

Current Biology

Mountain lions avoid burned areas and increase risky behavior after wildfire in a fragmented urban landscape

Highlights

- After the wildfire, mountain lions avoided burned areas and increased risky behavior
- Post-fire risky behavior included increased road crossings and daytime activity
- Altered movement and space use post-fire increased risk of intraspecific conflict
- Risky behavior may increase mortality risk for animals in urban fire-prone regions

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In brief

When wildfires and urbanization coincide, animals trade off risks of burned landscapes with those of anthropogenic environments. Blakey et al. find that after an exceptionally large wildfire in an urbanized region, mountain lions avoided burned areas and increased activities that elevated their risk of negative interactions with humans and conspecifics.

Report

Mountain lions avoid burned areas and increase risky behavior after wildfire in a fragmented urban landscape

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SUMMARY

Urban environments are high risk areas for large carnivores, where anthropogenic disturbances can reduce fitness and increase mortality risk.¹ When catastrophic events like large wildfires occur, trade-offs between acquiring resources and avoiding risks of the urban environment are intensified. This landscape context could lead to an increase in risk-taking behavior by carnivores if burned areas do not allow them to meet their energetic needs, potentially leading to human-wildlife conflict.^{2,3} We studied mountain lion behavior using GPS location and accelerometer data from 17 individuals tracked before and after a large wildfire (the 2018 Woolsey Fire) within a highly urbanized area (Los Angeles, California, USA). After the wildfire, mountain lions avoided burned areas and increased behaviors associated with anthropogenic risk, including more frequent road and freeway crossings (mean crossings increased from 3 to 5 per month) and greater activity during the daytime (means from increased 10% to 16% of daytime active), a time when they are most likely to encounter humans. Mountain lions also increased their amount of space used, distance traveled (mean distances increased from 250 to 390 km per month), and intrasexual overlap, potentially putting them at risk of intraspecific conflict. Joint pressures from urbanization and severe wildfire, alongside resulting risk-taking, could thus increase mortality and extinction risk for populations already suffering from low genetic diversity, necessitating increased connectivity in fire-prone areas.

RESULTS

Direct effects of wildfire on mountain lions

Direct and immediate effects of wildfire on mountain lions can include injury and mortality. Of the 11 individual mountain lions being tracked at the time of the Woolsey Fire that had the potential to be affected by it, two died or were presumed to have died during or soon after the fire.

Do mountain lions avoid burned areas after a large wildfire?

At the population level, mountain lions avoided burned areas after the wildfire (Figures 1 and 2) and no individual animal showed significant selection for them. Males avoided burned areas more than females, as indicated by their generally larger and more negative effect sizes (Figure 1). Proportions of locations within burned areas compared before and after the fire showed the same trend as selection analyses (Table S1), specifically, much

lower proportions of locations in burned areas post-fire. Excluding the two males that had less than 10% of their pre-fire locations within the burn perimeter (P56 and P61, Table S1), all 3 males showed strong and significant avoidance (effect size -0.63 to -1.45). The response of females to the fire was more variable (Figure 1). The post-fire burned area use that did occur was concentrated (61%) in the patchily burned region in the southeast corner of the outer burn perimeter, and within the Simi Hills (north of the US-101 freeway) where the majority of the landscape (66%) burned (Figure 2).

Do mountain lions increase behaviors that put them at anthropogenic risk after a large wildfire?

While there was support for mountain lions increasing use of urban areas after the wildfire, the magnitude of this increase was negligible (Figure 3A). The probability of urban use was low before the fire ($\sim 4.3\%$), and while this increased after the fire, it remained low ($\sim 5.4\%$); this 1% change was much lower than

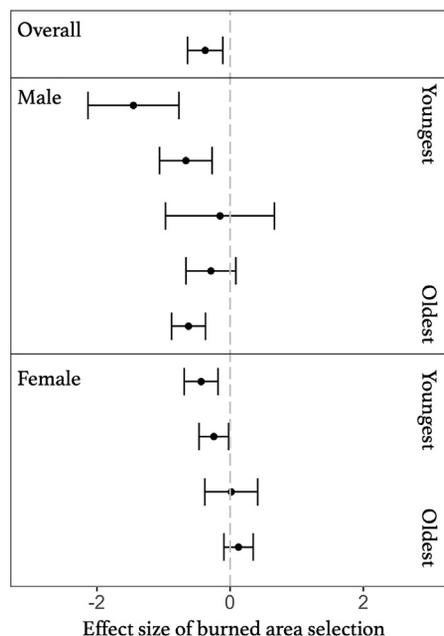


Figure 1. Results of resource selection analysis for burned areas after the fire by the 9 individual mountain lions who were tracked both before and after the fire

The two individuals assumed to have perished during or soon after the fire were excluded. Each point shows the effect size comparing selection for burned areas before and after the fire using step selection functions, for each individual mountain lion. The overall effect size was calculated using a meta-analytic approach and all error bars show 95% confidence intervals. Negative effect sizes indicate selection against burned areas while positive effect sizes indicate selection for burned areas following fire. See also [Table S1](#).

the range of variability in proportion of urban use by mountain lions across the population (0%–15%) ([Table S2](#)). Regardless of fire, mountain lions used urban areas rarely (mean for study animals was 5% of the time, including time periods before and after the fire) and use of urban areas was variable among individuals ranging from one female who used urban areas less than 1% of the time to two females who used urban areas > 10% of the time. All sex and age classes were variable in urban area use.

Consistent with our predictions, mountain lions tended to increase road crossings after the wildfire, with the fitted relationship indicating an increase from ~3 crossings per month before the fire to ~5 crossings per month 15 months after the fire ([Figure 3B](#)). Mountain lions also increased their daytime activity after the fire from 10% of the day to 16% of the day, although the continuous response model indicated a potential slight increase prior to the wildfire event ([Figure 3C](#)). Our analysis pooled all major road crossings (major roads shown in [Figure 4](#)), though mortality risk (both perceived and actual) is likely to vary with the size and traffic volume of roads. California has the busiest roads in the USA and the busiest interstate in any USA city runs through our study area (I-405).⁴ The first successful crossing of the I-405 freeway over the 16 years of the broader study was recorded in the months after the fire; comparing crossing frequencies of the busy US-101 freeway, we observed roughly one crossing every 2 years before the fire, compared to one crossing every 4 months after the fire.

