



Research Article

Puma Response to the Effects of Fire and Urbanization

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ABSTRACT In southern California, wildfire and urbanization influence landscape condition and features. We explored the synergistic effects of these disturbances on puma (*Puma concolor*) movement and habitat preference in southern California, USA using a telemetry dataset of >40 individuals from 2001 to 2011. We examined post-fire movement of tracked pumas to consider the relationship between habitat use and availability as animals used the landscape. We also explored puma response to burned areas to examine the influence of vegetation cover, time since fire, fire frequency, and the synergistic effects of urbanization on puma landscape use. We compare our results to those of others by using a complementary approach to evaluate how habitat relationships change with additional puma data and with consideration of the fire history of the landscape. Our analyses suggest that after fires, pumas use burned habitats opportunistically, responding to post-fire changes in prey density. Additionally, time since fire and fire frequency were useful predictors of puma presence at the individual- and population-level. Our puma habitat models showed a strong relationship between puma habitat use, vegetation, and human developments. Our analysis suggests that fire is an important landscape element to consider when evaluating puma habitat; pumas opportunistically used recently burned areas in the first few years after fire. We identified that pumas avoided grassland vegetation types and areas of sparse cover, suggesting that increasing fire frequency could affect puma habitat suitability and connectivity in the future. Fire frequencies in parts of southern California have already increased beyond the threshold to which the ecosystem is resilient, and if this trend continues across the region, suitable puma habitat may be lost through vegetation-type conversion to homogenous non-native annual grasslands, a habitat avoided by pumas during foraging and resting. We suggest monitoring responses to increasing fire frequency to assess how pumas and other carnivores will be affected by large-scale changes that may pose a threat to landscape integrity and persistence of puma populations in southern California. © 2015 The Wildlife Society.

KEY WORDS cougar, habitat selection, mountain lion, *Puma concolor*, southern California, urbanization, wildfire.

Disturbance influences the patterns and processes of landscapes (Turner 1989). Both human-caused (e.g., logging, development, road construction) and natural disturbances (e.g., floods, fire, and tornados) alter the landscape, creating spatially and temporally heterogeneous mosaics (Turner 2005a) that affect ecosystem composition and function. Disturbances that occur at large spatial scales often change landscape characteristics like vegetation structure and type. This can then lead to changes in key metrics of landscape integrity, such as resource availability, core habitat features, and corresponding responses in populations and communities (Sousa 1984, Pickett and White 1985, Fraterrigo and Rusak 2008, Turner 2010). Furthermore, multiple

disturbances act synergistically to shape population and community dynamics across species and landscapes (Sauvajot et al. 1998, White et al. 1999, Riley et al. 2003, White 2006). Multiple disturbances, particularly compounded anthropogenic perturbations, can intensify or dampen disturbance effects, and can change the probability of disturbance co-occurrence and the normative recovery time of the community (Paine et al. 1998, Turner 2010), as is the case with expanding anthropogenic development and increasing frequency of wildfires (Syphard et al. 2007b).

In the highly urbanized landscape of southern California, the 2 primary landscape disturbances that overlap and interact are fire and anthropogenic development. The shrublands of southern California evolved with fire as a natural disturbance. Many of the native species of shrubs are adapted to respond quickly after fire, regenerating by reseeding, resprouting, or both (Keeley 2006), and many wildlife species that inhabit these areas are equally

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well-adapted to the natural fire regime. This resilience to fire as a disturbance can be observed in the post-fire environment where initial resprouting and new growth can appear just days or weeks after the fire. Within 15–20 years, depending on vegetation type, abiotic conditions, and fire frequency, the system returns to a more mature successional state, similar to pre-fire conditions, with a contiguous closed canopy that provides cover and food for wildlife.

Historically, wildfires in this region served as a natural disturbance pulse that had beneficial effects for many species through a reset of the successional state of the system, resulting in increased heterogeneity in the landscape. However, recent research reported a shift in the fire disturbance regime in southern California (Keeley and Fotheringham 2003) with respect to fire intensity, size, frequency, type, seasonality, and severity (Flannigan et al. 2000). Unlike much of the fire-suppressed forested lands (e.g., ponderosa pine [*Pinus ponderosa*] forest) in the western United States where fire frequency has declined (Covington and Moore 1994, Hessburg et al. 2005, Stephens and Fulé 2005), the shrubland ecosystems in southern California are facing more frequent fire. Fire-return intervals (i.e., the average time between fire events) in the shrublands of southern California have historically ranged from 30 to 100 years but are now 33% more frequent (Keeley et al. 1999, Lombardo et al. 2009, Safford et al. 2011). The cumulative impact of more frequent and larger fires is, eventually, homogenization of vegetation and habitat structure resulting in negative consequences for the ecosystem that outweigh any potential benefits of individual fires. This shifting disturbance with shortened intervals between fires interrupts the vegetation successional cycle, reduces plant diversity, and results in vegetation association changes from native to non-native and grass-dominated landscapes (Keeley 2005).

This increase in fire frequency can be attributed to 3 anthropogenic factors: the spatial distribution and density of development on the landscape, increases in human-caused ignitions, and climate change. Southern California is home to nearly 20 million people living in the 3 major metropolitan areas of coastal southern California that abut and are interspersed with expanses of protected areas composed of fire-prone vegetation. The resulting interface between these wildlands and areas of development (e.g., residential, commercial, industrial, agricultural) has created a landscape threatened by human-induced habitat loss and habitat shifts (i.e., changes in use of vegetation associations and expanding development) associated with development and increasing fire frequencies. Expanding development, particularly areas of low-density housing (<50 houses/km²) and intermediate population densities (35–40 people/km²), is partially accountable for this shift in fire regime because the incidences of human-caused ignitions coincident with contiguous vegetation available to burn are highest in these areas (Syphard et al. 2007b, 2009). These fires can have lasting effects on the landscape and wildlife habitat as anthropogenic development and wildfire can independently, and when coupled, result in persistent landscape changes (Syphard et al. 2009). Additionally, shifting weather patterns

resulting from climate change contribute to further alteration of fire regimes in southern California. Climate models predict that temperatures will increase and humidity will decrease (Miller and Schlegel 2006), and under these conditions, strong, dry winds (i.e., Santa Ana winds) may occur more often and later in the season when fuel loads are highest and fuel moistures lowest (Miller and Schlegel 2006).

Pumas (*Puma concolor*) are the ecosystem's largest predator with wide-ranging movement behaviors and a high level of sensitivity to habitat fragmentation (Crooks 2002), and they serve as an indicator species for ecosystem integrity (Ripple and Beschta 2006, 2008; Thorne et al. 2006). There is a growing concern that persistence of puma populations in southern California is uncertain with previous studies reporting pumas are becoming genetically isolated from each other (Ernest et al. 2003, 2014; Riley et al. 2014; Vickers et al. 2015), and immigration into these populations is necessary to prevent extirpation from the region within the next 100 years (Beier 1993). We focused on this region as development pressure threatens to transform nearly 10% of the study area from suitable to unsuitable puma habitat by 2030 (Burdett et al. 2010).

In this study, we investigated the indirect and long-term effects of fire and anthropogenic development on pumas in the Santa Ana and eastern Peninsular Range populations of southern California. We developed this study building on previous research analyzing the impacts of urbanization and human-induced habitat fragmentation on this same population of pumas (Burdett et al. 2010). In Burdett et al. (2010), pumas were reported to have a neutral response to chaparral within their home ranges; the authors speculate the lack of response could be related to the density of mature chaparral, which limits movement of mule deer (*Odocoileus hemionus*) and puma and could result in less abundant prey in those stands. Burdett et al. (2010) raise the question of whether fire history may explain the scale-dependent response to chaparral. We answer that question using a similar data set and methodological approach as Burdett et al. (2010), and incorporate new data on additional individuals and data on fire and fire history. Our goal was to determine how pumas respond to the post-fire environment in an urbanized landscape in an effort to explore the synergistic effects of wildfire and urbanization on this species of conservation concern in southern California.

