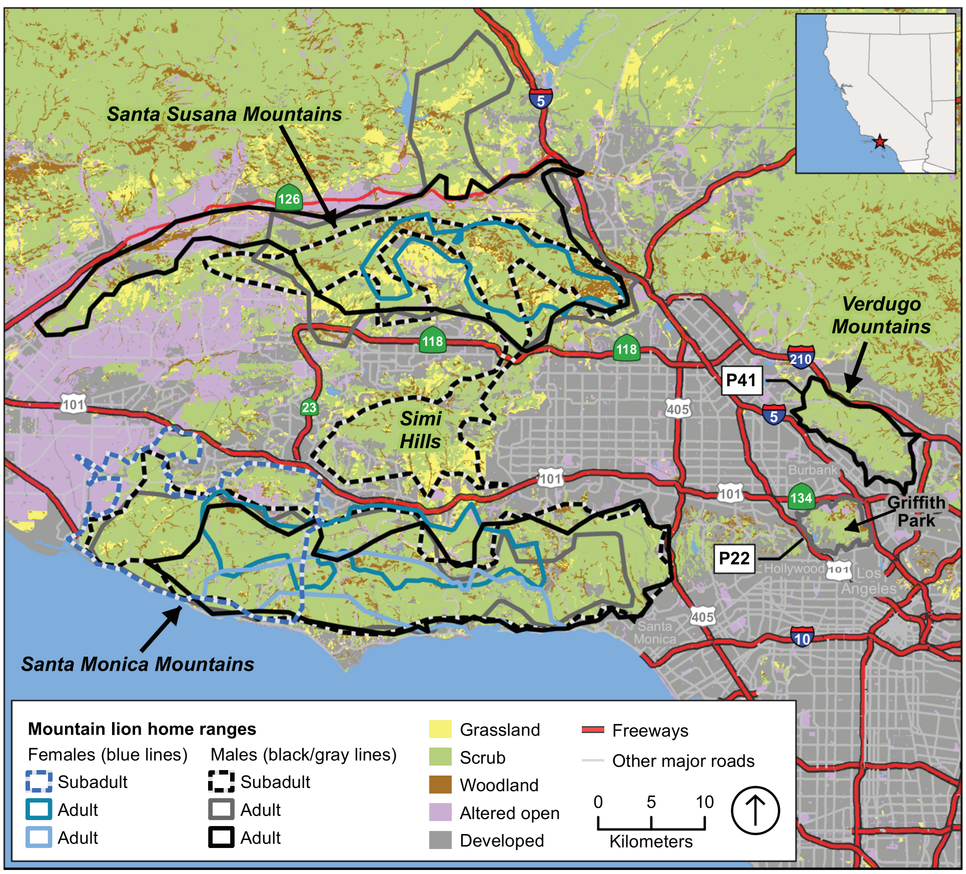

Figure 1. Study area and selected home ranges for global positioning system collared mountain lions in the Los Angeles area, California, USA, 2002–2016. The background is from the land-cover map used in habitat use and selection analyses. Altered open areas were those modified by humans, often with landscaped vegetation (e.g., golf courses, cemeteries). Adult males P22 and P41 had extremely small home ranges isolated by freeways and urban development.

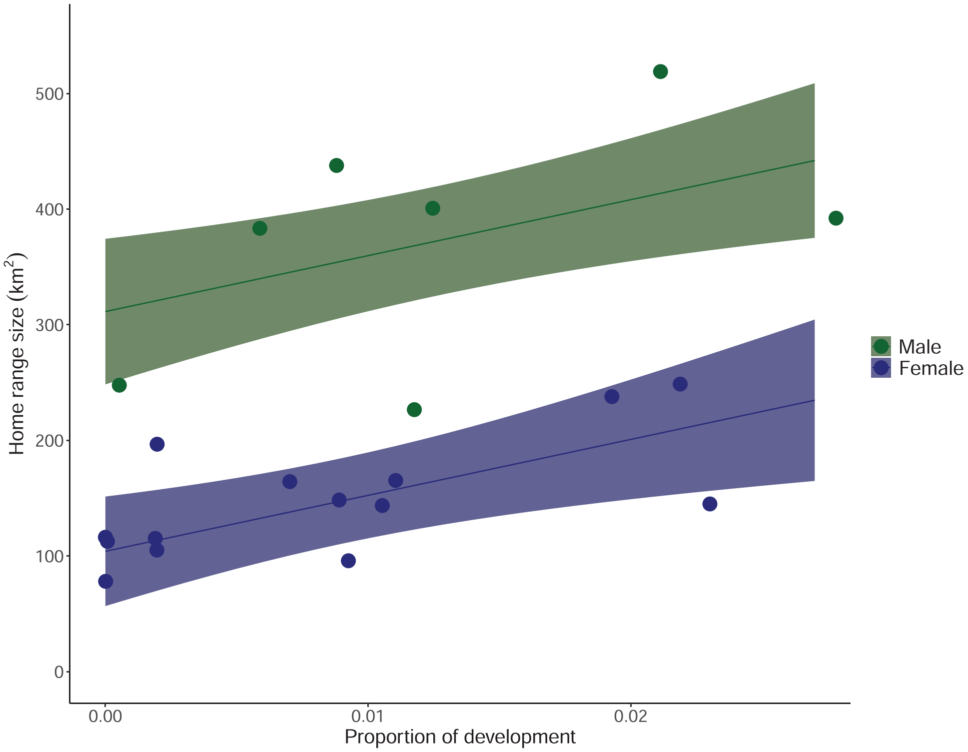

Figure 2. Positive, linear relationship between home range size and proportion of development within home ranges of resident mountain lions in the Los Angeles area, California, USA, 2002–2016 as estimated with a generalized additive mixed model. We show the raw datapoints along with the predicted trends and the 95% confidence intervals (shaded area).

woodlands and savannas, riparian woodlands, and non-native annual grasslands. Bobcats and coyotes occurred throughout most of the study area. The only wild ungulates were mule deer (*Odocoileus hemionus*), the main prey for mountain lions (Benson et al. 2016*b*).

METHODS

Capture and Telemetry

We captured mountain lions using foot cable-restraints (i.e., Aldrich foot snares), baited cage-traps, or by treeing them with trained hounds during 2002–2016. We immobilized mountain lions with ketamine hydrochloride combined with either xylazine hydrochloride or medetomidine hydrochloride administered intramuscularly. We monitored captured animals for the duration of the time they were immobilized and estimated age based on body size and tooth wear measurements (Anderson and Lindzey 2000, Laundré et al. 2000). We deployed global positioning system (GPS)-collars (Followit AB, Simplex and Tellus models, Stockholm, Sweden; North Star Science and Technology, Globalstar Tracker model, King George, VA, USA; or Vectronic Aerospace, GPS Plus model, Berlin, Germany) equipped with very high frequency beacons on adults and subadults (independent animals prior to reproduction: females 14–25 months, males 14–42 months). Fix schedules of GPS-collars varied, but we programmed most collars to obtain 1–2 day locations and 5–7 night locations every 24 hours. Capture and handling procedures were permitted through a scientific collecting permit with the California Department of Fish and Wildlife (number 5636) and the National Park Service Institutional Animal Care and Use Committee, and our use of animals was consistent with the American Society of Mammalogists guidelines (Sikes et al. 2011).