Do mountain lions increase behaviors that could increase the risk of conflict with conspecifics after a large wildfire?

Mountain lions increased both their distance traveled and the amount of space used after the fire ([Figures 3D and 3E](#)). Distance travelled increased from $\sim 250 \pm 48$ (predicted 95% confidence interval [CI]) km per month to $\sim 390 \pm 48$ km per month, a more than 50% increase from pre-fire distances. Although adult males either decreased or retained similar amount of space used after the fire, subadult males and all females, the groups most at risk in intraspecific encounters, increased their amount of space used by ~15%–24%. Results of the age-sex class analyses should be interpreted cautiously due to the low number of individuals per class and wide confidence intervals ([Figure 3E](#) and [Table S3](#)).

Where analyzed, trends towards increases in spatial overlap in mountain lion landscape use after the fire did not perform better than the null model ([Table S4](#)), potentially due to the relatively low sample size and the confounding factor of two males perishing in the fire and an additional three males perishing of anticoagulant rodenticide poisoning and vehicular collision during the 15 months post-fire. However, we saw a trend towards an increase in spatial overlap after the fire between the dominant male and other males in the study area after the fire ([Figure 4](#)). Additionally, mean observed overlap was greater for all age-sex classes after the fire across all iterations of the model validation expressed as a proportion of male and female home ranges, though this difference was negligible for male-female overlap ([Figure S1](#)). Specifically, important components of intrasexual overlap in this territorial species more than doubled: overlap of the dominant male on other males increased from 10% to 23% post-fire ([Figure 4C](#)) and overlap between females increased from 7% to 18% post-fire ([Figure S1](#)).

DISCUSSION

In an urban landscape after the wildfire, we found support for the prediction that mountain lions avoided burned areas post-fire, and increased behavior that could expose them to risk. Changes in behavior by mountain lions post-fire are likely due to a complex trade-off balancing the necessity to acquire food and breed, while avoiding conspecific conflict and encounters with humans in a transformed and fragmented landscape. These kinds of trade-offs between anthropogenic disturbances and other major disturbance events are an increasing reality for carnivores persisting in human-dominated landscapes worldwide.^{5–7}

Carnivores have varying responses to fire, and this is likely to be strongly influenced by how fire changes the structure of vegetation, and with it, the ability to capture prey.^{8,9} In the case of cursorial carnivores, such as wolves and coyotes, fire may increase their abilities to capture prey.^{10,11} Whereas ambush predators such as mountain lions, lynx, and African lions may require more heterogeneity, including retained vegetation cover, in post-fire landscapes in order to successfully stalk prey.^{12–15} The mountain lions in our study mostly avoided burned areas in the 15 months after the fire. This contrasted with studies that indicate opportunistic use of burned landscapes by carnivores,^{7,16,17} but was consistent with Eby et al.,¹³ who found that despite abundant prey in burned areas, African lions (*Panthera leo*) avoided the burned landscape, likely due to reduced

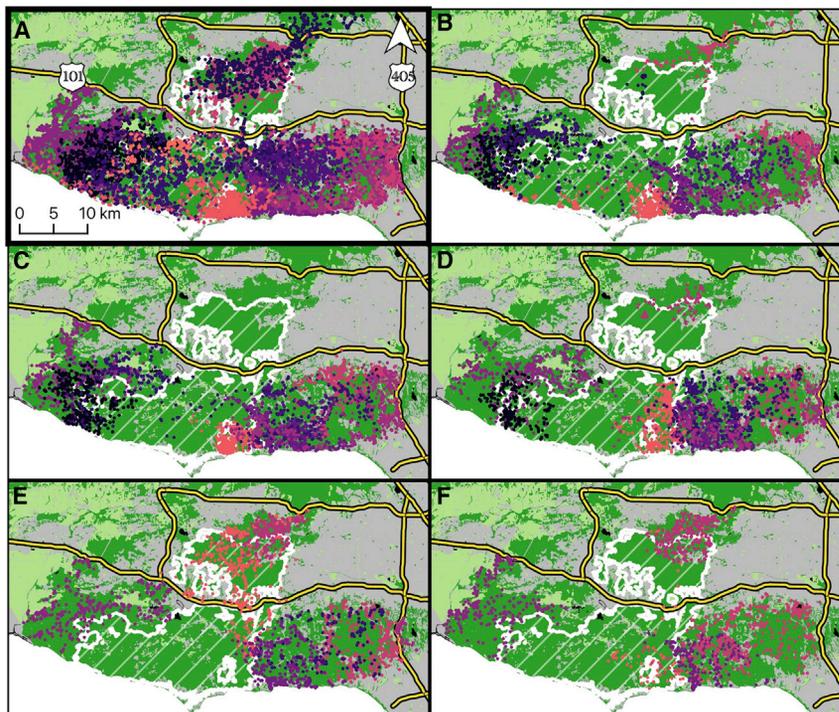


Figure 2. Study area within the Los Angeles and Ventura County areas of California, USA, showing locations of 17 individual mountain lions in periods before and after the 2018 Woolsey Fire

The study area includes the Santa Monica Mountains (south of the 101 freeway) and Simi Hills (north of the 101 freeway).