STUDY AREA

This study tracked pumas over approximately 20,000 km² across the Peninsular Range of southern California. Roughly 70% of the study area was dominated by natural habitats, but only 45% of the area was formally protected land. Human populations are increasing in California (Syphard et al. 2007a, Sanstad et al. 2011), and have resulted in increased fragmentation and loss of wildlife habitat (Underwood et al. 2009); over 12% has been developed into urban or suburban use and an additional 16% of the study was characterized as land altered by anthropogenic activities (e.g., vacant lots, golf courses). Even on protected lands, the proximity of large

population centers was evident from the degree of human presence within preserved areas. Both consumptive recreation, such as hunting and fishing, and non-consumptive activities such as hiking, biking, and horseback riding were commonly observed throughout the study area regardless of proximity to the coast or suburban and urban development.

The extent and intensity of development was varied over the study area, allowing for an examination of puma habitat selection across differing levels of development and a range of fire histories and frequencies. Anthropogenic development was most intense along the coast with densely populated metropolitan areas located between the coast and the foothills. Lower housing densities in exurban development were located in the foothills and valleys farther from the coast and rural areas, interspersed with protected lands, were in the mountains and deserts of the eastern portions of the study area, farthest from the coast. Areas dominated by both exurban and rural development included farms, orchards, and ranches with livestock grazing, with a range of small- to large-scale operations.

Pumas were the largest carnivore within the study area, although there were a number of sympatric carnivores, including American badger (*Taxidea taxus*), coyote (*Canis latrans*), bobcat (*Lynx rufus*), raccoon (*Procyon lotor*), and gray fox (*Urocyon cinereoargenteus*) that co-occurred with pumas. The 2 ungulate species within the study area were mule deer and desert bighorn sheep (*Ovis canadensis nelsoni*), with mule deer being widely distributed and bighorn sheep restricted to the rugged terrain of the desert habitats of the study area.

The study area encompassed the Santa Ana Mountains in eastern Orange County and the western portions of Riverside and San Bernardino counties and the eastern Peninsular Range including the San Jacinto, Santa Rosa, and Palomar mountains in Riverside and San Diego counties, and extending into Baja California, Mexico (Fig. 1). Elevation in this area ranged from below sea level in the eastern deserts to 3,202 m at San Jacinto Peak. The majority of the study area was publicly held open space and included the Cleveland National Forest, Chino Hills State Park, Irvine Ranch Natural Landmarks, Santa Rosa Plateau Reserve, the Nature Reserve of Orange County, Marine Corps Base Camp Pendleton, the San Bernardino National Forest, Palomar State Park, Cuyamaca Rancho State Park, and Anza Borrego Desert State Park.

Vegetation associations were predominantly shrubland types that varied with elevation and distance from the coast as those are the 2 primary factors influencing weather patterns and vegetation communities in the region. Closest to the coast and at lowest elevations were coastal scrub habitats dominated by California sagebrush (*Artemisia californica*) and laurel sumac (*Malosma laurina*). Chaparral was found from the inland valleys and foothills to the mountains in the east and was dominated by chamise (*Adenostoma fasciculatum*), manzanita (*Arctostaphylos* spp.), redshank (*Adenostoma sparsifolium*), scrub oak (*Quercus berberidifolia*), or lilac (*Ceanothus* spp.). Grasslands often composed of non-native annual grasses, and oak woodlands dominated by coast live oak (*Quercus agrifolia*) also occurred

at these intermediate elevations in the foothills. Riparian zones in the study area frequently had an oak (*Quercus agrifolia*), sycamore (*Platanus racemosa*), and cottonwood (*Populus fremontii*) overstory with herbaceous understory. The easternmost parts of the study area were desert scrub dominated by creosote bush (*Larrea tridentata*) and ocotillo (*Fouquieria splendens*). The vegetation at the highest elevations within the study area were black oak (*Quercus kelloggii*) and coniferous forests dominated by Jeffrey pine (*Pinus jeffreyi*), Coulter pine (*Pinus coulteri*), incense cedar (*Calocedrus decurrens*), and white fir (*Abies concolor*).

The Mediterranean climate of the study region was characterized by hot, dry summers and mild, wet winters with annual precipitation often less than 300 mm, virtually all coming during the winter months. Both precipitation and temperature varied across the study area, and were dependent on distance from the coast, elevation, and local topographic features. Temperatures ranged from averages of 14.8–31.8°C in summer to averages of –0.1–14.1°C in winter. In this area, fires occurred year round, although the most intense and largest fires commonly occurred in October and November in conjunction with Santa Ana (foehn) winds (Keeley 2006).

METHODS

Animal Capture and Telemetry

We captured and tracked pumas with global positioning system (GPS) collars between 2001 and 2011 as part of the University of California, Davis Karen C. Drayer Wildlife Health Center Southern California Puma Project (California Department of Fish and Wildlife Scientific Collecting Permit #9875, University of California, Davis, Institutional Animal Care and Use Committee Protocol #17233). We captured pumas using baited cage traps, foot-hold snares, or by treeing them with hounds. Once captured, pumas were sedated with Telazol (tiletamine HCl and zolazepam HCl) or medetomidine and ketamine HCl, weighed and measured, sexed, ear-tattooed, sampled for blood, tissue, and disease testing, and fitted with an ear-tag and a GPS collar. Over the course of the 10-year sampling period, we deployed 4 different models of GPS collar (TGW-3580, Telonics, Mesa, AZ; Simplex P-1D, Televilt, Lindsberg, Sweden; 3300S or 4400S, Lotek Wireless, Newmarket, Ontario, Canada). We set collars to various sampling intervals dependent on study goals during each collaring effort, with the longest interval being 6 hours. We attempted data retrieval via remote download approximately once/month. Prior to analysis, we checked and filtered data for inaccurate and erroneous locations by visualizing locations and removing improbable locations and all locations with poor quality, undefined location (1-dimension) fixes. During the course of the study, we conducted field visits on a regular basis to complement telemetry data and to verify animal and collar condition. We also visited kill sites opportunistically to document species and location of cached prey.

The collars were deployed from 21 days to 3 years (\bar{x} = 266 days; over multiple collar deployments). After eliminating animals with <30 days of telemetry data and those that did