We attempted to catch every individual that we were aware of and continued to track previously collared animals by recapturing them. We used remote motion-sensitive cameras throughout the study area to document uncollared animals. In the Santa Monica Mountains, we generally followed about 75% of the adults and subadults, especially later in the study period. In the Simi Hills, 3 animals moved through or used them periodically, but there was no evidence of resident animals there during this study. We tracked a smaller proportion of animals in the Santa Susana Mountains. Adult male P22 was the only mountain lion that was documented using Griffith Park. In the Verdugo Mountains, there was an uncollared adult female, along with adult male P41.

Home Range Analyses

We estimated adaptive local convex hull home ranges in R version 2.15.1 (R Core Team 2020) with the package adehabitat (Calenge 2006) using GPS telemetry data for each mountain lion included in our analysis to calculate the 100% isopleth. We set the *a* parameter as the maximum distance between any 2 points in each dataset (Getz et al. 2007). We filled in internal holes for home range polygons because we used them to estimate availability in our resource selection analyses. Thus, our goal was to define the outer

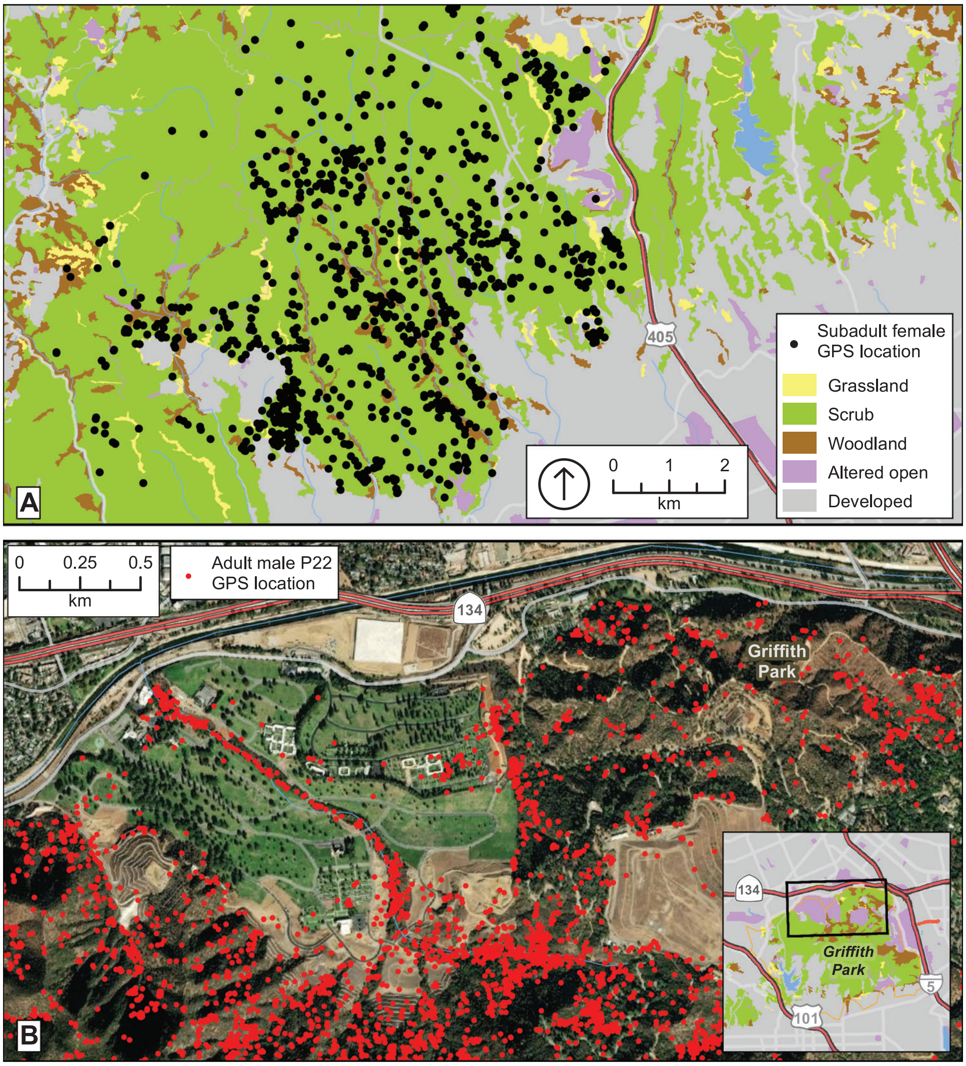

Figure 3. A) Locations from the global positioning system (GPS)-collar for a subadult female mountain lion in the eastern Santa Monica Mountains, California, USA, 2015–2016. The background is from the land-cover map used in habitat use and selection analyses. Altered open areas were those modified by humans, often with landscaped vegetation (e.g., golf courses, cemeteries). Although this female was often close to development, just 1 location of 2,067 (0.05%) used in our analysis was within it. B) The GPS-collar locations for adult male P22, in the Griffith Park Area, California, USA, 2012–2106. The inset shows the land-cover map for his whole home range. Male P22 was rarely located in altered open areas and resource selection analyses indicated significant avoidance of these areas.

boundaries of areas that were used by each mountain lion, and we assumed that the areas within these polygons were within their home ranges and available to that individual. We estimated home range separately for adults ($n = 16$; 7 females, 9 males) and subadults ($n = 17$; 8 females, 9 males). Overall, we estimated 33 home ranges for 29 mountain lions (4 were tracked as both adults and subadults) using all data collected from the period we monitored each animal (min. = 94 days) in the relevant age class.

We investigated the influence of intrinsic (sex, age class) and environmental (proportion of development) factors on home range size using generalized additive mixed models (GAMMs). In these models, the response variable was home range size, and we included a parametric, dummy-coded predictor variable for male (reference female). We also included a non-parametric predictor for the proportion of development that we fit as a smooth function (spline) to capture potential non-linear relationships. We included a random intercept of individual to account for the lack of independence of data from animals tracked as both adults and subadults. First, we conducted our main analysis with non-dispersing residents only but excluded the 2 animals tracked in highly urban environments, specifically relatively small patches of natural area surrounded by dense residential and commercial development (P22, P41; Fig. 1) and dispersing animals (all subadult males and 1 subadult female). Next, we conducted a second analysis with home range estimates for all animals. This second analysis allowed us consider the influence of development on space use more broadly and to consider the influence of higher levels of development experienced by the 2 males occupying the small, isolated habitat patches. In this second model, we also included a dummy-coded variable for adult (reference subadult) and an interaction between male and subadult because we included subadults and adults of both sexes.

Landscape Use

We evaluated use of the landscape by classifying GPS telemetry locations of mountain lions by natural land-cover type and anthropogenic land-use type, and calculating the proportion of home ranges classified as each natural land-cover type and anthropogenic land-use type. We modified 2 existing vegetation layers (Classification and Assessment with Landsat of Visible Ecological Groupings-CALVEG 2013, National Park Service 2014) by combining similar land-cover types to produce a layer with 7 broad land-cover classes: chaparral, coastal sage scrub, grassland, upland woodland, riparian woodland, other, and water. The other category included the remaining rare land-cover classes, mainly exotic vegetation but also areas classified as rock, sand, or other features. For areas where land cover was developed or otherwise altered for anthropogenic activities, we generalized a digital land-use map (Southern California Association of Governments 2005) for 2 classes of anthropogenic land use: development and altered open. Development included commercial and industrial areas and residential areas with ≥2.5 houses/ha. Altered open were areas modified by humans to a lesser extent than developed areas and included golf courses, schools, landscaped areas such as city parks, low-density residential areas (<2.5 houses/ha), cemeteries, horse ranches, and agricultural areas. The Southern California Association of Governments map (2005) was the most accurate available land-use data for the region, and it was reflective of the landscape throughout the study period from 2002–2016 for the development and altered open classifications that we used in these analyses. The geographic information system (GIS) program monitors land use in and around the park as part of the National Park Service Inventory and Monitoring Program.