(A–F) Locations of 17 individual mountain lions studied within the periods from 15 months prior to the fire (A) and 15 months after the fire (B)–(F) (in 3-month intervals) are shown in different colors for each individual. Time periods shown include 15 months pre-fire to time of fire (A); time of fire to 3 months post-fire (B); 3–6 months post-fire (C); 6–9 months post-fire (D); 9–12 months post-fire (E); and 12–15 months post-fire (F). Of the 17 individuals, 12 were tracked both pre- and post-fire (though of these, 1 individual was suspected to have perished in the fire and 1 individual died soon after) and 5 individuals were tracked only after the fire (Figure S3). Land use is shown by dark green (natural areas), light green (altered open areas) and gray (urban areas). The area burned by the Woolsey Fire (2018) is shown in white outline with white hatching. Freeways are shown in yellow.

See also Table S1.

cover decreasing ambush hunting success. In the Santa Monica Mountains, the most intensive use of burned areas in our study occurred in areas surrounding a patchily burned area in the southeastern part of the outer burn perimeter of the Woolsey Fire (Figure 3), an area that was more heterogeneously burned and that included some sizable unburned patches. Use of these areas could be due to hunting advantages and prey availability in landscapes where burned areas are patchy, and near the edges of burns.^{14,18} We did not account for differences in burn severity across the landscape, which can be an important predictor of wildlife post-fire habitat use, because fires within Southern Californian shrubby vegetation tend to burn with uniformly high-intensity, stand-replacing fire.¹⁹ Our findings are overall consistent with the reduction in predator-prey interactions for ambush predators after the fire proposed by Doherty et al.⁹, and the need to find suitable habitat to capture prey is likely one of the drivers of the risk-taking behaviors we observed.²

There is extensive evidence globally that large carnivores avoid areas of high human footprint (areas of relatively greater human population and infrastructural development) in space and time.^{20,21} Our study indicated that even after a considerable disturbance that transformed the structure of over half the landscape used by the resident population, urban areas remained a strong deterrent. However, mountain lions did increase their exposure to anthropogenic risk by increasing road and freeway crossings and by increasing activity during the day when human activity is greatest. Human killings of mountain lions (in response to depredation of livestock) may be more likely in areas of intermediate housing density than in more urban areas,²² and vehicle strikes are also a very high cause of mountain lion mortality²³ in this population. Therefore, mountain lions in our study area may be experiencing an assessment risk-response mismatch,

whereby the animals' assessment of risk does not accurately reflect mortality risk.²⁴

Reduction of suitable habitat after fire has the potential to result in greater risk of intraspecific conflict in carnivore populations within urban environments, where dispersal is constrained by multiple barriers. Though carnivore home ranges tend to be smaller and population densities higher in urban areas,²⁵ during the study period, the population we studied presented a relatively extreme example, given that the Santa Monica Mountains, south of the 101 freeway, were being used by at least eight males (most being subadults), though its size is the equivalent of 1 to 2 home ranges for adult males.^{26,27} In this context, multiple behavioral changes by the mountain lions in our study, including a 50% increase in distance traveled, use of 15%–24% larger areas by females and subadults, and a trend towards greater intrasexual overlap, have the potential to increase the risk of intraspecific conflict, especially between males. In our study area, intraspecific conflict, specifically being killed by an adult male, is the biggest cause of mortality for subadult mountain lions, and adult males have also been recorded to kill adult females and kittens, including their own offspring and past mates.^{23,26} Intraspecific conflict (fatal or otherwise) is likely to be exacerbated in urban areas where barriers prevent subadults from dispersing into new territories.^{23,26,28} Therefore, after a severe wildfire, when space available for hunting and moving within cover is reduced, animals must trade-off energetic demand with perceived risk of encountering adult males, weighing behaviors that put them at greater risk of conflict against greater flexibility in space use and, potentially, diet.²⁹

The increases in amount of space used and distance traveled that we observed could be influenced by multiple factors. A severe wildfire like the Woolsey Fire could allow mountain lions to move