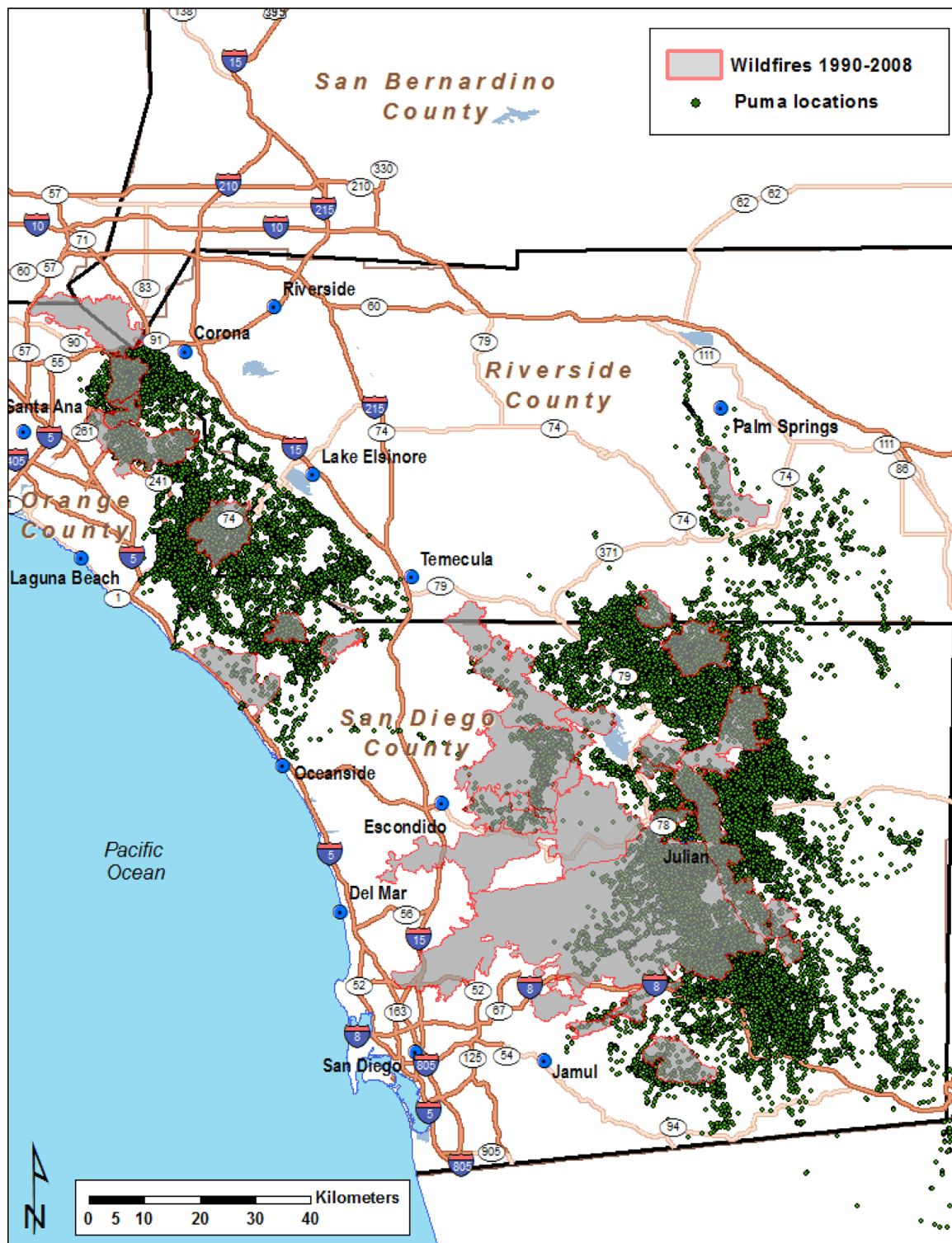


Figure 1. Puma location points in southern California, 2001–2011, and fire perimeter overlay.

not have both burned and unburned habitat available within their home ranges, we used 44 pumas (21 M and 23 F) for analysis. Our study included data from an additional 16 pumas (9 M and 7 F) not analyzed in Burdett et al. (2010). We tracked these animals between 2007 and 2011 and the majority of them were located in the Santa Ana Mountains portion of the study area.

Data Analysis

Using the previously analyzed and new data, we considered 1) puma habitat use with respect to burn status and fire age in a use-availability framework, 2) puma foraging patterns relative to burned areas by analyzing movement rates and kill sites, 3) how landscape features and anthropogenic land use influenced puma habitat selection via modeling, and 4) the effects of

potential shifts in fire frequency on puma habitat use. We conducted a 3-step process to examine the interaction of fire, vegetation association, topography, land protection status, and intensity of development, and to explore the influence of fire frequency and anthropogenic development on puma response to the landscape. First, we evaluated habitat preference at the individual home range level to compare the use versus availability of burned and unburned habitats. To determine whether pumas were hunting in burned areas in proportion to their availability, we analyzed movement metrics and kill site locations relative to burned and unburned habitat. Finally, to explore the factors influencing puma movement and landscape use, we used a multivariate analysis to determine whether the landscape features of vegetation, fire age, fire frequency, or urbanization were significant predictors of puma presence.

For all analyses, we identified burned habitat using the fire history database from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program (FRAP). Shrublands, the predominant vegetation association in most of our study area, are adapted to wildfire and overall shrub cover (although not necessarily shrub density or height) generally recovers within 15–20 years of a fire event (Rundel 1981, Keeley 1986, Keeley et al. 2005). We, therefore, selected fires that had burned within 20 years prior to a puma being tracked in the area and limited our analysis to fires >1,000 ha. We included 27 fires in our analyses (Table 1), and mapped all data in a geographic information system (ArcGIS 10.0; Environmental Systems Research Institute, Inc., Redlands, CA).

Habitat Preference

We used a type II, or third-order (Johnson 1980), habitat selection analysis conducted using compositional analysis (Aebischer et al. 1993, Calenge 2006) with the Adehabitat package in R 2.15.1 (R Development Core Team 2011) to determine whether pumas used burned habitat in proportion to its availability. Because telemetry sampling effort varied by individual and to account for spatial autocorrelation, we subsampled locations for pumas with finer scale movement data at a 6-hour interval to establish a common interval across all individuals. We generated 95% minimum convex polygon (MCP) home ranges (km²) for each individual in Geospatial Modelling Environment (Beyer 2012) to represent the maximum area available for use in the habitat selection study. We then classified each MCP home range using the fire history dataset to identify the proportion of available habitat that had been burned and time since last fire classified into 5 categories: <1 year, 1–4 years, 5–9 years, 10–14 years, and >15 years post-fire. For animals tracked >1 year or individuals with home ranges overlapping >1 fire, we used the classification that reflected the time since the last fire across the majority of the home range of each individual. Lastly, for the population-level habitat (i.e., burn vs. unburned) preference analysis, we identified used habitat by the condition (burned or unburned) at each puma point location, which we summed for each individual. We also generated an individual preference index based on the expected number of locations in burned and unburned habitat, generated from the proportions of each available habitat, compared with the number of observed locations, calculated as (observed–expected)/√expected. We calculated the index with respect to burned habitat, so negative

Table 1. Ignition, date, and final size (ha) of wildfires in southern California, USA between 1990 and 2008 included in compositional analysis. We gathered data from the California Department of Forestry and Fire Protection's Fire and Resource Assessment Program fire history database.

| Fire name | Start date | Cause | Hectares burned |
|-----------------|-------------|-------------------------|-----------------|
| Morrettis | 28 Jun 1990 | Arson | 1,341 |
| Eagle | 14 May 1993 | Campfire | 2,106 |
| Guejito | 27 Oct 1993 | Power line | 7,211 |
| Ortega | 27 Oct 1993 | Miscellaneous | 8,503 |
| Bailey | 1 Jun 1994 | Unknown | 2,867 |
| Second | 26 Jun 1994 | Miscellaneous | 2,339 |
| Palm | 1 Jul 1994 | Lightning | 7,860 |
| Butterfield | 19 Jun 1995 | Arson | 2,708 |
| Baker | 13 Oct 1997 | Unknown | 2,557 |
| Laguna 100 | 14 Aug 1999 | Arson | 1,785 |
| La Jolla | 7 Oct 1999 | Debris | 3,175 |
| Pechanga | 29 Jul 2000 | Unknown | 4,749 |
| Viejas | 3 Jan 2001 | Smoking | 4,224 |
| Gavilan | 10 Feb 2002 | Debris | 2,292 |
| Pines | 29 Jul 2002 | Power line | 24,965 |
| Coyote | 16 Jul 2003 | Lightning | 7,570 |
| Roblar 2 | 21 Oct 2003 | Equipment use | 2,789 |
| Cedar | 25 Oct 2003 | Equipment use | 109,542 |
| Paradise | 26 Oct 2003 | Arson | 22,883 |
| Mataguay | 13 Jul 2004 | Arson | 3,546 |
| Sierra | 6 Feb 2006 | Escaped prescribed burn | 4,286 |
| Horse | 23 Jul 2006 | Campfire | 6,749 |
| Santiago | 21 Oct 2007 | Smoking | 11,505 |
| Witch | 21 Oct 2007 | Arson | 65,587 |
| Ammo | 23 Oct 2007 | Playing with fire | 8,698 |
| Poomacha | 23 Oct 2007 | Arson | 19,996 |
| Freeway Complex | 15 Nov 2008 | Vehicle | 12,264 |

numbers represent an avoidance of and positive numbers a preference for burned areas.