Resource Selection

We estimated resource selection within home ranges (third-order selection; Johnson 1980) for mountain lions. To estimate resource availability, we systematically sampled 30-m pixels separated by 150 m throughout each home range, resulting in 44 pixels/km^2 (Benson 2013). We then calculated distances from the centroid of all 30-m pixels used by (telemetry) and available to (systematic locations) mountain lions to the closest patch of each land-cover or land-use type (Table S1, available online in Supporting Information). We did not include the water and other variables in resource selection analyses. The water areas were very rare and not likely used, and the other category included a number of land-cover classes that were rare in most home ranges and selection of which would not have clear biological meaning. We calculated these distances using the Euclidean distance tool in the Spatial Analyst toolbox in ArcGIS 10.2.2 (Esri, Redlands, CA) using GIS methods described by Benson (2013). We also estimated distances from unpaved roads and trails (i.e., trails = fire roads, other unpaved roads, and hiking trails). Although we initially intended to consider 3 classes of paved roads, primary roads (major highways) were rare within home ranges, whereas secondary and tertiary roads (intermediate and smaller paved roads) were highly correlated with our anthropogenic land-use classes, specifically development, so we excluded paved roads from the analysis. We estimated slope and elevation from digital elevation models in ArcGIS and classified all used and available pixels with respect to these topographic variables (Table S1). Digital elevation model data were estimated at 9.5-m resolution, but we averaged these data across 30-m used and available pixels for our analyses.

Distance-based variables are effective for assessing habitat selection (Conner et al. 2003), and using continuous, distance-based variables for natural land-cover types and land-use classes (rather than categorical variables) also eliminated the need to base inference on subjectively chosen reference categories in our regression models (Beyer et al. 2010). Distance-based approaches for habitat selection analysis are also robust to error in location data (Conner et al. 2003) and can mitigate GIS error. Finally, distance-based analyses are especially effective for evaluating selection for areas that animals may be attracted to but rarely actually enter (e.g., water or developed areas; Benson et al. 2015, 2016*b*).

We modeled resource selection with generalized linear mixed models implemented in the R version 3.1.1 (R Core Team 2020) package lme4 (Bates et al. 2015) with a binary (0 = available, 1 = used) response variable. We included random intercepts for individual in each model to mitigate effects of unbalanced telemetry data across individuals (range = 796–10,407 locations, $\bar{x} = 3{,}883$) and the lack of independence between used locations from the same individual, and to pair used and available data for individuals within our models. After excluding paved roads, correlation between predictor variables was modest or low ($r < 0.50$) so we included all remaining variables in our global model (Table S1). Prior to modeling, we rescaled values for all continuous variables by subtracting their mean and dividing by 2 standard deviations (Gelman 2008).

The use-available design for resource selection models estimates the relative probability of use of resource variables (i.e., relative to their availability). We use the terms selection and avoidance throughout to indicate that used locations were significantly closer to (selection) or farther from (avoidance) distance-based resource variables (vegetation types, land-use types, trails) than were available locations, or values of classification-based resource variables (elevation and slope) were significantly greater or lower at used locations relative to available locations. Specifically, we inferred selection or avoidance of resource variables when 95% confidence intervals of fixed-effect beta coefficients did not overlap zero.

We investigated potential sex- and age-specific patterns in resource selection. Initially we created models with 3-way interactions between dummy-coded variables of male (female = 0, male = 1) and adult (subadult = 0, adult = 1), and each resource variable. These exploratory analyses indicated there were strong differences in resource selection among age and sex classes, but interpretation of these interactions was cumbersome. Thus, we created male- and female-specific models and included 2-way interactions between adult and each resource variable, which again showed differences between age-classes within both sexes. We next created separate models for each of the 4 sex and age-class combinations (adult females, subadult females, adult males, subadult females) to provide simpler interpretation without interactions. We also created exploratory models separated by time of day (day, crepuscular, and night, with crepuscular defined as an hour before and after sunset and sunrise). At the population-level, selection patterns were generally similar across the different time periods. Thus, for simplicity we pooled data across time periods for our population-level analysis. We investigated individual-level variation in selection of human-altered areas (development and altered open) relative to time of day and degree of urbanization within each home range.

Because resource selection models with large numbers of GPS telemetry locations have considerable power to detect statistical significance, we evaluated biological significance by examining the relative effect sizes (beta coefficients) from these models. Thus, strongest selection and avoidance patterns by mountain lions can be inferred from resource variables that separated from zero most strongly. We present beta coefficients and confidence intervals to allow readers to evaluate statistical and biological significance.

We tested the predictive ability of our models using k-fold cross validation implemented in lme4 as described by Boyce et al. (2002). Specifically, we used 80% of the data (training data) to build a model that we then used to predict the relative probability of use of the remaining 20% (test data). We repeated this procedure 5 times until all data had been used as both training and test data. We ran Spearman rank correlations to assess relationships between the frequency of cross-validated locations and 10 probability bins of equal size representing the range of predicted values. A model with good predictive ability is expected to show a strong correlation with higher numbers of locations falling into higher probability bins (Boyce et al. 2002).

Individual-Level Modeling

We also explored additional individual variation in selection of areas modified by humans. First, we hypothesized that the distance of mountain lions to development or altered open areas might vary as a function of the availability of these areas, consistent with a functional response in resource selection (Mysterud and Ims 1998). We estimated individual-level responses of mountain lions to anthropogenic land use by including a random slope term for development and altered open in resource selection models with all resource variables described above also included as predictors (Gillies et al. 2006). We ran separate models for day, night, and crepuscular periods to derive individual-level coefficients that were specific to these periods across the 24-hour period. We then explored potential functional responses to development and altered open using generalized additive models (GAMs) with the time-period-specific individual-level coefficients as response variables. We specified predictor variables ($\bar{x}$ distance to development or altered open across each individual's home range) as non-parametric smooth functions (splines) in the GAMs to allow for the possibility of non-linear relationships. Second, we hypothesized that individual mountain lions might change their behavior relative to development and altered open between time periods (day, night, crepuscular) as a function of increasing human presence. We subtracted the day—night, day—crepuscular, and crepuscular—night coefficients to derive values reflecting the change in selection between each time period following Benson et al. (2015). We included these values as the response variable in GAMs with a predictor variable for distance-based availability of development or altered open to investigate whether animals changed their behavior across the 24-hour period as a function of increasing urbanization.

Response to Fire

Fire is part of the natural disturbance regime in our study system. Previous researchers of mountain lions occupying shrub-dominated mountains south of Los Angeles reported that mountain lions responded opportunistically to burned areas and that there was considerable individual variability in the response, and they suggested that mountain lions may benefit in the short-term from fire disturbance (Jennings et al. 2016). In our study, only 9 mountain lions that we tracked interacted with 4 separate fires that burned significant portions (≥5%) of their home ranges. Therefore, we conducted a subset analysis with these 9 mountain lions. For these fires, we used polygons that documented the extent of each fire and reclassified these areas as burned in our land-cover and land-use layers and recalculated availability for each of the 9 mountain lions. To examine relatively short-term responses to fires, we used all telemetry data for these mountain lions for up to 3 years following the fire as the used data. We ran a new resource selection model and evaluated selection and avoidance of all resource variables and the additional burned variable. We also included a random slope term for burned to evaluate individual-level variation in response to fire. Although we realize our analysis is a simplification of the complex response of mountain lions to fire disturbance, we wanted to investigate this relationship using the relatively small subset of relevant data available.

