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RESEARCH ARTICLE

Mountain lions reduce movement, increase efficiency during the Covid-19 shutdown

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Abstract

1. Wildlife strongly alter behaviour in response to human disturbance; however, fundamental questions remain regarding the influence of human infrastructure and activity on animal movement. The Covid-19 pandemic created a natural experiment providing an opportunity to evaluate wildlife movement during a period of greatly reduced human activity. Speculation in scientific reviews and the media suggested that wildlife might be increasing movement and colonizing urban landscapes during pandemic slowdowns. However, theory predicts that animals should move and use space as efficiently as possible, suggesting that movement might actually be reduced relative to decreased human activity.
2. We quantified space use, movement, and resource-selection of 12 GPS-collared mountain lions (eight females, four males) occupying parklands in greater Los Angeles during the Spring 2020 California stay-at-home order when human activity was far below normal. We also tested the hypothesis that reduced traffic on Los Angeles area roadways increased permeability of these barriers to animal movement.
3. Contrary to expectations that wildlife roamed more widely during pandemic shutdowns, resident mountain lions used smaller areas and moved shorter distances relative to their historical behaviour in greater Los Angeles. They also relaxed avoidance of anthropogenic landscape features such as trails and development, which likely facilitated increased travelling efficiency. However, there was no detectable change in road-crossing, despite reduced traffic volume.
4. Our results support the theoretical prediction that animals maximize movement efficiency and suggest that carnivores incur energetic costs while avoiding humans. While mountain lions may restrict movement at the landscape level relative to barriers, they appear to increase distances moved at finer scales when avoiding human activity – highlighting the scale-dependent nature of animal responses to human disturbance.
5. Avoiding humans can reduce direct mortality of large carnivores and is often suggested to be an important mechanism promoting coexistence in shared landscapes. However, energetic costs incurred by increased movement and space-use while

avoiding human activity may have important consequences for population viability, predator–prey interactions, community structure, and human–wildlife conflict. Management providing sufficient wild prey and education regarding best practices for protection of domestic animals are important for conserving large carnivores in human-dominated landscapes.

KEYWORDS
carnivores, human activity, mountain lions, resource selection, road crossing, space use

1 | INTRODUCTION

Wildlife around the world have altered their movement in time and space in response to expanding human activity and infrastructure (Gaynor et al., 2018; Tucker et al., 2018). These changes in behaviour can have important consequences for wildlife population viability, the structure of ecological communities, and ecosystem function (Bauer & Hoye, 2014; Benson et al., 2016a). A recent global study documented restricted movements of wildlife in areas of greater human footprint and attributed this partly to anthropogenic barriers (Tucker et al., 2018). However, regardless of human disturbance, theory predicts that animals use the smallest home ranges within which they can acquire sufficient resources (Mitchell & Powell, 2007; Wilson, 1975). Thus, rather than restricting movement in human-dominated areas, in some cases animals may need to increase space use as they travel between fragmented patches of suitable habitat to acquire resources (Gehrt et al., 2009; Riley et al., 2003). Importantly, responses to human disturbance are highly species and context specific (e.g. Nickel et al., 2020), such that general understanding of these patterns remains elusive (Tablado & Jenni, 2017).

Behavioural shifts by wildlife to avoid humans in time or space may be adaptive if they reduce direct mortality (Benson et al., 2015) or promote coexistence by mitigating human–wildlife conflict (Carter et al., 2012). However, such behavioural alterations may come at the cost of movement and foraging efficiency if animals travel farther or fail to visit areas with valuable food resources while avoiding areas of human disturbance, which could result in indirect costs similar to those experienced by prey that avoids predators (Frid & Dill, 2002). Thus, quantifying animal movement and resource selection when wildlife are released from the constraints of human activity may provide critical insight into indirect costs associated with navigating human disturbance. However, experimental reduction of human activity in anthropogenic landscapes is generally not possible.

Additionally, fundamental questions remain regarding whether animals respond behaviourally to anthropogenic changes to the physical environment or the presence of humans themselves (Nickel et al., 2020). Indeed, many studies use infrastructure like roads or development as measures of human disturbance (e.g. Wang et al., 2017). The global response to the Covid-19 pandemic created a natural experiment in Spring 2020, providing a unique opportunity to quantify changes in animal behaviour relative to reductions in human activity associated with park closures, commercial shutdowns and shelter-in-place orders (Rutz et al., 2020; Manenti et al., 2020). Importantly, the pandemic decoupled human activity from infrastructure in many areas, making it possible to disentangle mechanistic drivers of behavioural responses by wildlife to human disturbance. Perceived changes in animal behaviour in response to pandemic shutdowns have captured the imagination of scientists and the public alike (e.g. Rutz et al., 2020; Sahagun, 2020; Zellmer et al., 2020). For instance, Zellmer et al. (2020) suggested that decreased traffic and human activity might lead to increased dispersal capability and gene flow between isolated populations. However, we are unaware of empirical studies quantifying changes in animal space use and movements of individually tracked animals relative to reduced human activity during the pandemic or a similarly widespread reduction in human activity.