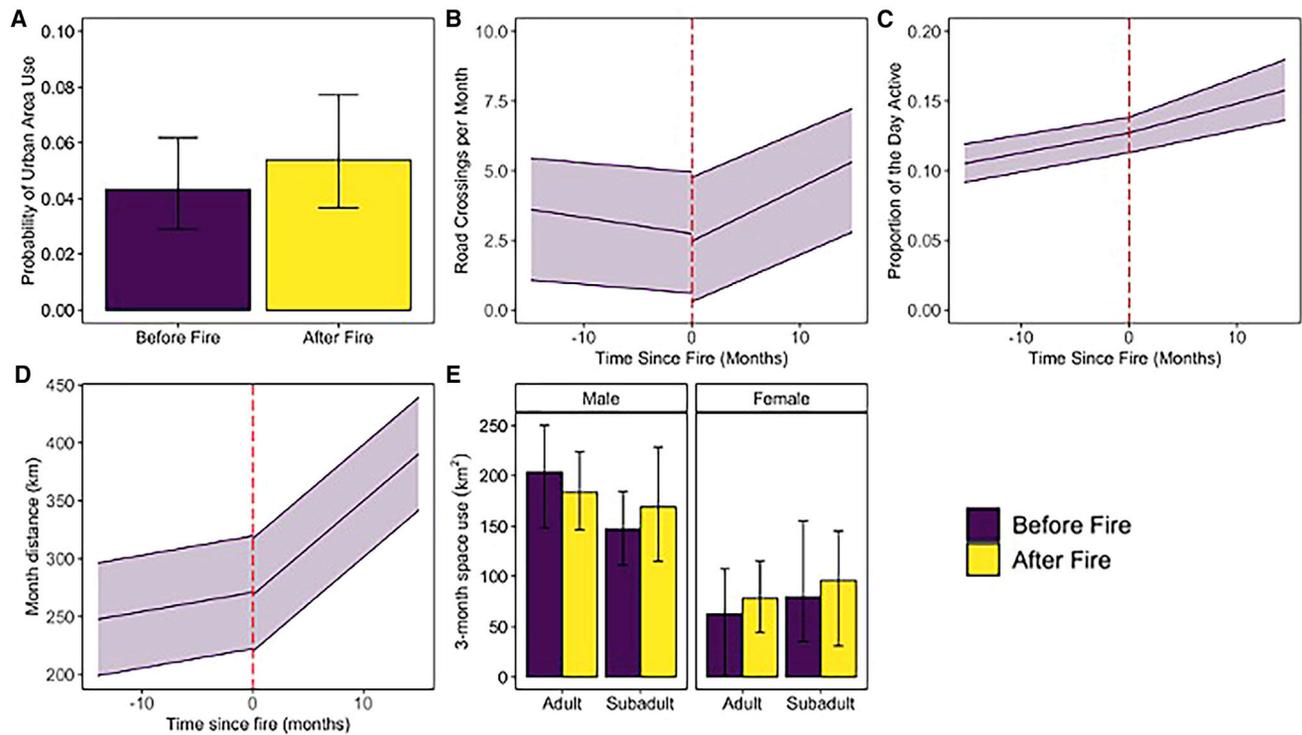


Figure 3. Predicted changes in risky behaviors by mountain lions after the 2018 Woolsey Fire, based on mixed effects models comparing probability of mountain lion use of urban areas

(A–D) Comparing probability of mountain lion use of urban areas (A), frequency of road crossings per month (B), proportion of day spent active (C), monthly distance traveled (D), and mean area of amount of space used over 3-month periods separated by sex and age class before and after the 2018 Woolsey Fire (E). The periods before and after fire were defined by the 15 months prior to and following the Woolsey Fire.

Models used to predict relationships included a mixed effects logistic regression model (A), segmented linear mixed effects models (B) and (C), segmented mixed effects meta-regression (D), and a linear mixed effects model (E).

Error bars and bands show 95% confidence intervals around fitted relationships.

See also [Table S2](#).

more efficiently by removing dense cover in the landscape and due to the reduction in human recreational use in the short-term after fire.^{30,31} Alternatively, increased space use could indicate an increase in avoidance of either humans or adult males, in the more sparse landscape where concealment is more challenging, given that mountain lions generally avoid open areas.²⁷ Alternatively, or perhaps concurrently, hunting could be more difficult for mountain lions due to the lack of cover on the landscape to ambush deer, as observed for African lions in savanna habitats.¹³ All of these scenarios are likely to influence energy expenditure, indicating that a major disturbance, such as the wildfire in this study, could lead to energy deficits in carnivore populations.³²

Our study was an opportunistic study of a population of mountain lions who were tracked before, during, and after a wildfire. The limited number of individuals who were not impacted by the wildfire precluded a natural experiment (such as a BACI design), therefore we must consider the possibility of other factors that could have influenced the behavior of mountain lions in our system over the 30 months of the study. Variability in human activity is unlikely to have contributed to changes in mountain lion behavior because our study ended (March 2, 2020) prior to local and state-wide restrictions on public movement due to COVID-19 in the state and county (beginning March 19, 2020). Over the study period, rainfall varied, with greater rainfall after the fire than before, and

two and a half mule deer (*Odocoileus hemionus*) calving seasons (important periods for mountain lion hunting) occurred, with one and a half prior to the fire and one after the fire (Figure S2). We cannot rule out the possibility that fluctuations in, and interactions between, weather and mule deer abundance influenced mountain lion behavior during our study. However, it is unlikely that these variables resulted in the findings we report here. The greater rainfall after the fire would be expected to increase deer forage and subsequently decrease, rather than increase, mountain lion space use and therefore reduce road crossings.^{33,34} Further, given that mule deer tend to be crepuscular, the increase in daytime activity is unlikely to be explained by variability in environmental conditions changing deer abundance.^{35,36}

Conservation implications

Our findings have important implications for the conservation of large carnivore populations living near urban areas, showing that wildfire can not only result in direct mortality, but could also influence carnivore behavior in ways that increase anthropogenic risks, like vehicular collisions and encounters with humans, as well as increase the risk of intraspecific conflict. These risks can interact. For example, one subadult male in this study was hit and killed by a vehicle on a freeway immediately after an altercation with an uncollared adult male. Behavioral changes observed in this

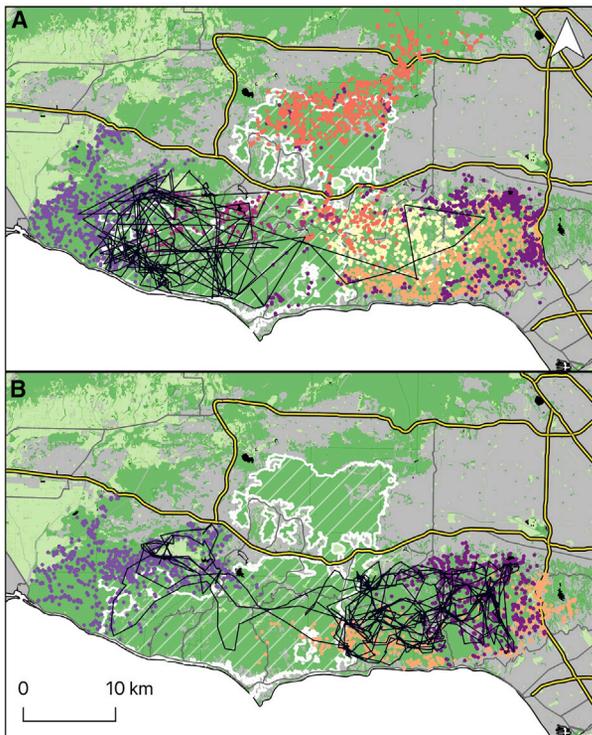


Figure 4. Observed overlap between the dominant adult male and subadult males before and after the 2018 Woolsey Fire

The dominant male (P30) is shown by a black line and subadult males are shown in colored points, different colors signify different individuals. Time periods include two ~6-month periods before (8th May 2018–8th November 2018) and after (21st March 2019–10th September 2019) the 2018 Woolsey Fire.