RESULTS

Home Ranges

Home range size.—From July 2002 through December 2016, we captured and GPS-collared 29 adult and subadult mountains lions, obtained 128,133 locations for analysis, and estimated 33 home ranges. Of the 29 animals tracked, 19 were in the Santa Monica Mountains, 7 in the Santa Susana Mountains, 1 in Griffith Park, 1 in the Verdugo Mountains, and 1 was a disperser between areas. Mean home range size was $372 \pm 103\,km^2$ (SD) for 7 adult males (we excluded home ranges for 2 males using highly urban environments), $134 \pm 22\,km^2$ for 7 adult females, $284 \pm 134\,km^2$ for 9 subadult males, and $162 \pm 68\,km^2$ for 7 subadult females (excluding 1 female who was dispersing throughout the monitoring period). Male home ranges were larger than those of females, particularly for adults. Two adult males (P22, P41) lived in isolated natural areas surrounded by dense residential and commercial development and freeways and had much smaller home ranges than any other animals, and in particular than any other adult males. Specifically, P22 inhabited a home range of 24 km^2 for 4.5 years in the Griffith Park Area, and P41's home range was 54 km^2 in the Verdugo Mountains (Fig. 1). There was considerable variability in home range size, especially for subadult males. For example, 3 subadult males had home ranges >400 km^2, larger than those of most adult males. In the Santa Monica Mountains, there were 5 males (2 adults, 3 subadults) that had home ranges encompassing essentially the entire isolated mountain range south of the 101 Freeway and west of the 405 Freeway (Fig. 1, 3 of these males portrayed). By contrast, home range size was relatively consistent across adult females (range = 105–165 km^2).

For the 4 animals for which we estimated both subadult and adult home ranges, the size of their home ranges did not change considerably, perhaps not surprisingly because 3 of these 4 animals were females, and subadult female ranges were on average just 28 km^2 larger than those of adults. Specifically, one female's range went from 164 km^2 (subadult) to 165 km^2 (adult), her daughter's declined from 197 km^2 to 116 km^2, and her granddaughter 's increased from 115 km^2 to 144 km^2. Only a single radio-collared male successfully transitioned to adulthood during this study; he dispersed north from the Santa Susana Mountains (Riley et al. 2014) and went from using 191 km^2 to 248 km^2.

Factors influencing home range size.—For our main analysis, excluding dispersing subadults (all subadult males and 1 subadult female) and the 2 males using small isolated fragments, the relationship between home range size and proportion of development within the home range was positive, in accordance with our prediction, and linear ($\beta = 4{,}839.0$, $t = 2.9$, $P = 0.010$; Fig. 2) and males had larger home ranges than females ($\beta = 207.3$, $t = 6.6$, $P < 0.001$; adjusted $R^2 = 0.77$). We conducted a second analysis with all animals, which resulted in a non-linear relationship that captured the positive relationship between home range size and development from low to moderate development (0–7% of home ranges; Fig. S1A, available online in Supporting Information) but transitioned to a strongly negative relationship at higher levels of development influenced by the 2 adult males occupying highly urban environments (16–18% development; Fig. S1B).

Landscape Use

Mountain lion use relative to human land use.—Overall, mountain lion use of urban areas was very low (Table 1), as we predicted. For all animals, including the 2 males in the highly urban environments, 0.9% of locations were in development and 2.6% were in altered open areas, meaning that they were located in natural areas >95% of the time. Adults were even more rarely in development, just 0.1% of locations for both males and females. Subadult males used development more than other age and sex classes, but only 1.0% of their locations were in development and 97.1% were in natural areas. Use of altered open areas was greater than that of development, although still very low (Table 1).

In terms of home range composition, the pattern was similar, with a very low proportion of mountain lion home ranges consisting of urbanized areas (Table 1). Overall development was just 2.9% of home ranges on average for all animals, with 7.3% of home ranges made up of altered open areas. Adult males used 1.3% development and 7.3% altered open, and thus were slightly more urban-associated than adult females (0.8% development, 5.4% altered open), but for both groups more than 91% of their home ranges consisted of natural land-cover types. Subadults were also a bit more urban-associated than adults, but again, even for subadults >89% of their home ranges on average consisted of natural land-cover types.

As with home range size, the 2 males in isolated patches surrounded by urban neighborhoods and freeways were exceptions to these patterns, using development 58 and 93 times more than other adults. Even for these 2 animals, 88.5–90% of their locations were in natural land-cover types. Similarly, for home range composition, these 2 males

Table 1. Landscape use for mountain lions in and around the Santa Monica Mountains, California, USA, 2002–2016, based on >128,000 locations from global positioning system radio-collars. Pts is the percent of the locations in each land-cover type and HR is the percentage of the home range consisting of that type. We obtained data from 29 different mountain lions, but overall $n = 33$ because 4 animals had both subadult and adult ranges. Home ranges were 100% local convex hull isopleths. We did not include the other classification, which contained multiple land-cover types of very low frequency, or the water classification, which was extremely rare and not likely used. Modified = Altered open + Development.

	Natural land-cover types										Anthropogenic land-cover types					
	Chaparral		Coastal sage scrub		Grassland		Riparian woodland		Upland woodland		Altered open		Development		Modified	
	Pts	HR	Pts	HR	Pts	HR	Pts	HR	Pts	HR	Pts	HR	Pts	HR	Pts	HR
Adult males[a] ($n = 7$)	0.46	0.44	0.20	0.26	0.03	0.06	0.09	0.02	0.14	0.07	0.04	0.07	0.00	0.01	0.04	0.09
Adult male P22	0.34	0.22	0.20	0.22	0.00	0.01	0.07	0.01	0.16	0.07	0.04	0.14	0.06	0.18	0.10	0.32
Adult male P41	0.60	0.59	0.12	0.14	0.02	0.00	0.00	0.01	0.11	0.03	0.02	0.04	0.09	0.16	0.12	0.21
Subadult males ($n = 9$)	0.50	0.43	0.23	0.27	0.03	0.05	0.03	0.02	0.15	0.08	0.02	0.07	0.01	0.04	0.03	0.11
Adult females ($n = 7$)	0.52	0.47	0.19	0.23	0.03	0.07	0.04	0.02	0.16	0.10	0.02	0.05	0.00	0.01	0.02	0.06
Subadult females ($n = 8$)	0.51	0.54	0.26	0.24	0.02	0.03	0.03	0.02	0.10	0.06	0.03	0.06	0.00	0.01	0.04	0.07
All animals ($n = 33$)	0.50	0.46	0.22	0.25	0.02	0.05	0.05	0.02	0.14	0.07	0.03	0.07	0.01	0.03	0.03	0.09

[a] Does not include P22 and P41, animals that occupied very small and isolated ranges.

used >2 times as much modified landscape (development + altered open) as other groups, but still on average only about 25% of their home ranges consisted of these human-altered areas (Table 1).