Large carnivores are excellent study species with which to investigate the influence of human activity on animal movement because of their large space requirements and aversion to humans. Isolated mountain lion (*Puma concolor*) populations persist in southern California in human-dominated landscapes but are at risk of local extinction in some areas due to a combination of demographic and genetic risk factors associated with anthropogenic barriers and activities (Benson et al., 2016a, 2019). Indeed, isolation of mountain lions in the Santa Monica and Santa Ana Mountains by Los Angeles area freeways and development has led to the lowest levels of genetic diversity documented for the species aside from the highly endangered Florida panther (Ernest et al., 2014; Riley et al., 2014). In April 2020, the California Fish and Game Commission voted to advance mountain lions as a candidate species for listing as 'threatened' under California's Endangered Species Act. Thus, increased understanding of behavioural responses by mountain lions in greater Los Angeles to human activity will inform management in California in addition to having broader implications for ecology and conservation.

Accordingly, we quantified movements, space use, and resource selection of mountain lions (*P. concolor*) relative to reductions in human activity in and adjacent to the city of Los Angeles during the Spring California statewide stay-at-home order and park closures associated with the Covid-19 pandemic. Specifically, we tested the hypothesis that large carnivores are able to use fragmented landscapes more efficiently with reduced human activity. If true, we predicted that mountain lions would use smaller areas (P1), move shorter distances (P2),

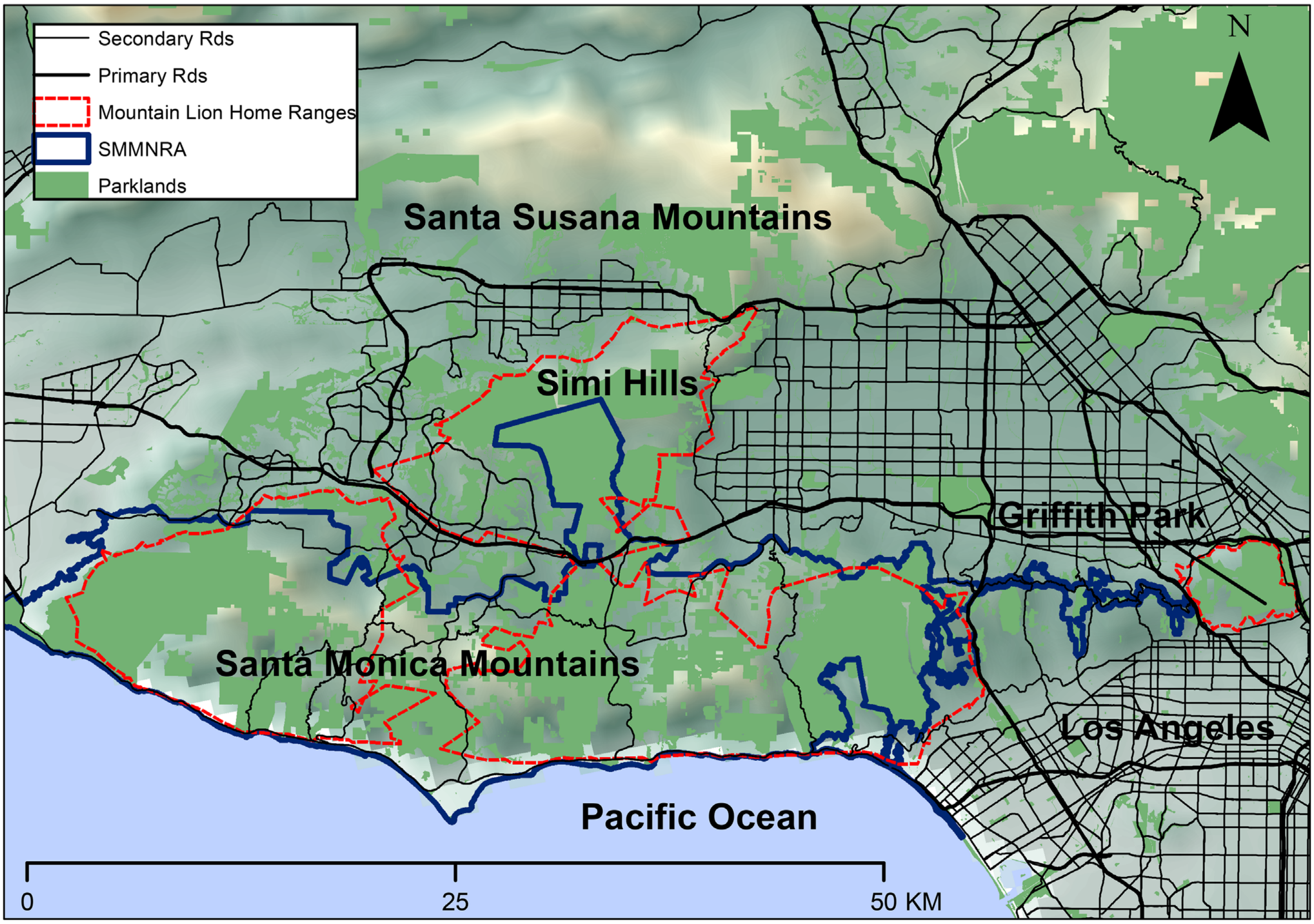

FIGURE 1 Greater Los Angeles in California, USA, showing areas used by mountain lions, the SMMNRA, and portions of our study area comprising parklands