Kill Site and Movement Metrics

Prey abundance and distribution serve as important predictors of puma presence (Laundré 2010). In our study area, mule deer are the primary prey for most pumas (Beier and Barrett 1993, Sweanor et al. 2008). However, there is very little information available on mule deer abundance and distribution in the region, specifically as those population parameters relate to fire. Therefore, we conducted a kill site analysis based on patterns in puma movement to consider whether pumas were using prey resources in burned areas and applied this as an indirect measure of the prey selection and availability that may be an influencing factor in puma use of burned habitats. We evaluated prey consumption patterns using the tested and validated kill cluster algorithm Python script (Knopff et al. 2009), which identifies kill clusters based on repeated visits to an area limited to approximately 200 m over the course of several nights, indicating a large prey item was killed, cached, and visited repeatedly for foraging bouts on successive nights after the kill. The algorithm is designed to identify clusters assuming handling time for prey items >8 kg (Knopff et al. 2009) and was developed in a region where deer are the primary prey for pumas as they are in our study area. Previous studies on pumas in southern California reported that, although smaller prey items are an important component to the puma diet based on examination of both scats and kill sites (Beier and Barrett 1993, Logan and Sweanor 2001), these prey species were generally consumed within 3–5 hour of the kill, whereas a puma would spend 3–4 days consuming a deer carcass (Beier and Barrett 1993). We, therefore, reasoned that the majority of kill clusters identified by the algorithm represented kills of mule deer. Because pumas often kill then cache their prey, dragging it up to 100 m to a suitable cache site, we also assessed the number of kill sites that occurred at the edge of burned areas where a deer could have been taken in a burned area, then cached in adjacent shrubs for cover. We analyzed kill sites with likelihood ratio goodness-of-fit G-tests to determine whether more kills occurred in burned areas than expected given the amount of burned habitat available to each puma.

We also examined movement metrics to determine whether movement patterns differed in burned and unburned habitats. To determine tortuosity of movement, we calculated step length, a measure of distance between 1 point and the next in time, and net displacement, the total distance between the first and each consecutive point. More tortuous movements may be indicative of foraging or hunting behavior. We compared average step length and net displacement for burned and unburned habitats with a non-parametric Mann–Whitney *U*-test.

Habitat Models

We designed our habitat modeling approach to mirror that of Burdett et al. (2010) to make a direct comparison of habitat associations given the inclusion of 16 additional pumas to the dataset and the incorporation of fire variables to evaluate the role of fire in influencing puma habitat selection.

To model puma response to fire and other biotic and abiotic factors, we considered 28 predictor variables, including the original 22 variables evaluated by Burdett et al. (2010) related to 5 different categories: fire, vegetation, topography, protection status, and anthropogenic development (Table 2). We did not evaluate the effects of seasonal variation on puma habitat selection because seasonal changes in this region are mild and previous research reported that, although home ranges are larger in the wet season, puma habitat preferences are consistent across seasons (Dickson and Beier 2002).

We derived our burn status and time since fire variables from the FRAP fire history data and extracted fire frequency data representing number of fires since 1908 from the Fire Return Interval Departure database (Safford et al. 2011). We defined and delineated vegetation association covariates from the Landscape Fire and Resource Management Planning Tools Project (LANDFIRE; Rollins and Frame 2006) using the same 10 vegetation categories to reclassify as in prior studies (Dickson and Beier 2002, Burdett et al. 2010). We also included distance to water as a habitat covariate, which we generated by creating a raster layer of the Euclidean distance to blue line streams from the United States

Table 2. Fire and land cover variables evaluated in habitat models for pumas, Southern California, USA, 2001–2011 (adapted from Burdett et al. 2010).

| Variable | Description |
|----------------------------|--|
| Fire | |
| Burned | Area burned within the last 20 yr |
| Time since fire (TIMEFIRE) | Time since fire categorized into 6 classes |
| Number of fires | Number of fires at a given location since 1908 |
| Habitat | |
| Agriculture | Pasture, cropland, orchards |
| Barren | Open areas lacking vegetation |
| Conifer forest | Pine/fir forests |
| Chaparral | Chamise-dominated areas |
| Coastal scrub | Coastal sage dominated areas |
| Desert scrub | Sagebrush/creosotebush-bursage-dominated areas |
| Grassland | Graminoid-dominated areas |
| Oak woodland | Oak-dominated open canopy woodlands |
| Riparian | Mixed coniferous/deciduous forest |
| Sparse | Sparsely vegetated areas |
| Distance to water | Euclidean distance to blue line stream |
| Topography | |
| Elevation | Meters above sea level |
| Slope | Degrees of slope |
| Aspect | Direction of slope |
| Ruggedness | Ruggedness metric |
| Protection status | |
| Private unprotected | Private land with no protection status |
| Private protected | Private land not open to development |
| Public protected | Public land not open to development |
| Tribal | Land in Native American ownership |
| Development | |
| Private undeveloped | Privately owned land with no housing units |
| Rural | Housing density >16.18 ha/unit |
| Exurban | Housing density 0.68–16.18 ha/unit |
| Suburban or urban | Housing density <0.68 ha/unit |
| Distance to major roads | Euclidean distance to major road |
| Distance to local roads | Euclidean distance to local roads |

Geological Survey National Hydrology Dataset stream layer because we observed riparian areas often recover more quickly from fire. We gathered our topographic data from digital elevation models (DEM), and calculated vector ruggedness measure (VRM) from the DEM to represent terrain variability (Sappington et al. 2007), which was previously identified as an important landscape feature for pumas (Dickson et al. 2005, Burdett et al. 2010). Data on protected areas were based on information from the Protected Areas Database of the United States (DellaSala et al. 2001). Our anthropogenic development covariates included data on housing density, which were based on the same spatially explicit regional growth models (Theobald 2005) used in Burdett et al. (2010), and Euclidean distances from major (e.g., freeways and secondary arterial roads and highways) and local roads (e.g., paved collector roads and gravel or native surface roads) developed from the 2007 TIGER datasets for California major roads and local roads (U.S. Census Bureau 2007).

As in Burdett et al. (2010), we analyzed puma habitat preference based on a use-availability framework. Use was represented by the telemetry points for each puma, and we generated stratified random points in proportion to the number of presences for each individual within their 100% MCP home ranges to represent available habitat using the Geospatial Modelling Environment (Beyer 2012). We then tested all variables using univariate binary logistic regression in Systat version 12 (Systat Software, San Jose, CA) to determine which were significant on their own and whether the response to each indicated selection or avoidance, which we then factored into our development of a resource selection function (RSF) model using generalized linear mixed models (GLMM). Our GLMMs included only variables that were significant predictors of puma presence in our univariate regression models, and to avoid multicollinearity, we used Spearman rank correlation to identify variables with $r \geq |0.6|$ so those variables would not be incorporated into the same model.