Use of natural land-cover types.—In terms of natural land cover, mountain lions were most often in the shrubland vegetation types of chaparral and coastal sage scrub, not surprisingly given that these are the dominant vegetation types in the region. For all 4 age-sex classes, chaparral was the most common vegetation type used, at close to or >50% (Table 1), followed by coastal sage scrub at about 20%. When combined as shrublands, this cover type accounted for 66% of adult male locations (excluding P22 and P41) and 71–77% of locations for the other 3 age-sex classes. Upland woodland (mostly oak woodland) was the next most common vegetation type (10.3–15.9%), followed by riparian woodland (3.0–9.0%), and finally grasslands (1.7–3.1%). Males P22 and P41 were relatively similar to other mountain lions in terms of their use of natural land-cover types (more detailed results for P22 and P41 are available online in Supporting Information).

Third-Order Resource Selection

Selection of human land-use types.—Mountain lions of all age and sex classes selected development within their home ranges (Fig. 3A), contrary to our prediction. This selection was especially strong for subadults of both sexes and adult females (Fig. 4). This selection of development was in a distance-based context, which does not necessarily mean they were frequently in development. In fact, the mean distances of mountain lions to development at their telemetry locations ranged from 1,280 m (subadult males) to 1,930 m (adult males) across the 4 age and sex classes (Table S2, available online in Supporting Information). All age and sex classes avoided altered open areas, with males avoiding these areas most strongly (Figs. 3B and 4). Mountain lions of the different sex-age classes differed in their response to trails. Adult females strongly avoided trails, adult males and subadult females selected trails, and subadult males had no significant response (Fig. 4).

Selection of natural land-cover types.—In terms of natural land cover, just as chaparral was the most commonly used vegetation type, it was also strongly selected by all 4 groups (Fig. 4). All 4 age-sex classes also selected coastal sage scrub, most strongly for subadult females (Fig. 4). Riparian woodland was also selected by all 4 classes, but only subadult males selected this vegetation type strongly (Fig. 4). Mountain lions consistently selected upland woodland, except for subadult females who showed no selection or avoidance (Fig. 4). For 3 out of 4 age-sex classes, the only natural land-cover type that was avoided was grasslands, strongly for subadult females, although subadult males selected it. We predicted that grassland would be avoided, but the consistent strong selection of chaparral was contrary to our prediction that riparian and upland woodland would be most strongly selected.

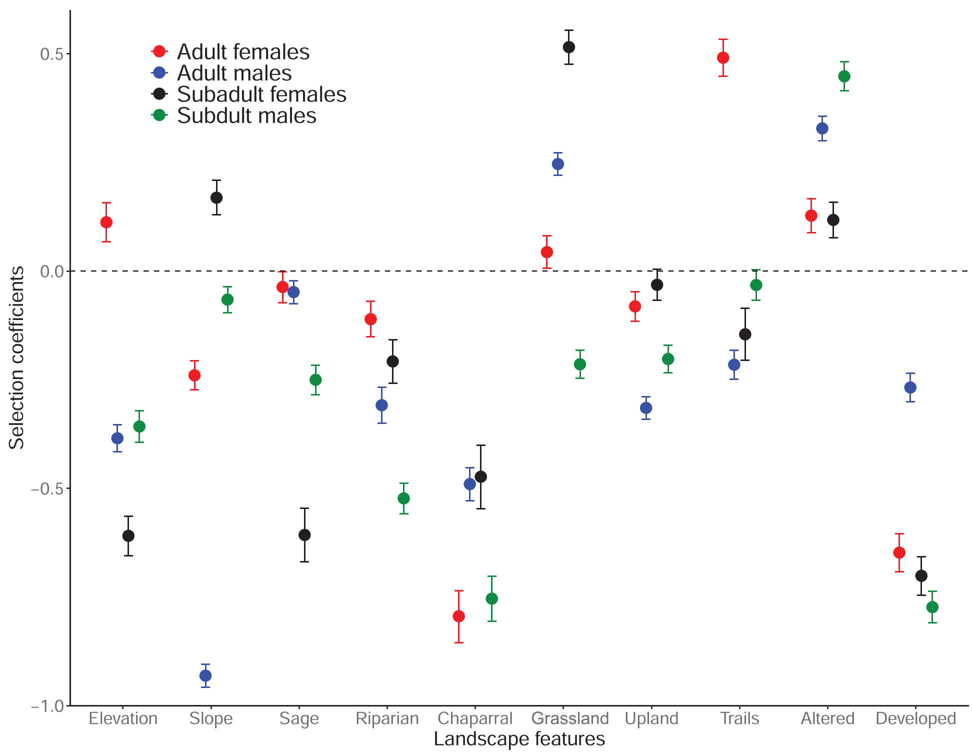

Figure 4. Beta coefficients and 95% confidence intervals from resource selection function models for the different age (adults and subadults) and sex classes of global positioning system collared mountain lions tracked in greater Los Angeles, USA, California, 2002–2016. For classification-based variables (elevation and slope), beta coefficients >0 indicate selection, whereas coefficients <0 indicate avoidance. All other variables were distance-based meaning that coefficients <0 indicate selection, whereas those >0 indicate avoidance. Coefficients with confidence intervals overlapping zero indicate no selection or avoidance. Sage = coastal sage scrub, riparian = riparian woodlands, upland = upland woodlands, altered = altered open areas.

For slope and elevation, there were also some differences between age-sex groups. For elevation, adult females selected higher elevations, whereas all other groups avoided higher elevations, subadult females strongly so. Adults avoided steep slopes, especially adult males (Fig. 4). Subadult males showed much weaker avoidance and subadult females actually selected steeper slopes (Fig. 4). For all 4 age-sex classes, the mean slope for lion locations was around 20% (Table S2). The k-fold cross-validation procedure indicated that the 4 sex- and age-specific models had strong predictive ability; the frequency of cross-validated locations within probability bins were highly correlated with bin ranks ($r_s = 0.915$–0.997).

Individual-level responses to human land use.—At the population-level, there was strong selection of development during all 3 periods of the day (day, crepuscular, and night) that did not vary strongly between these periods. In accordance with our prediction, P22 and P41 showed a similar pattern that differed from mountain lions occupying more remote areas, in that they shifted towards greater avoidance of development during the day and greater selection at night (more detailed results for P22 and P41 are available online in Supporting Information).

Overall, there were not significant functional responses in resource selection for development for any of the time periods (all $P \geq 0.12$). There were significant positive relationships between the difference in selection between crepuscular and night ($F = 8.9$, estimated degrees of freedom (edf) = 2.7, $P < 0.001$, % deviance = 57%, $n = 29$; Fig. 5A) and day and night ($F = 5.8$, edf = 2.3, $P = 0.005$, % deviance = 42%, $n = 29$; Fig. S2A, available online in Supporting Information) and proximity to development. These relationships were influenced by the 2 individuals that were in urban areas more than the other mountain lions that we tracked; both changed their behavior strongly across time periods (more detailed results for P22 and P41 are available online in Supporting Information).