(A–C) (A) indicates the period before the fire until the Woolsey fire, when P30 was dominant (8th May 2018–8th November 2018), and (B) shows a similar period of time ending with P30’s death (21st March 2019–10th September 2019). Before the fire, P30 regularly used the area within the fire perimeter and was rarely in the eastern half of the Santa Monica Mountains (A), whereas post-fire, he occasionally moved through the burned area and largely relocated to the eastern end, overlapping extensively with multiple subadult males. (C) shows the mean (\pm SE) proportion of P30’s space use that overlaps with six other individual mountain lions (3 males and 3 females), tracked concurrently with him, before and after the fire. We defined P30 as the dominant male since he showed behaviors including territorial marking through scraping, breeding, and regular use of core natural areas.

study (e.g., variable usage of burned areas, increased activity during the day, and increased distance traveled) could be indicative of increased hunting challenges or hunting flexibility. If the fire-transformed landscape reduces the ability of mountain lions to ambush deer, they might rely on other prey items, including smaller carnivores, which in turn put them at greater risk of poisoning from toxicants such as anticoagulant rodenticides.³⁷

Greater risk-taking behaviors by carnivores living near urban areas could lead to increased mortality in populations already suffering from low genetic diversity, leading to increased extinction risk.^{38–40} As the world continues to urbanize and as we see increasing frequency of high severity fires in many of the world’s fire-prone landscapes,⁴¹ we are likely to see similar challenges for carnivore conservation in a broader range of global regions and taxa. Increasing the connectivity among urban habitat patches through a system of wildlife overpasses or underpasses,⁴² already known to be important for increasing genetic exchange, could be particularly critical in fire-prone areas when the quantity of already limited suitable habitat can be greatly reduced post-fire.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at <https://doi.org/10.1016/j.cub.2022.08.082>.

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Land use is shown by dark green (natural areas), light green (altered open areas), and gray (urban areas) and the extent of the Woolsey Fire (2018) is shown in white outline with white hatching. Primary and secondary roads are shown with gray lines with freeways in yellow (both were used in the road crossing analysis).

See also [Figure S1](#).

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AUTHOR CONTRIBUTIONS

R.V.B., S.P.D.R., D.T.B., and J.A.S. conceived the ideas, J.A.S. and S.P.D.R. collected the data, R.V.B. conducted the analysis, wrote the paper and made graphs. J.A.S., S.P.D.R., and D.T.B. edited and provided feedback on the manuscript throughout development.

DECLARATION OF INTERESTS

The authors declare no competing interests.

INCLUSION AND DIVERSITY

We worked to ensure sex balance in the selection of non-human subjects. One or more of the authors of this paper self-identifies as a member of the LGBTQ+ community. While citing references scientifically relevant for this work, we also actively worked to promote gender balance in our reference list.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data and code	Dryad data repository	Data and code are available at Dryad: https://doi.org/10.5068/D1M97D
Software and algorithms		
R v 3.6.1	R Development Core Team	https://www.r-project.org/
Rstudio v. 1.3.1093	Rstudio Team	https://www.rstudio.com/
adehabitatHR v. 0.4.16	The Comprehensive R Archive Network (CRAN)	https://cran.r-project.org/web/packages/adehabitatHR
adehabitatLT v 0.3.25	CRAN	https://cran.r-project.org/web/packages/adehabitatLT
amt v. 0.1.4	CRAN	https://cran.r-project.org/web/packages/amt
ctmm v. 0.5.11	CRAN	https://cran.r-project.org/web/packages/ctmm
ggplot2 v. 3.3.0	CRAN	https://cran.r-project.org/web/packages/ggplot2
lme4 v 1.1-23	CRAN	https://cran.r-project.org/web/packages/lme4
metafor v. 2.4-0	CRAN	https://cran.r-project.org/web/packages/metafor
momentuHMM v. 1.5.1	CRAN	https://cran.r-project.org/web/packages/momentuHMM
QGIS v. 3.4	QGIS Development Team	https://qgis.org

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources or reagents should be directed to and will be fulfilled by the lead contact, Rachel Blakey (rvblakey@cpp.edu).

Materials availability

The study did not generate new unique reagents.

Data and code availability

The data and code generated during this study are available at Dryad: <https://doi.org/10.5068/D1M97D>.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We captured and tracked mountain lions using global positioning system (GPS) collars (*Puma concolor*) as part of a long-term study conducted by the National Park Service (2002–present).^{26,27,43} Mountain lions were captured using foot cable-restraints, baited cage-traps, or by treeing them with trained hounds; and immobilized with ketamine hydrochloride combined with medetomidine hydrochloride, administered intramuscularly. All animals were monitored throughout the time they were immobilized, during which time we estimated age, based on body size and tooth wear measurements. Age classes were: kittens (dependent offspring with their mother, 0–14 months), subadults (independent animals prior to reproduction: females 14–25 months, males 14–42 months), and adults (breeding animals: females >25 months, males >42 months).⁴⁴ We fitted adult and subadult animals with Vectronic Aerospace GPS collars (Berlin, Germany; Vertex Plus and Vertex Lite models) equipped with VHF beacons. Animal capture and handling procedures were permitted through a scientific collecting permit with the California Department of Fish and Wildlife (SCP # 05636) and the National Park Service Institutional Animal Care and Use Committee (Protocol PWR_SAMO_Riley_Mt.Lion_2014.A3). For this study, we used locational and accelerometer data for 17 individual mountain lions, collected over a 2.5-year period between 2017 and 2020, encompassing a large wildfire event, the 2018 Woolsey Fire. Individuals tracked for the study included 9 females (5 adult, 2 subadults, and 2 subadults that became adults during the study period) and 8 males (2 adult, 1 subadult, 1 kitten, and 4 subadults that became adults during the study period). Age was calculated for each three-month period, and the male kitten was treated as a subadult for the purposes of the study, given that he was estimated to be close to subadult age (~1 year old) and his mother was not observed during his capture.