We ran binomial GLMMs of puma presence and our random points representing available habitat (Pearce and Boyce 2006, Aarts et al. 2012) using the PROC GLIMMIX function in SAS (SAS Institute, Cary, NC). Generalized linear mixed models are a robust tool to analyze habitat selection with telemetry data because the random effects resulting from spatial and temporal correlation in location data and unbalanced number of locations from each individual can be estimated to allow for more accurate and appropriate analysis of population-level effects (Gillies et al. 2006, Bolker et al. 2009, Koper and Manseau 2009, Burdett et al. 2010). Because the dataset of GPS-tracked individuals included both males and females across age classes, we assumed that the presence data represented an appropriate level of inter-individual variability. Models calculated random effects using the random intercept method with a standard variance components covariance structure and the Huber-White Sandwich variance estimator to calculate empirical standard errors that are robust to the lack of independence in telemetry data due to both the spatial

autocorrelation of locations and correlation of points from each individual (Clark and Stevens 2008).

To determine whether the data from the additional 16 collared pumas resulted in changes in habitat associations reported in Burdett et al. (2010), we ran the same suite of 15 a priori models and then ran a complement of those models that included our fire covariates (Table 5). We based model selection on an information-theoretic approach using Akaike's Information Criterion for small sample sizes (AIC_c) and compared overall differences between models with ΔAIC_c to determine which model best fit the data. We also calculated model weights (w_i) or the likelihood of a model, according to Burnham and Anderson (2002). To further evaluate model fit, we separated the data into 5 groups, each incorporating approximately 80% of all data points, while withholding all data from several individuals, to determine whether we had overfit our models. We ran each group separately and compared results to determine whether removing all the location information from select individuals would vary the model output, which would suggest that certain individuals were having undue influence on our results. To better understand which variables in the best model were influencing patterns of puma presence, we recorded the odds ratios for each variable and the 95% confidence limits for those odds ratios. Odds ratios with confidence limits that bound 1 are considered less influential in the model.

RESULTS

Habitat Preference

Data from the 44 pumas included 99,078 point locations, ranging from 245 to 8,664 ($\bar{x} = 2,252$ points collected/individual). Subsampling the location data at 6-hour intervals resulted in 33,465 points across all individuals for evaluation in the population-level habitat preference analysis. The compositional analysis revealed there was moderate preference for burned areas over unburned habitats by pumas (Wilk's $\lambda = 0.8854$, $P = 0.03$). We observed individual variation in the amount of burned habitat that was available to individual pumas and the amount of burned habitat individual pumas used based on the habitat preference analysis. Despite the individual variation, the population-level trend was of greater use of burned habitats relative to their availability. The mean burned habitat available within an individual puma home range was 25.0%, whereas 29.3% of the puma locations were in burned habitats (Wilk's $\lambda = 0.8854$, $P = 0.03$). The maximum value for percentage of burned habitat in an available MCP was 72.6%, whereas the maximum percentage of that individual's point locations in burned habitat was 93.4%, demonstrating a more striking case of selection of burned habitat.

The individual preference index also suggested that most individuals exhibited a moderate preference for burned habitats over unburned habitat, regardless of time since fire ($\bar{x} = 2.44$, max. = 16.53, min. = -8.19; Fig. 2). However, we did observe differences in the post-fire response among individuals. Although most animals demonstrated

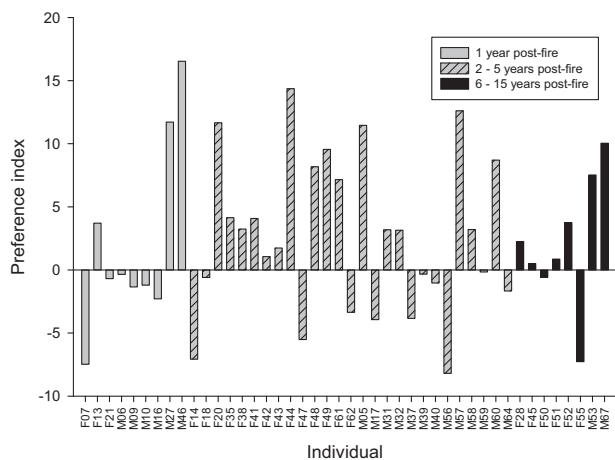


Figure 2. Individual burn preference index for pumas in southern California, 2001–2011, based on use versus availability with respect to the time since last fire. We identified time since fire from the date of the wildfire that burned the majority of the home range area for each puma. Mean home range size for all pumas was 627.4 km² (\bar{x} = 454.6 km² for females, \bar{x} = 793.1 km² for males). Positive numbers indicate a preference for burned areas and negative values, an avoidance of burned areas. Individual pumas are located on the *x*-axis.

a moderate preference for burned habitat, some animals showed a strong preference, whereas others exhibited avoidance of burned areas. This variation did not appear to be linked to sex-specific patterns (e.g., M56 and F07 showed strong avoidance of burned areas [preference indices = -8.19 and -7.47], respectively), whereas at the opposite end of the spectrum, male M46 and female F44, showed a very strong preference for burned area (preference index = 16.53 and 14.35, respectively). Although average burned habitat preference was slightly less for females than males (\bar{x} preference index values of 1.89 and 3.04, respectively), overall, there was no difference in burned habitat preference between male and female pumas ($t_{42} = -0.606$, $P = 0.547$). In general, it appeared that pumas avoided habitats that had been burned <1 year prior to use, and preferred habitat within 2–5 years of a fire.

Kill Site and Movement Analysis

We identified 9,598 putative kill or cache sites from the 44 pumas analyzed using the kill cluster algorithm (Knopff et al. 2009). For all pumas combined, the majority of kill sites occurred in unburned areas, but there were more kill sites observed in burned areas than expected given the amount of available burned habitat ($G_1 = 195.8$, $P < 0.001$; Table 3). Additionally, 60 putative kill sites (<1%) were located 100 m from a burned edge, which may be indicative of kills occurring within the burn that were subsequently cached on the unburned edge of the fire perimeter. When grouped by sex, the results were the same with more kills observed in burned areas than expected for males ($G_1 = 179.9$, $P < 0.001$) and females ($G_1 = 45.7$, $P < 0.001$). To better understand these hunting patterns, we evaluated the observed kill site distribution across successional states and found that 70% of all kills were in unburned habitats, 24% in early successional (burned 0–6 yr prior), 3% in mid-successional (burned

Table 3. Observed and expected distributions of kill site clusters for all pumas, male pumas, and female pumas in burned versus unburned areas, with percentages in parentheses for collared pumas in southern California, 2001–2011. We identified kill clusters using a Python algorithm (Knopff et al. 2009) and classified them as occurring in burned or unburned habitats.

| Group | Burn status | Observed | Expected |
|-----------|-------------|-------------|-------------|
| All pumas | Burned | 2,891 (30%) | 2,291 (24%) |
| | Unburned | 6,685 (70%) | 7,285 (76%) |
| Males | Burned | 1,519 (39%) | 1,129 (29%) |
| | Unburned | 2,349 (61%) | 2,739 (71%) |
| Females | Burned | 1,372 (24%) | 1,162 (20%) |
| | Unburned | 4,336 (76%) | 4,546 (80%) |

6–12 yr prior), and 4% in late successional (burned >12 yr prior) habitats.

The mean step length or distance from one point to the next, was shorter for pumas in burned habitats 1,260.3 m (± 16.8 m SE) compared to 1,393.7 m (± 13.1 m SE) in unburned areas ($U = 1.199\text{E}+08$, $P < 0.001$). We observed a similar pattern with net displacement, such that mean net displacement was shorter in burned areas compared to unburned habitats (burned = 17,069.5 m \pm 183.4 m SE, unburned = 19,834.1 m \pm 135.5 m SE, $U = 1.251\text{E}+08$, $P < 0.001$).