For altered open areas, there was a functional response in resource selection during the day, such that avoidance of altered open areas increased with proximity to them (i.e., $\bar{x}$ distance to altered open decreased across their home range; $F = 4.3$, edf = 6.5, $P = 0.003$, % deviance = 63%, $n = 29$). And as with development, the difference in selection between crepuscular and night ($F = 10.0$, edf = 5.2, $P < 0.001$, % deviance = 74%, $n = 29$; Fig. 5B) and between day and night ($F = 12.5$, edf = 6.0, $P < 0.001$, % deviance = 81%, $n = 29$; Fig. S2B) varied significantly with proximity to altered open areas. Again, the relationships of the differences in selection between time periods were influenced by a few animals who had a lot of altered open area in their home ranges and strongly avoided it (Fig. 3B).

Fire.—Collectively, the 9 mountain lions who had ≥5% of their home range burned by wildfire during the study exhibited a non-significant trend towards selection for burned areas ($\beta = -1.02$, 95% CI = −2.27, 0.23). Variation was high, both between and within individuals, as only 1 mountain lion, a subadult female, showed a clear individual-level response indicating strong selection of burned areas (Fig. S3, available online in Supporting Information). The responses of the other 8 mountain lions varied from trends toward selection or avoidance, but variation was high such that confidence intervals overlapped zero for the remaining 8 individual-level responses (Fig. S3).

DISCUSSION

Response to Development

The fact that mountain lions still persist in and around Los Angeles, one of the largest and most densely populated metropolitan areas in the world, is a testament to the amount of intact natural land cover that remains in and around the city. Our results indicate that mountain lions also exhibited a strong behavioral response to areas dominated by people, supporting our overall hypothesis that anthropogenic landscape modification reduces the value of these areas for mountain lions. First and most importantly, most collared mountain lions were virtually never in developed areas. The fact that for resident (non-dispersing) mountain lions, home range size was positively related to the proportion of development within it also indicates that developed areas reduce the value of otherwise suitable habitat for mountain lions. And the 2 animals that used the highest proportion of development occupied, to our knowledge, 2 of the smallest home ranges ever recorded for adult males of the species, indicating that when faced with a choice between venturing across freeways and through intense urbanization, they instead greatly restricted the size of their home ranges. Access to females is thought to be the primary motivator for the large home ranges of adult male mountain lions. For P22 in Griffith Park, he has never shared that area with females based on extensive remote camera data. In the Verdugo Mountains, P41 did have access to a single female, again based on remote camera detections, whereas adult males often have access to multiple females. Thus, the freeways and urbanization surrounding these habitat fragments appeared to represent such substantial barriers to movement that these males constrained their space use despite the limited mating opportunities.

Our results also highlight the flexibility of mountain lions, in that they can take advantage of opportunities provided by human activities and navigate even intense development when necessary. After selection of chaparral, the most consistent result of our resource selection analyses was the selection of development (Fig. 4), indicating that they were regularly closer to it than expected. This was consistent with previous work showing that mountain lions in this population killed and consumed deer closer than expected to development (Benson et al. 2016*b*). We speculate that mule deer may be taking advantage of lush vegetation in developed and altered areas (DeStefano and DeGraaf 2003, Bender et al. 2004, Wilmers et al. 2013), thus attracting mountain lions to urban edges. The behavior of P22 and P41 (Fig. S4, Discussion, available online in Supporting Information) suggests that individual animals are able to alter their behavior patterns to take advantage of human landscapes at times when people are less active.

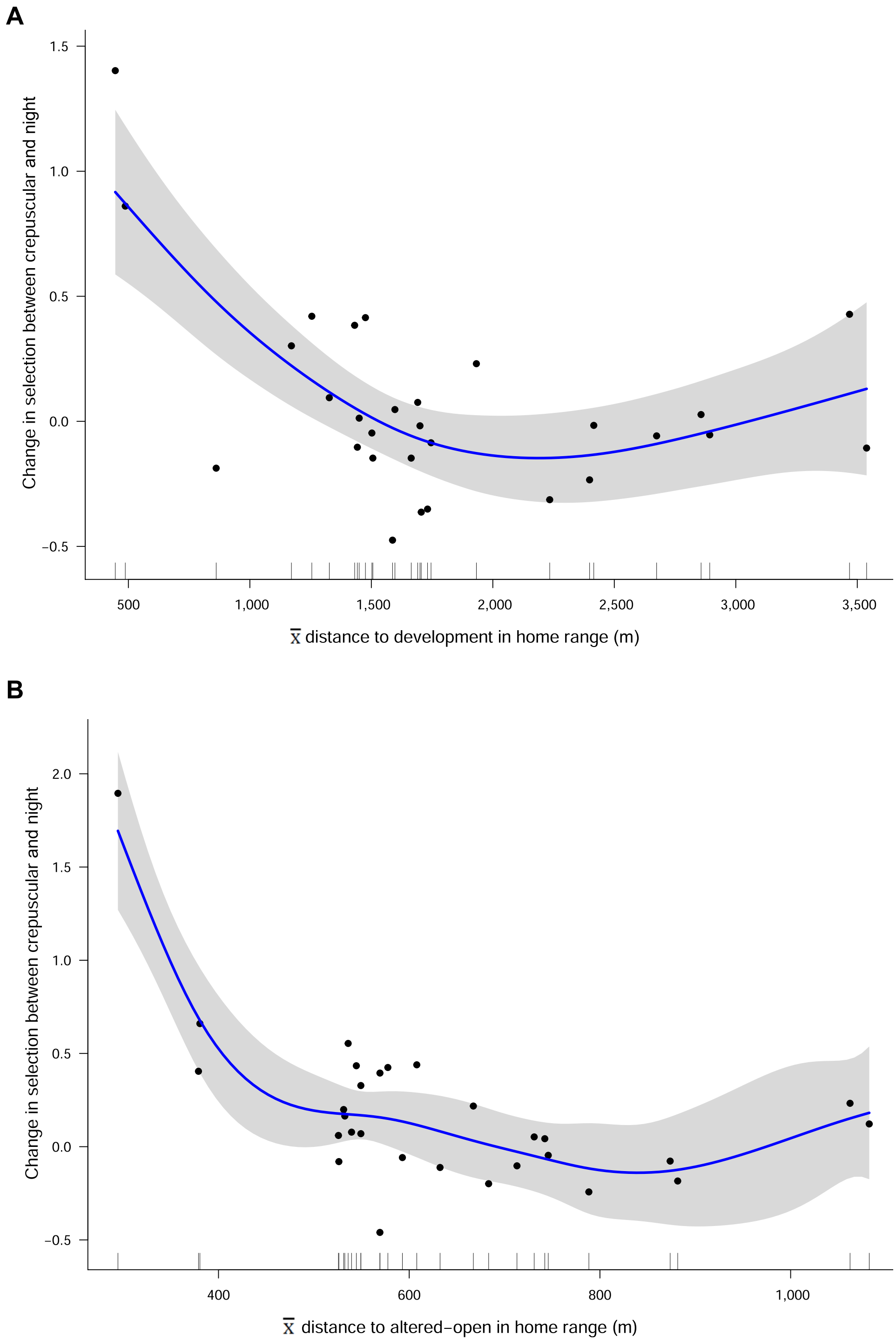

Figure 5. Relationships with 95% confidence intervals (shaded areas) estimated from generalized additive models of the differences in individual-level selection coefficients between crepuscular and night periods relative to distance-based availability of development (A) and altered open areas (B) for mountain lions in greater Los Angeles, California, USA, 2002–2016.