We programmed collars to collect 8 locations per 24-hour period (7 at night, 1 during the day). The seven fixes at night were at 2 h intervals beginning at 5:00pm Pacific Standard Time (PST), while the day location was collected at 1:00pm PST. On average, 90% of programmed fixes for periods used in this study were successful, with individual mountain lion fix rates ranging from 69% to 98%. Collars also collected activity data on two axes (X: anterior-posterior/surge, Y: lateral/sway), averaged across every 5 minute period. A third axis (Z: dorso-ventral/heave) was only available for two of the seventeen individuals, so these data were not used

in the analysis. Accelerometer measurements were 99% successful on average, with all individuals recording > 96% of expected measurements.

METHOD DETAILS

Study area

We studied an urban population of mountain lions within Los Angeles and Ventura counties, California, in the Santa Monica Mountains and Simi Hills (34°05'N, 118°46'W) (Figure 2). All patches of natural habitat were bordered by major freeways, urbanization, agricultural development, or the Pacific Ocean. The study population in the Santa Monica Mountains, in particular, has been genetically isolated from nearby populations by roads and urbanization,^{26,38} leading to high extinction risk.⁴⁴ Land-use was variable across the study area, and included federal, state, and local parklands, as well as urban areas consisting of high-density residential, commercial, and industrial areas, low-density rural or suburban residential areas, and agricultural areas. Natural vegetation in the study area consisted of mixed chaparral, coastal sage scrub, oak woodlands and savannas, riparian woodlands, and non-native annual grasslands. The only wild, large ungulates were mule deer, which are the predominant prey for mountain lions in the region,⁴³ and two-and-a-half mule deer (*Odocoileus hemionus*) calving seasons occurred during the study period (Figure S2). The climate of the study area was Mediterranean, with cool, wet winters and hot, dry summers. Rainfall varied over the study period, with greater rainfall after the fire than before. The area is prone to drought and wildfire,⁴⁵ with two major wildfires occurring within less than a decade prior to this study, the Springs Fire in 2013, 9,814 ha, and the Woolsey Fire in 2018, 39,234 ha. The Woolsey Fire was the largest fire on record to have affected the Santa Monica Mountains and burned > 40% of the natural area in the Santa Monica Mountains and > 66% of the natural area in the Simi Hills (Figure 3).

QUANTIFICATION AND STATISTICAL ANALYSIS

Study design

We included locational data for 17 individual lions during 15 months leading up to and 15 months following the Woolsey Fire (2018). Mountain lion tracking periods varied (Figure S3), and more individuals were tracked after the fire (F: 9; M: 6) compared to before the fire (F: 5; M: 7). We therefore used resampling methods that balanced numbers of individuals among age classes to validate our findings (Table S3).

Do mountain lions avoid burned areas after a large wildfire?

To evaluate whether mountain lions decreased use of areas after they were burned in the Woolsey Fire, we compared selection coefficients for individual mountain lions derived from step selection functions before and after the fire using a meta-analytic approach.⁴⁶ Individual mountain lions were excluded from this analysis if an adaptive Local Convex Hull (LoCoH), calculated from every location recorded during the study period (the period spanning 15 months before and after the focal fire), overlapped with the burned area from the focal fire by less than 10%, or if they were not tracked during both periods (both before and after fire). We used the *adehabitatHR v0.4.16* package⁴⁷ within the *R v3.6.1* environment⁴⁸ to fit LoCoH home ranges and used the maximum number of nearest neighbors as all those points which were within the maximum distance between any 2 points recorded for animals in this analysis.

We first fitted a separate step selection function to each individual mountain lion during the periods before and after the fire separately using the *amt v 0.1.4* package.⁴⁹ These functions compared observed “steps” (movements connecting successive locations) with random possible steps generated from distributions of turning angles and step lengths from the broader population. We used only night locations for the step selection analysis, defined as locations collected between one hour after sunset and one hour before sunrise. The observed and random (i.e., “available”) steps were compared to estimate selection coefficients using a conditional logistic regression to match observed to related randomly selected steps as strata. We used a sample rate of 2 h with a tolerance of 1 h and generated 1000 random steps for each observed step. The high tolerance level was not necessary and unlikely to have influenced the analysis, given > 99.96 of steps were within ± 5 minutes of the 2 h interval. Steps were separated into “bursts” for each night, to ensure sample intervals were regular (2 h intervals between each step). We then calculated effect sizes (y_i) representing the change in selection of areas within the fire perimeter before and after they were burned by subtracting the “before fire” coefficient ($coef_{before}$) from the “after fire” coefficient ($coef_{after}$) for each individual. This meant that positive coefficients indicated selection for burned areas was higher after the fire, and negative values indicated that selection for burned areas was lower after the fire. We calculated the sampling standard error (se_i) using the following approach recommended by Senn, Gavini, Magrez, & Scheen,⁵⁰ where se_{before} and se_{after} are the standard errors of the selection coefficients before and after the fire for each individual and ri is the correlation between the coefficients before and after the fire.

$$y_i = coef_{after} - coef_{before}$$

$$se_i = \sqrt{se_{after}^2 + se_{before}^2 - (2 \times ri \times se_{after} \times se_{before})}$$

Our sample size was small (5 males and 4 females tracked both before and after the fire), so we were chiefly interested in population-level selection for or against burned areas. We therefore estimated a population-level effect size using random effects meta-analysis⁴⁶ using the *metafor v. 2.4-0* package.⁴⁶ Along with the step-selection analyses and for comparison with them, we calculated mountain lion use of areas within the burn perimeter before and after the fire as the number of point locations whose 10 m radius intersected with the burned area (to allow for some variability in GPS location and fire layer accuracy).

Do mountain lions increase behaviors that put them at anthropogenic risk after a large wildfire?