Habitat Model

The results of univariate logistic regression models revealed that many variables were highly significant predictors of puma presence, including several covariates that were not significant in the analysis in Burdett et al. (2010; Table 4). Puma presence was positively associated with burned areas, particularly in the first 9 years after fire. The presence was also associated with conifer, oak woodland, and riparian landscapes and pumas preferred to be close to water. There was a small positive relationship between the number of repeat fires since 1908 and puma presence, and the presence was also positively influenced by the amount of private, protected land or tribal land, and private undeveloped land. Finally, pumas preferred rugged terrain and higher elevations, which are generally correlated with distance from the coast and degree of open, contiguous habitat. The presence was negatively associated with the amount of barren, sparse, grassland, and desert scrub vegetation associations, and private, unprotected land. Puma presence was also negatively associated with exurban, and suburban or urban housing densities. Our binary fire variable (burned vs. unburned) was highly correlated with time since fire and slope was highly correlated with VRM. We tested each variable in our models and selected the better performing for each, which were time since fire and VRM.

When we ran our GLMM models, those that included our fire variables performed better than those that did not, and the selected model was the global vegetation, anthropogenic development, and fire model, which clearly outperformed all other models ($w_i > 0.999$; Table 5). This model was also similar to the composition of the selected model from Burdett et al. (2010), but included our fire variables (which

Table 4. Results of univariate binary logistic regression for each model variable predicting habitat selection of pumas in Southern California, USA, 2001–2011. Variables are classified by parameter type. The coefficient for each model variable with standard error is presented, as well as the *P*-value ($\alpha = 0.05$) for each parameter. TIMEFIRE represents the time since the last fire in 6 categories: 0 (<1 yr), 1 (1–4 yr), 2 (5–9 yr), 3 (10–14 yr), 4 (15–19 yr), and 5 (>20 yr).

| Variable | Coefficient \pm SE | <i>P</i> |
|----------------------------------|-----------------------------------|----------|
| Fire | | |
| Fire (0, 1) | -0.355 ± 0.029 | <0.001 |
| TIMEFIRE 0 (<1 yr) | 0.749 ± 0.134 | <0.001 |
| TIMEFIRE 1 (1–4 yr) | 0.409 ± 0.035 | <0.001 |
| TIMEFIRE 2 (5–9 yr) | 0.494 ± 0.072 | <0.001 |
| TIMEFIRE 3 (10–14 yr) | 0.000 ± 0.099 | 0.999 |
| TIMEFIRE 4 (15–19 yr) | 0.052 ± 0.068 | 0.448 |
| TIMEFIRE 5 (>20 yr) | Reference | |
| Number of fires | 0.118 ± 0.010 | <0.001 |
| Vegetation | | |
| Agriculture | -0.253 ± 0.170 | 0.137 |
| Barren | -1.367 ± 0.100 | <0.001 |
| Conifer ^a | 0.541 ± 0.055 | <0.001 |
| Chaparral | 0.006 ± 0.028 | 0.829 |
| Coastal scrub ^a | 0.005 ± 0.039 | 0.905 |
| Desert scrub ^b | -0.607 ± 0.058 | <0.001 |
| Grassland | -1.199 ± 0.063 | <0.001 |
| Oak woodland | 0.631 ± 0.042 | <0.001 |
| Riparian | 1.916 ± 0.096 | <0.001 |
| Sparse ^a | -1.510 ± 0.124 | <0.001 |
| Distance to water | $(-1.35 \pm 0.06) \times 10^{-3}$ | <0.001 |
| Protection status | | |
| Private unprotected | -0.104 ± 0.028 | <0.001 |
| Private protected ^a | 0.730 ± 0.104 | <0.001 |
| Public protected ^b | -0.019 ± 0.026 | 0.452 |
| Tribal ^a | 0.264 ± 0.054 | 0.023 |
| Development | | |
| Private undeveloped ^a | 0.354 ± 0.059 | <0.001 |
| Rural ^b | 0.067 ± 0.035 | 0.054 |
| Exurban ^a | -0.395 ± 0.045 | <0.001 |
| Suburban/urban ^a | -1.378 ± 0.116 | <0.001 |
| Distance to major road | $(-1.6 \pm 0.30) \times 10^{-5}$ | <0.001 |
| Distance to local road | $(-2.0 \pm 11.0) \times 10^{-6}$ | 0.862 |
| Topography | | |
| Elevation | $(1.65 \pm 0.26) \times 10^{-4}$ | <0.001 |
| Slope ^a | $(-8.53 \pm 1.31) \times 10^{-3}$ | <0.001 |
| Aspect ^a | $(-3.49 \pm 1.22) \times 10^{-4}$ | 0.004 |
| Ruggedness | 5.150 ± 0.496 | <0.001 |

^a Variables identified as significant predictors of puma presence that were not significant in Burdett et al. (2010).

^b Variables that were not found to be significant that Burdett et al. (2010) found to be marginally significant.

includes the mean intercept $\beta_0 = 0.298$, and random intercept $\gamma_{0j} = 0.063$):

$$\begin{aligned} \text{logit}(w(x)) = & 0.298 + (0.602 \times \text{conifer}) + (0.534 \times \text{oak}) + (1.437 \times \text{riparian}) \\ & + (-0.104 \times \text{distance to water}) + (-1.262 \times \text{barren}) \\ & + (-0.636 \times \text{desert scrub}) + (-1.059 \times \text{grassland}) \\ & + (-0.974 \times \text{sparse}) + (-0.403 \times \text{exurban}) \\ & + (-0.991 \times \text{suburban-urban}) + (-0.003 \times \text{distance to major road}) \\ & + (0.056 \times \text{number of fires}) + (0.520 \times \text{TIMEFIRE0}) \\ & + (0.122 \times \text{TIMEFIRE1}) + (0.391 \times \text{TIMEFIRE2}) \\ & + (-0.099 \times \text{TIMEFIRE3}) + (-0.354 \times \text{TIMEFIRE4}) + 0.063 \end{aligned}$$

where TIMEFIRE0 represents less than 1 year post-fire, TIMEFIRE1 1–4 years post-fire, TIMEFIRE2 5–9 years

post-fire, TIMEFIRE3 10–14 years post-fire, TIMEFIRE4 15–19 years post-fire, and TIMEFIRE5 >20 years since the last fire. Our second best model was the global vegetation, anthropogenic development model, which had the most support in Burdett et al. (2010), demonstrating the importance of those 2 categories of variables. Beyond the second model, the majority of our best performing models were the same as the top models in Burdett et al. (2010), and in the same order (except for a shift between the global vegetation, land protection model and the global vegetation, topography model) but included our fire variables. Overall, across all our models, we consistently saw that selected and avoided vegetation, development, and fire were the variables that resulted in large improvements in model performance, indicating these are the habitat features that are most influential on puma presence.

Odds ratios from the selected model output indicate that the strongest habitat association for pumas was with areas of riparian habitat, and to a lesser degree oak woodlands and coniferous forest (Fig. 3 and Supplementary Table S1). Conversely, pumas were least likely to be found in grasslands and areas with suburban-urban housing densities (<0.68 ha/unit). There was also a negative response to sparse, barren, and desert scrub habitats, and areas of exurban housing density in our final GLMM. (Fig. 3 and Supplementary Table S1).

Model validation with our 5 data partitions showed agreement in model selection and relationships of the predictor variables with puma presence. There were varying results in the relationship between puma presence and time since fire, which could have been influenced by the variation in individual responses we observed in the individual preference index or by availability of burned habitat at different successional states. Despite the cross-partition differences in time since fire that most likely played a role in our non-significant response, when looking across partitions, we did still see a trend of more positive responses in the first 3 time steps since fire (<1–9 yr) and a predominantly negative response beyond 15–20 years after fire.