Most mountain lions in our study selected development regardless of time of day, perhaps because their primary prey species (mule deer) responded positively to urbanization. The 2 mountain lions in areas of greater development exhibited strong differences in selection of development between day and night, in a way that mountain lions in more remote areas did not. This was likely a direct response to urbanization and the disturbance that it causes for animals that are faced with it on a regular basis. To more directly address our hypothesis of the selection of development being related to abundance and activity of deer, we would need more information on how mule deer interact with urban and suburban landscapes in our system. Unfortunately, there are very few studies about urban mule deer generally, or about their movements and habitat use in urban landscapes specifically (Bender et al. 2004, McClure et al. 2005). Preliminary information from 6 GPS-collared mule deer in our study area showed intensive and regular use of residential developed areas and altered open areas such as golf courses (J. L. Brown, National Park Service, unpublished data).

If mountain lions are indeed selecting urban edges because of heavy use of those edges by mule deer that are taking advantage of anthropogenic vegetation, then this would be an example of a secondary urban resource subsidy (Dunagan et al. 2019). Omnivorous species such as raccoons and coyotes that reach high densities in urban areas (Gehrt and Riley 2010, Hadidian et al. 2010) can receive a primary urban resource subsidy by directly consuming anthropogenic resources such as trash, ornamental fruit, or pets (Larson et al. 2020), and obligate carnivores such as mountain lions or bobcats may benefit indirectly from urbanization if their prey populations are augmented (e.g., bobcats and rabbits; Dunagan et al. 2019).

Response to Natural and Altered Open Land-Cover Types

Overall, the mountain lions in our study consistently selected native vegetation types with dense cover: chaparral, riparian woodland, and coastal sage scrub (Fig. 4). The 2 features of the landscape that they consistently avoided were grasslands and altered open areas, which were also the most open portions of the landscape. These results are consistent with previous work showing that mountain lions select areas with dense stalking cover and avoid open areas to facilitate hunting success (Atwood et al. 2007), and in a statewide analysis including 13 different study areas, Dellinger et al. (2020) reported selection for shrub cover and avoidance of open areas. Mountain lions are ambush predators, and predators may select areas where the probability of killing is maximized, rather than areas where encounter rates are highest (Hopcraft et al. 2005). Mountain lions rarely killed deer in grasslands (referred to as prairie-meadow) or altered open areas relative to thicker vegetation types (Benson et al. 2016*b*). Because encounters with prey are virtually impossible to directly observe, relatively little is known about the specific factors associated with mountain lion hunting success. Prey species appear to be more vulnerable to, and wary of, mountain lions in more closed vegetation types, whereas coursing predators such as wolves may be more of a threat in open areas (Atwood et al. 2009). Recently burned areas may also lack sufficient stalking cover for mountain lions to successfully prey on deer, providing a potential explanation for why these areas were not strongly selected by all mountain lions.

The consistent avoidance of altered open areas (Figs. 3B and 4) indicates that although these land-cover types may have value for bobcats and coyotes (Riley et al. 2003), it may not be the case for mountain lions. The selection of dense cover and avoidance of open areas could also be because some mountain lions, particularly females and subadult males, are at risk for violent and even deadly encounters with adult males (Riley et al. 2014, Benson et al. 2020). Finally, in the altered open areas, they may feel threatened by people, as suggested by the diel variation in selection; an avoidance response to humans has been documented in other mountain lion populations in California (Smith et al. 2015).

Comparison with Other Studies of Mountain Lions and Development

A number of other recent studies of mountain lions and human development in the western United States included resource selection analyses, which collectively indicated that mountain lions avoided residential areas, although generally these studies were largely in lower density suburban or exurban areas (Kertson et al. 2011, Wilmers et al. 2013, Nicholson et al. 2014, Blecha et al. 2018) as opposed to higher density urban areas. This accords with our results of almost no use of development by 94% of lions and of consistent avoidance of altered open areas. The strong distance-based selection of development that we documented is potentially different from what has been found in other places, but these other studies also consistently determined that mountain lions were flexible in their ability to take advantage of available resources in the complex landscapes created by humans. For example, in western Washington, mountain lions used remaining natural areas and corridors within the exurban residential areas (Kertson et al. 2011), and in Colorado mountain lions hunted near residences, especially as hunger increased (Blecha et al. 2018). In the Santa Cruz Mountains, mountain lions avoided residences during reproductive behaviors, but avoidance was much weaker while moving and feeding (Wilmers et al. 2013). In all 3 areas, diet studies indicated that mountain lions expanded their diets in residential areas to include smaller omnivorous or domestic animals (Kertson et al. 2011, Moss et al. 2016, Smith et al. 2016). Similarly, in a reserve outside Jaipur, India, the leopard diet consisted of 90% domestic species, mostly dogs (Kumbhojkar et al. 2021). In combination, our landscape use and selection results reflect the behavioral response of mountain lions to development in the Los Angeles area, where being close to humans has costs (e.g., human-caused mortality; Benson et al. 2020) and benefits (e.g., higher probability of killing mule deer; Benson et al. 2016*b*).

There were important differences between age and sex classes, and on an individual level for the 2 males occupying highly urban environments. Other studies, while also reporting significant individual-level variation, in general have not seen a functional response (Burdett et al. 2010, Kertson et al. 2011, Wilmers et al. 2013); although Knopff et al. (2014) reported that individuals exposed to agricultural and low-density development avoided these areas less than wilderness animals. Lions P22 and P41 did modify their behavior in response to development by using and selecting it at night but avoiding it more than other mountain lions during the day (Supporting Information). Similarly, Kertson et al. (2011) reported that when mountain lions moved between patches or covered greater distances in residential areas, it was only at night and movement rates were significantly higher. Wang et al. (2017) also reported faster rates of movement and therefore higher caloric cost for mountain lions when using exurban residential areas in central California.

In terms of age and sex differences, Blecha et al. (2018) and Alldredge et al. (2019) reported that males avoided residential development more than females in Colorado, as did Wilmers et al. (2013) in Santa Cruz. Kertson et al. (2013) did not report sexual differences in residential use in Washington. Though in our study area, both sexes were almost never found in urban areas, both selected areas closer than expected to development, and females did so more than males, a similar trend to the greater male avoidance in other regions.

Importance of the Use and Configuration of Development

In general, other researchers have reported selection relative to development or residential areas but almost never its actual use, as we have done here (Table 1). It would be valuable to more regularly report the actual numbers, and proportions, of locations that were in developed or residential areas (Riley et al. 2010) because this is very relevant for human-wildlife conflicts and people's perception of risk from mountain lions. In Washington, Kertson et al. (2013) did report that mean home range overlap of mountain lions with residential areas was 18.35%; however, this was generally in low-density, exurban development. Alldredge et al. (2019) computed mountain lion use of urban (>10 houses/ha) and suburban (1.47–10 houses/ha) areas of Colorado's Front Range and reported the percentage of animals that never used urban (85% of males, 74% of females) or suburban (33% of males, 14% of females) areas, and that use of both occurred overwhelmingly (85% for urban, 62% for suburban) between 2200 and 0500. They also reported that older females regularly used higher density housing areas. Burdett et al. (2010) presented habitat composition for home ranges in the Santa Anas and Peninsular Ranges, California, although urban and suburban areas were combined. Only 0.6% of home ranges on average was made up of urban-suburban areas, with a range of just 0.3% to 0.9%. In contrast, we had an average of 2.9% of home ranges made up of urban development, with a range of 0.0 to 18.0%. Dickson and Beier (2002) reported habitat use in the Santa Anas, where developed areas made up <5% of home ranges and <5% of locations were in them, with males being more urban than females.