We calculated three metrics associated with behaviors that may place mountain lions at additional risk from humans and anthropogenic threats: use of urban areas; number of road crossings; and proportion of daytime period active. We defined urban areas as commercial, and industrial areas and residential areas with ≥ 2.5 houses/hectare identified within the Southern California Association of Governments land use map.⁵¹ This map was the most accurate available land-use data for the region, because later versions classified land uses at the parcel scale, rather than based on observed boundaries between different land uses. The dataset we used was reflective of the landscape throughout the study period from 2017–2020 for the broad development and altered-open classifications that we used in these analyses. The geographic information system (GIS) program for the park monitors land use in and around SMMNRA as part of the National Park Service Inventory and Monitoring Program. We defined mountain lion use of urban areas before and after the fire as a binary variable where point locations whose 10 m radius intersected urban areas were recorded as used (1), and those locations whose buffer did not intersect with urban areas were unused (0). We compared use of urban areas before and after the fire using a mixed effects logistic regression with period (before and after fire) as a fixed effect and individual mountain lion as a random intercept using *lme4 v 1.1-23*⁵² (see [Tables S3](#) and [S5](#) for details of all analyses). We compared 3 models to investigate how the probability of mountain lion use of urban areas changed after the fire including: null (no effect of fire); step response (an abrupt change in urban use after the fire compared to before the fire); continuous response (a change in the relationship between urban use and time after the fire) ([Table S5](#)). We compared models using Akaike's Information Criterion adjusted for small sample size (AICc) and identified the most parsimonious model as the model with the lowest AICc, that was separated from a less complex nested model by $\Delta\text{AIC} > 2$. Modelled coefficients and fitted relationships are presented with 95% confidence intervals, and confidence intervals around the fixed effects were calculated for fitted relationships using parametric bootstrapping.

To quantify road crossing behavior, we first exported each month of locations for each mountain lion into a movement trajectory using the *adehabitatLT v0.3.25* package.⁴⁷ We classified a major road as all freeways and secondary roads using road data from the U.S. Census Bureau,⁽⁵³⁾ adding roads that had similar amount and speed of traffic based on observations by National Park Service biologists. Specific roads included are shown in [Figure 4](#). We added a 50 m buffer (50 m either side) to each road, to allow for road width and spatial uncertainty in road and mountain lion datasets. Road crossings were identified manually as “minimum road crossings”, using lines between two consecutive points that traversed any buffered road, using QGIS v. 3.4.⁵⁴ When the line drawn between two consecutive point locations traversed a single road more than once, and the starting point was on one side of the road, whereas the ending point was on the other side, this was counted as one crossing. When the line drawn between two consecutive point locations traversed a road any number of times, but both starting and ending points were on the same side of the road, this was counted conservatively as zero crossings. As point locations were separated by a minimum of 2 h, we cannot discount the possibility of the animal taking an alternative (rather than the shortest) route to traverse between the two points. However, in all cases where we have recorded a crossing, the alternative route would have resulted in at least one road crossing, so our measure of “minimum road crossings” remains consistent with these possibilities.

We analyzed the relationship between road crossings and fire in a similar way to the urban use analyses ([Tables S3](#) and [S5](#)). We used linear mixed effects models with the number of road crossings per individual per month as the response variable and individual mountain lion as a random intercept, and we used model selection to assess support for either an abrupt (step) response or a gradual (continuous) response to fire ([Table S5](#)). To account for unequal fix rates among months and individuals, we included fix rate (the number of locations recorded for an individual mountain lion during the month when road crossings were counted) as a fixed effect in all road crossings models.

To estimate the proportion of the daytime period spent active, we analyzed accelerometer data for lions where it was available ([Figure S3](#) & [Table S3](#)). Given that we did not have field observations to inform our estimations of behavioral state, we used unsupervised Hidden Markov Models (HMMs) to estimate two states approximating “resting” and “active” behavior.⁵⁵ The HMM method explicitly models temporal dependence which is inherent in accelerometer data and assumes that the observed acceleration data time series is driven by an unobserved (hidden) behavioral state process.⁵⁵ We split the data into separate individuals.⁵⁵ We fitted a 2-state HMM using two data streams (activity of the X and Y axes), for which we assumed Gaussian distributions. We estimated starting values for our two states by examining distributions of the two data streams. We also fitted HMMs considering time of day as a covariate ($\cos(2\pi \cdot (\text{hour of day}/24))$) using starting values extracted from the simpler models. These models did not improve fit compared to the simpler models based on AICc, so we retained the simpler models. Prior to analysis we standardized activity measurements by dividing all values for separate individuals and collars by the maximum recorded value during the period the collar was worn by the animal, given collar tightness can affect acceleration values measured by the sensor.⁵⁶ We fitted HMMs using the *momentuHMM v1.5.1* package.⁵⁷

Next, we separated daytime activity data, including all data collected from one hour after sunrise to one hour before sunset to avoid crepuscular periods.²⁷ We removed 24 h periods from the dataset if they had $< 95\%$ of expected recordings. We then

calculated the proportion of daytime active as the proportion of time that was classified as “active” using the HMM method. We used logit-transformed proportion of daytime active as the response variable in linear mixed effects models (LMM) with individual as a random intercept to account for variability in activity levels among individuals (Tables S3 and S5). Consistent with the urban use and road crossings analyses, we used model selection to assess support for either an abrupt (step) response or a gradual (continuous) response to fire (Table S5).

Do mountain lions increase behaviors that could increase risk of conflict with conspecifics after a large wildfire?

We calculated three metrics to quantify behaviors that could place mountain lions at additional risk due to increased chance of conspecific interactions: distance travelled, amount of space used, and spatial overlap with other mountain lions.