DISCUSSION

Landscape-scale disturbances are critical processes for creating landscape heterogeneity, providing mosaics of diverse habitat for a variety of species (Turner 1989, 2005a,b). Building on previous work examining puma response to urbanization and human-induced habitat alteration and fragmentation (Dickson and Beier 2002, Beier et al. 2010, Ernest et al. 2014, Riley et al. 2014, Zeller et al. 2014), particularly Burdett et al. (2010), we found that pumas appear to benefit in the short term from fire disturbances in a shrubland ecosystem, using these areas opportunistically. However, shifts in disturbance regimes such as the shortened fire-return intervals that have been observed in southern California (Keeley et al. 2009) and multiple, interacting disturbances (e.g., fire in urbanized ecosystems; Syphard et al. 2007b, 2009), create the potential for synergistic effects that may threaten the integrity of these landscapes and the persistence of species most sensitive to

Table 5. Models of puma presence, Southern California, USA, 2001–2011 with regard to fire and other landscape variables, ranked by second-order Akaike's Information Criterion (AIC_c) with difference in AIC_c (ΔAIC_c) and model weights (w_i).

| Model structure ^a | AIC _c | ΔAIC _c | w _i |
|--|------------------|-------------------|----------------|
| All vegetation/development/fire | 34,454.47 | 0.00 | >0.999 |
| All vegetation/development | 34,536.16 | 81.69 | <0.001 |
| All vegetation/topography/fire | 34,592.50 | 138.03 | <0.001 |
| All vegetation/protection status/fire | 34,595.08 | 140.61 | <0.001 |
| All vegetation/fire | 34,616.22 | 161.75 | <0.001 |
| All vegetation/protection status | 34,650.91 | 196.44 | <0.001 |
| All vegetation/topography | 34,659.67 | 205.20 | <0.001 |
| All vegetation | 34,685.87 | 231.40 | <0.001 |
| Selected vegetation/development/fire | 34,948.55 | 494.08 | <0.001 |
| Selected vegetation/topography/fire | 35,142.81 | 688.34 | <0.001 |
| Selected vegetation/protection status/fire | 35,152.63 | 698.16 | <0.001 |
| Selected vegetation/fire | 35,175.37 | 720.90 | <0.001 |
| Avoided vegetation/development/fire | 35,219.27 | 764.80 | <0.001 |
| Selected vegetation/topography | 35,276.74 | 822.27 | <0.001 |
| Selected vegetation/protection status | 35,284.66 | 830.19 | <0.001 |
| Selected vegetation | 35,328.17 | 873.70 | <0.001 |
| Selected vegetation/development | 35,339.59 | 885.12 | <0.001 |
| Avoided vegetation/development | 35,339.59 | 885.12 | <0.001 |
| Avoided vegetation/topography/fire | 35,371.31 | 916.84 | <0.001 |
| Avoided vegetation/protection status/fire | 35,375.87 | 921.40 | <0.001 |
| Avoided vegetation/fire | 35,406.99 | 952.52 | <0.001 |
| Avoided vegetation/topography | 35,468.67 | 1,014.20 | <0.001 |
| Avoided vegetation/protection status | 35,472.72 | 1,018.25 | <0.001 |
| Avoided vegetation | 35,515.70 | 1,061.23 | <0.001 |
| Development/fire | 36,001.03 | 1,546.56 | <0.001 |
| Topography/fire | 36,164.39 | 1,709.92 | <0.001 |
| Protection status/fire | 36,229.39 | 1,774.92 | <0.001 |
| Development | 36,233.25 | 1,778.78 | <0.001 |
| Topography | 36,367.09 | 1,912.62 | <0.001 |
| Protection status | 36,450.34 | 1,995.87 | <0.001 |

^a All vegetation = conifer + oak woodland + riparian + distance to water + barren + desert scrub + grassland + sparse, Development = exurban + suburban or urban + distance to major road, Fire = time since fire + number of fires, Topography = elevation + ruggedness + aspect, Protection status = private protected land + tribal land, Selected vegetation = conifer + oak + riparian + distance to water, Avoided vegetation = barren + desert scrub + grassland + sparse.

habitat fragmentation (Crooks 2002) and degradation, such as the puma.

Examining puma response to a post-fire landscape, we see a preference for burned habitats at several different levels. Our population-level habitat preference analysis suggests that pumas use burned areas more than would be expected, given the availability of burned areas, even accounting for individual differences. Although the numerical differences in use versus availability of burned areas are not large, these moderate differences have statistical and biological significance and they likely suggest opportunistic use of burned areas by pumas. The kill site analysis provides some insight as to potential influences of this preference pattern. Although the majority of kill sites were located in unburned habitats, there were a disproportionate number of kills in burned areas given the amount of burned habitat available. We assert that the majority of these kill site locations were mule deer kills. Based on kill site visits during the study (Sweaner et al. 2004) and previous studies of puma diet in

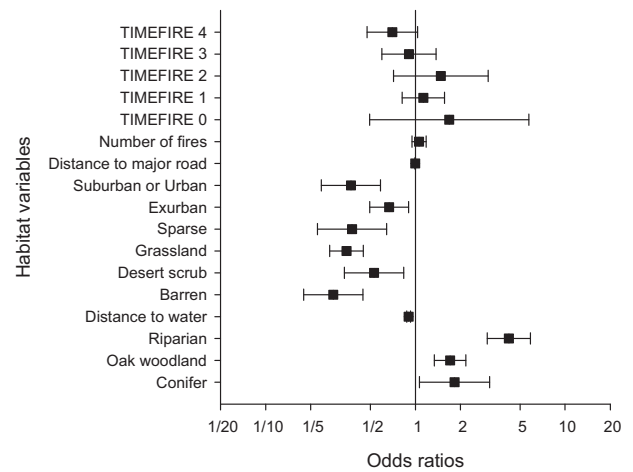


Figure 3. Odds ratios with 95% confidence intervals showing puma response in southern California, 2001–2011, to habitat variables from the selected generalized linear mixed model habitat suitability model. TIMEFIRE represents the time since the last fire in 6 categories: 0 (<1 yr), 1 (1–4 yr), 2 (5–9 yr), 3 (10–14 yr), 4 (15–19 yr), and 5 (>20 yr).

southern California, mule deer make up the majority of biomass in the puma diet in this region (Beier and Barrett 1993, Logan and Sweaner 2001). Most other prey species in the region are too small to necessitate a foraging bout longer than several hours (Beier and Barrett 1993) and therefore would not be detected by the kill cluster algorithm. This kill site data and previous studies on mule deer response to burned areas (Lawrence 1966, Ashcraft 1979, Klinger et al. 1989) lead us to conclude that mule deer use of the post-fire landscape may help explain the observed puma use of burned habitat, particularly in the first few years after fire when vegetation is growing most quickly, providing fresh forage for mule deer. Both step length and net displacement were smaller in burned than unburned habitats, which may also be a reflection of increased time spent foraging and hunting in the preferred burned habitat (Moorcroft and Barnett 2008). Studies on mule deer support this hypothesis; deer abundance increases in burned areas in the first few growing seasons after fire (Lawrence 1966, Ashcraft 1979, Klinger et al. 1989) as a result of resprouting and fire-induced seeding (Keeley 2006). For deer, mosaic burns, fires that leave pockets of unburned habitat, have been identified as creating preferred habitat with easy access to cover (Biswell 1989). These findings are further supported by observations gathered from telemetry and tracking on site visits after the 2003 Cedar fire of pumas moving through burned areas and preying on deer within or at the fire perimeter. A complementary telemetry study of mule deer movement in eastern San Diego County also tracked deer traveling and foraging in recently burned areas after the 2003 Cedar fire (Sweaner et al. 2004).