The configuration of development and roads relative to large natural areas is also very likely to affect results. In Colorado, Washington, and Santa Cruz, there were extensive natural areas immediately adjacent to the most intense development. By contrast in our study area, the Santa Monica Mountains are isolated from additional natural areas by anthropogenic barriers, and the Verdugo Mountains and Griffith Park are isolated and small (Fig. 1). Thus, in our study virtually every animal, particularly adult males and subadults but even adult females, was relatively close to humans and their structures. South of Los Angeles, the Santa Ana Mountains are similarly isolated by the ocean, freeways, and development, but it is unclear if mountain lion behavior there varies from that in nearby areas. In some studies, the Santa Anas were combined in analyses with the Peninsular Ranges, which were less isolated by freeways and development (Burdett et al. 2010, Jennings et al. 2016). In an earlier study, Dickson and Beier (2002) reported that mountain lions in the Santa Anas were avoiding human-dominated areas including agriculture and urban development for third- (within home range) and second-order (landscape level) resource selection. Given evidence that mountain lions use or select developed areas more at night (Alldredge et al. 2019, this study), the lack of night locations (12%) may have underrepresented the use of development (Dickson and Beier 2002).

Importance of Shrublands to Mountain Lions

In terms of natural vegetation types, our study area differed in terms of habitat composition from those in Colorado (Blecha et al. 2018) and Washington (Kertson et al. 2011), where the natural areas were heavily forested, and conifer forest presence and canopy cover were important positive predictors of mountain lion selection. In the Santa Cruz Mountains, also a much more forested environment, mountain lions selected forests and shrublands during movement (Wilmers et al. 2013). The other southern California studies have repeatedly emphasized selection of riparian woodland, oak woodland, and the conifer forest present in the Peninsular Ranges (Dickson and Beier 2002, Burdett et al. 2010, Jennings et al. 2016, Zeller et al. 2017). The response of mountain lions to shrub vegetation types such as chaparral and coastal sage scrub has generally been reported as neutral, or in some cases even as avoidance (Burdett et al. 2010), such that the importance of these vegetation types has not been emphasized. Our research highlights the importance of shrub communities for mountain lions based on the consistent selection of chaparral and coastal sage scrub, and on average >70% of GPS locations were in shrub vegetation types (Table 1). Dellinger et al. (2020) also reported consistent selection of shrub cover in their statewide analysis. Available habitat use data from other southern California studies similarly reflect the dominance of shrub vegetation types, where they made up >50% of home ranges (Burdett et al. 2010) or of both locations and home ranges (Dickson and Beier 2002). Dickson and Beier (2002) mentioned that scrub vegetation in the Santa Anas typically had vegetation height <0.5 m and likely provided little stalking cover. In our study area, coastal sage scrub and certainly chaparral include extensive areas where vegetation is ≥1 m tall, and in an analysis of mule deer kill-sites (Benson et al. 2016*b*), 77% of the 420 kills were in chaparral or coastal sage scrub. We argue that shrub communities, chaparral in particular, are by far the most important natural vegetation types supporting mountain lion populations in coastal southern California.

Mountain Lion Conservation in Urban Landscapes

When sufficient natural land cover is maintained, even when surrounded by major freeways and intense urbanization, mountain lions can navigate the landscape, find and effectively hunt sufficient prey, find mates, breed, and raise young.

And importantly they can do so without significant direct conflict with humans. As of 2021 we studied >90 mountain lions for 19 years in the Santa Monica Mountains area, and we have just one record of a mountain lion behaving aggressively towards people, a 10-month-old kitten that attacked a 5-year-old boy (J. A. Sikich, National Park Service, unpublished data). It is likely that every animal in our study has been close to (i.e., within 100 m of) humans regularly, if not daily, as people recreate in the park or just inhabit their homes. The spatial and temporal behavioral responses we documented highlight that mountain lions, an apex predator and large carnivore, are effective at living in human-dominated landscapes and rarely interacting directly with humans. Alldredge et al. (2019) specifically studied mountain lion-human interactions on Colorado's Front Range, and the interactions were limited to sightings, lions preying on pets or livestock, and animals in undesirable locations. Similarly, Kertson et al. (2013) documented just 21 interactions over 4 years in their study area in Washington: 14 depredations, 3 sightings, and 4 encounters. Fortunately, mountain lions do not generally consider humans to be suitable prey.

Two of our results are particularly important for the conservation of urban mountain lion populations. One is the consistent, distance-based selection of development by mountain lions, despite rarely entering it. We hypothesize that developed areas are beneficial to and used by mule deer, their main prey, and that this explains the strong selection by mountain lions. If our hypothesis is correct, areas along the edges between urban areas and wildlands, or in lower density residential areas in other parts of the west such as the Santa Cruz Mountains or Colorado's Front Range, may have the highest potential for interactions between mountain lions and people and for conflict with pets or other domestic animals. If true, land or wildlife managers wishing to reduce these potential conflicts could consider working with local residents to reduce the attractiveness of neighboring residential or landscaped areas to deer. Another possibility is that mountain lions are closer to development to prey on denser populations of smaller species such as raccoons (Hadidian et al. 2010), rabbits (Dunagan et al. 2019), or domestic cats (Fig. S5, available online in Supporting Information), which has been cited as a cause for mountain lion use of exurban areas in Colorado (Moss et al. 2016), Washington (Robins et al. 2019), and the Santa Cruz Mountains (Smith et al. 2016).

The other notable result is the heavy use and strong selection of shrublands, namely chaparral and coastal sage scrub, by mountain lions in southern California. Mountain lions are often thought of as a species of the forests and mountains across the West, but they are clearly also strongly associated with shrub-covered hills in southern California. Although rarer vegetation types such as oak woodlands or riparian areas may be strongly selected, given the dominance of shrublands among natural vegetation in coastal southern California and their strong use and selection by mountain lions, conservation of chaparral and coastal sage scrub communities should be a high priority to aid in the persistence of the species throughout the region.

MANAGEMENT IMPLICATIONS

Wildlife and land managers should be aware that mountain lions may persist in urban landscapes, even in and around a megacity such as Los Angeles. Our results indicate that the amount of actual use of development may be very low, but it may be more common for individuals that occupy smaller habitat fragments surrounded by intensive human land use, particularly during the night. Moreover, mountain lions in larger patches that may rarely enter urban areas may be closer than expected to development, likely because of the presence of a resource such as prey. Other forms of developed open space, including landscaped areas such as cemeteries, golf courses, or parks, may be avoided, perhaps because of the lack of cover. Therefore, interactions in urban areas between people, pets, or livestock and mountain lions may be more likely near habitat fragments occupied by them. In larger natural areas, such interactions may be more likely closer to development rather than in the most remote regions. Managers should also be aware that shrublands such as chaparral are preferred and regularly used by mountain lions, so habitat patches dominated by shrubs should be actively preserved to conserve threatened populations. An important requirement for the effective conservation of at-risk mountain lion populations in southern California is preserving and enhancing connectivity between larger natural areas. The use and selection of shrublands and the avoidance of landscape elements without cover (grasslands, landscaped areas) can be used to restore or prioritize habitat linkages aimed at providing that connectivity. Finally, as the state of California is considering mountain lions along the coast, including the population that we studied, for listing under the state Endangered Species Act during 2020–2021, our results about landscape use can help planners in many jurisdictions evaluate how to best protect the habitat that mountain lions require.

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