We quantified distance travelled using a continuous time movement modelling (CTMM) approach.⁵⁸ The continuous time approach aims to separate the sampling processes from the animal’s underlying movement processes by fitting a model accounting for the positional and velocity autocorrelation properties inherent in movement data, and then simulating multiple possible trajectories based on this model.⁵⁹ We used model selection to fit a movement model to each monthly period for each individual mountain lion that best described the positional and velocity autocorrelation of the animal’s movement for that period. For 38 out of 257 individual-months analyzed, the movement showed no statistically significant evidence for velocity autocorrelation, so we were unable to estimate distance for these months. We estimated monthly distance travelled and variance of these estimates for the remaining 219 months. Given that the CTMM approach allows for estimation of uncertainty, we used a mixed effects meta-regression approach, fitted via restricted maximum likelihood, using estimated distance as the effect sizes and variance of distance as the sampling variances, with individual mountain lion as a random effect (Tables S3 and S5). Our estimated values of distance travelled were normally distributed around a mean of 330 ± 120 km (SD) per month. Moderators (covariates) were defined in the same way as fixed effects for the models of urban use, road crossings, and daytime activity (Table S5). We compared 3 models to investigate whether mountain lions changed their distance travelled after the fire including: null (no effect of fire on distance travelled); step response to fire (abrupt change in distance travelled after the fire); and continuous response (a change in the relationship between distance travelled and time after the fire) (Table S5). We fitted continuous time movement models and estimated distance travelled using the *ctmm v 0.5.11* package.⁵⁸

We quantified the amount of space used and estimated home range overlap using adaptive local convex hulls (LoCoH),⁶⁰ implemented within *adehabitatHR v0.4.18*. While we recognize that this method can underestimate the amount of space used and is sensitive to sampling rates,⁶¹ it performs well when animal movement is constrained by barriers like roads and urban areas,⁶⁰ and our sampling rate was generally consistent among individuals. Since we were more interested in comparative space use (before and after fire), rather than absolute measurements of area, we believe this approach is robust.

We quantified the amount of space used by calculating the adaptive LoCoH for every individual mountain lion and every 3-month period which contained a $\geq 75\%$ fix rate (Table S3). We analyzed the relationship between amount of space used and fire using linear mixed effects models with individual mountain lion as a random intercept (Table S5). We used model selection to assess support for an abrupt (step) response to fire and did not investigate a gradual response to fire as space use was calculated for 3-month periods (Table S5). We also fitted models including the interaction between period (before and after fire) and age-sex class, given the known disparities between amount of space used across age-sex classes,²⁷ though we interpret these results cautiously due to the low number of individuals in each group (Table S3).

We took two approaches to investigating changes in home range overlap before and after the fire. For the first approach, we focused on an adult male who held the largest territory within the Santa Monica mountains prior to the Woolsey Fire, P30, which we refer to as the “dominant male”. We examined all animals that had the potential to overlap with P30 (individuals that used the Santa Monica Mountains area as part or all of their home range) and that were tracked at the same time as P30 for at least 3 months both before and after the fire. This resulted in a dataset of 6 mountain lions (3 males and 3 females), who were tracked for periods ranging from 5 to 11 months (both before and after fire) concurrently with P30. For space use calculations, we limited tracking periods to the same period of time before and after the fire for each individual. For each individual we calculated amount of space used over the period they were tracked concurrently with P30 using adaptive LoCoHs. We then calculated areal overlap of the LoCoH with the corresponding LoCoH for P30 during the same period. Given the small sample size (6 individuals with one measure of overlap per period for a total of 12 measures of overlap), we interpreted the results graphically rather than conducting a formal analysis. Our second approach to quantifying overlap involved calculating the overlap between every pair of mountain lions that were tracked during concurrent 3-month periods (Table S3). We restricted this to animals that used the same region (e.g., animals that exclusively used the Simi Hills portion of the study area were only compared to other animals that used this part of the study area). We analyzed the overlap data in the same way as the first overlap analysis, but separated into two datasets, one expressing overlap as proportions of female home ranges overlapped and the other expressing overlap as proportions of male home ranges overlapped. We fitted linear mixed effects models to each of those two datasets using pair category (male-male, male-female, female-female) as a fixed effect and overlap pair (pair of individual mountain lions for which overlap was calculated) as a random intercept (Table S5). Similar to the space use analysis, we used model selection to assess support for an abrupt (step) response to fire (Table S5).

All analyses were conducted within *R v3.6.1*⁴⁸ using *Rstudio v. 1.3.1093*,⁶² all plots were made using *ggplot2 v. 3.3.0*⁶³ and all map figures were made using *QGIS v. 3.4*.⁵⁴

Resampling for model validation

In order to account for the variability in sampling across individuals and age-sex classes, we resampled observations in each dataset 100 times to provide equal numbers of locations across sex and age classes and re-ran the model selection analysis. The specific approaches for each analysis are listed in [Table S3](#). We recorded the percentage of iterations for which the most parsimonious models from the full dataset were selected as well as the proportion of models that resulted in fitted relationships in the same direction (e.g. greater or lower magnitude after compared to before fire) as the full-data model for all analyses. Where the majority of the relationships were in the same direction as the full dataset and the majority of iterations showed the same direction in relationships, we classified the relationships as robust. An additional validation step was performed for the urban use analysis. Given the female who used urban areas the most frequently (P75 — 15% of use was urban) was only sampled after the wildfire, we performed an additional check and removed her from the dataset and re-fit the models. We found that the strength and direction of the relationships were similar and that the same model type was found to be the most parsimonious, so we retained the full dataset.

Most of our analyses showed that the most parsimonious model and the direction of relationships were consistent across 100% of iterations, and we report only the exceptions below. In the analysis of urban use, models predicting abrupt changes were selected as the most parsimonious 76% of the time, with continuous responses to fire 24% of the time. In the road crossings analysis, 78% of model iterations showed an increase in road crossings after fire with 25% of models showing an abrupt change and 62% showing a continuous response. For the space-use analysis, direction of the relationships (increase in space use after fire) was consistent across 83 % of iterations. When space use was separated into sex and age classes, model selection was consistent across all iterations, but the consistency of relationship directions (increase or decrease after fire) varied among sex and age classes (adult male: 63 %, subadult male: 100 %, adult female: 81 %, subadult female: 92 %).