The outputs of our puma habitat models confirmed the validity of the habitat associations and response to anthropogenic development identified in Burdett et al. (2010). However, our analyses demonstrate that fire and fire history also affected puma habitat use. Our habitat models

and those of other studies (Dickson and Beier 2002, Burdett et al. 2010, Ordeñana et al. 2010) confirm that pumas in southern California primarily associate with areas of dense cover and woody vegetation. However, our data demonstrate that pumas also preferentially use burned areas for several years after the first post-fire growing season. Although our models indicate that puma habitat selection is not influenced by the presence of chaparral, our findings of puma selection for recently burned areas lend support to the hypothesis from Burdett et al. (2010) that the scale-dependent response to chaparral by pumas may be influenced by accessibility to that habitat, which dominates much of the southern California landscape where pumas occur. Our models reveal the role fire plays in puma habitat use in shrub-dominated landscapes and highlight the importance of habitats that provide cover (e.g., selection of riparian and oak woodlands and avoidance of grasslands and open habitats; Burdett et al. 2010). Our results confirm that puma presence is tightly linked to the availability of natural habitats with adequate cover that likely have high prey density. As in Burdett et al. (2010) and other studies (Dickson and Beier 2002, Beier et al. 2010, Zeller et al. 2014), there was a strong negative response to developed areas with moderate-to-high levels of housing density.

Although puma response to anthropogenic development is clear, understanding how more frequent and intense fires that result from increasing human populations and development pressure (Syphard et al. 2007b, 2009) affect pumas and their habitat is more complex. Although puma presence had a slightly positive relationship with the number of fire events within the last 100 years, we caution that several factors suggest that increasingly large and more frequent fires may negatively affect habitat suitability and connectivity for pumas in an area where urbanization and habitat fragmentation already occur. First, a trend toward increasing fire spatial extent is underway, demonstrated by 7 of the 27 (26%) fires we examined in our study that were over 100 km², approximately an entire home range for a puma. The largest of these fires, which was also the largest in state history, occurred in 2003 and burned 1,095 km², likely affecting the entire home range of multiple pumas. Second, in this time period, a number of fires have reburned areas that were burned within the last 10 years, a much shorter fire-return interval than the 30–100 years presumed for most shrubland ecosystems (Keeley et al. 2009). Although individual fire events may increase landscape heterogeneity and edges that pumas prefer, increased fire activity and shortened intervals between fires in shrublands inhibit the ability of native shrub species to regenerate and recolonize burned areas. This creates increased opportunities for non-native plants to invade, which over time, leads to degraded habitats, reduced heterogeneity, and large scale shifts from shrub-dominated habitats to non-native grasslands (Bachelet et al. 2001, Lenihan et al. 2003, Jacobsen et al. 2004). It is possible we did not detect a response to these types of shifts because our data did not overlap areas already experiencing type conversion or because we did not consider fire frequency with respect to the historical fire-return

interval. Furthermore, the areas most likely to shift are those adjacent to intermediate levels of population and housing density (Syphard et al. 2007b, 2009), which pumas avoid, confounding our assessment of puma response to fire frequency.

The strong, negative relationship between puma presence and sparse, barren habitats and grasslands suggest that converted habitats likely to result from higher fire frequencies may not support core habitat for puma populations in the region (Burdett et al. 2010, Zeller et al. 2014). We found that grasslands are a strongly avoided vegetation association for pumas as did Burdett et al. (2010) and other studies focused on southern California pumas (Dickson et al. 2005). Grasslands have also been identified as an association that may be used during movement behavior but not typically during resource use behavior (Zeller et al. 2014). Whether grasslands and areas of open habitat are unsuitable or merely suboptimal, we submit that wide-spread shifts to grasslands have the potential to result in reduced habitat for puma foraging, resting, and reproduction in areas that are already facing significant habitat loss influenced by anthropogenic development and activities. We expect that as urbanization expands and climate change creates warming, drying, and more frequent episodes of drought, the effects of increased fire starts and larger fires will begin to become apparent in areas beyond the wildland-urban interface (Syphard et al. 2007b, 2009), which are currently undeveloped, protected refugia for pumas in southern California. If areas of open, sparse habitats and grassland and urbanization expand, puma habitat will become more degraded and disconnected across the region, further endangering the persistence of healthy puma populations in southern California.

Pumas exhibit a particularly strong sensitivity to urbanization and habitat fragmentation (Crooks 2002, Ernest et al. 2003, Burdett et al. 2010), and have been extirpated from many coastal areas in southern California with high housing densities; 35% of the privately owned habitat in our study area that was suitable for pumas in 1970 is expected to be lost by 2030 (Burdett et al. 2010). Furthermore, this sensitivity to anthropogenic landscape features, especially roads, has led to reduced gene flow (Ernest et al. 2003, 2014; Riley et al. 2014) such that the populations in parts of our study area are genetically depauperate, isolated, and display signs of a recent and significant bottleneck (Ernest et al. 2014). Understanding the impacts of the interacting disturbances of wildfire and anthropogenic development on this wide-ranging and sensitive top predator is fundamental to preserving habitat suitability and connectivity for pumas in southern California. Understanding puma response to these anthropogenic-influenced landscape changes may also provide insight into ecosystem integrity considering similar analyses of the species in other regions have found support for pumas as important regulators of the ecosystem and therefore, an indicator species (Terborgh et al. 1999; Miller et al. 2001; Ripple and Beschta 2006, 2008). Although our analysis did reveal that burned habitats are a resource that pumas appear to use opportunistically in southern California shrublands, we also found that areas of core vegetation that provide cover

for the species, and an avoidance of the most heavily human-dominated features of the landscape, appear to most strongly influence puma habitat selection and use. Given puma sensitivity to habitat fragmentation and anthropogenic development, and that the spatial and temporal aspects of the natural fire regime of southern California shrublands are changing as a result of this human environment, we believe more attention toward detecting fire-related landscape-scale changes in vegetation and resulting puma response are warranted. When the effects of habitat loss and landscape fragmentation caused by urbanization are coupled with the potential impacts to habitat features by increasing fire frequency, the persistence of healthy puma populations within the region will be threatened. Of particular concern is the degree of change expected for fire frequencies in exurban areas where pumas are still present but at risk because of expanding urbanization. In our study area, 10% of the landscape is expected to transform from undeveloped, rural, or exurban to suburban or urban development by 2030 (Burdett et al. 2010). These areas of moderate human population densities where adequate natural vegetative cover can burn have been correlated with the largest spikes in ignitions and fire frequencies (Syphard et al. 2007b, 2009). As more of these habitats become degraded and fragmented, pumas will become more constrained in their movements and face the additive threats of mortality from roadways, depredation (Burdett et al. 2010, Vickers et al. 2015), and further loss of genetic variability (Ernest et al. 2014).

MANAGEMENT IMPLICATIONS

Although our findings support the conclusion that pumas are adapted to the natural historical wildfire disturbance process in southern California ecosystems and opportunistically use these burned areas, we found evidence that the relationship between wildfire and puma habitat is shifting. Further consideration of wildfires in conservation planning for pumas is warranted. Given that a trend in increased fire size and fire frequency is already underway in southern California, fire-induced habitat changes in an urbanizing landscape will reduce the quality or availability of puma habitat in an ecosystem where their persistence is already threatened by urbanization and habitat fragmentation. The indirect effects of these anthropogenic landscape changes on natural processes, namely wildfire, cause additional landscape shifts such as vegetation-type conversion from shrublands to non-native annual grasslands that cross threshold levels for continued puma persistence. Further research is needed to integrate projected fire frequency and magnitude in the near future with expected shifts in habitat condition and land-use change to understand how these alterations will affect puma viability in southern California. Long-term monitoring of response to increasing fire frequency, especially where vegetation-type conversions occur, is needed to assess how pumas and other carnivores will be affected by large-scale changes in landscapes. These landscape-scale analyses must also be integrated in the context of connectivity to ensure adequate protection of

suitable puma habitat to maintain landscape integrity and connectivity for the many species that rely on southern California landscapes.

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