and exhibit greater selection (or lesser avoidance) of anthropogenic landscape features (P3) during Spring 2020. We also tested the hypothesis that reduced traffic volume increased permeability of these barriers to animal movement. If true, we predicted that mountain lions would cross major roads more frequently in response to reduced traffic in the Los Angeles area (P4). Our work provides a novel glimpse into the behaviour of large carnivores occupying a major urban centre during an unprecedented period of reduced human activity.

2 | MATERIALS AND METHODS

2.1 | Study system

We conducted research in and adjacent to the city of Los Angeles (LA) in LA and Ventura counties, California (Figure 1). Specifically, we tracked mountain lions in Santa Monica Mountains National Recreation Area (SMMNRA; 634-km^2 unit of the National Park System), the Santa Monica Mountains, Simi Hills, Santa Susana Mountains, and Griffith Park (Figure 1). Griffith Park was a municipal park lying within the city of LA (Figure 1). The mountain lions we studied occupied areas that were mainly parklands bordered by major freeways, urbanization, or agricultural development (Figure 1).

On 19 March 2020, an executive order directed citizens of California to stay at home except as needed to pursue designated essential job activities or to shop for essential needs. Most parks within the LA area closed from 27 March to 9 May 2020, including trails throughout our study area. We used data on human activity from three sources to confirm that there was lower human activity in parks and on roads in LA and Ventura Counties during the park closures. First, we used publicly available Covid-19 Community Mobility data (Google, Mountain View, CA, USA) for parks, which estimated trends in human movement at the county level by comparing information on the number of visits and lengths of stay in parks on a given date to a baseline of mobility (https://www.google.com/covid19/mobility/). We also used estimates of daily vehicle miles travelled (StreetLight Data, Inc., San Francisco, CA, USA) in LA and Ventura counties to estimate reductions in traffic volume during our study (https://www.streetlightdata.com/). Finally, as the majority (7 of 12) of animals we tracked were within SMMNRA, we used data from the National Park Service (NPS) to compare monthly human activity (number of visitors) in SMMNRA from January to August 2020 to the same months in previous years

(Integrated Resource Management Applications, NPS; https://irma.nps.gov/Portal/). These data were publicly available and provided estimates of the number of visitors entering the park on a monthly basis.

2.2 | Capture and telemetry

We captured 12 mountain lions using cable restraints (Aldrich foot-snares), baited cage-traps, or by treeing them with trained hounds. We deployed global positioning system (GPS) radio-collars on adult and subadult mountain lions (Vectronic Aerospace, Berlin, Germany). We programmed collars to collect fixes every 2 h starting in the evening (1700) and ending in the morning (0500) and to collect a single location during the day (1300). However, we remotely increased the fix schedule during the park closures for collars on three animals to collect fixes every 2 h continuously from 24–25 April to 8–10 June 2020 to increase the number of diurnal locations during the pandemic. We could not remotely change the fix schedule for other collars due to differences in remote communication specifications. We captured and handled all animals following procedures approved through a scientific collecting permit with the California Department of Fish and Wildlife (SCP #5636) and the NPS Institutional Animal Care and Use Committee.

2.3 | Space use and movement

We estimated space use of mountain lions with 100% adaptive local convex hulls (a-LoCoH) for mountain lions and estimated the *a* parameter as the distance between the farthest two locations in each input dataset (Getz et al., 2007). The a-LoCoH method is preferable to other local convex hulls (r or k-LoCoH) as it is robust to variation in sample size and choices for selecting the *a*, *r*, or *k* parameters (Getz et al., 2007). We used the 100% local convex hull after inspecting data for spurious locations to provide estimates of total areas of space use during our monitoring periods. Mountain lions breed year-round and do not show strong seasonality in movements in the Mediterranean climate of our southern California study area, such that we assumed seasonal variation in space use would not strongly influence our results. We compared space use by resident, adult mountain lions during the 43-day Covid closure (27 March–9 May 2020) to their historical space use estimated during multiple 43-day periods for 1–8 years prior to the closure. Specifically, we investigated whether the estimated area used during the closure was outside of the 95% confidence intervals associated with the mean of their previous estimated space use. We believe this comparison is more meaningful than a simple 'before' and 'during' comparison using a single snapshot as the baseline because it allowed us to understand whether individuals were using space in a manner different from their historical patterns of behaviour documented over 1–8 years of monitoring. However, we refrain from using the term 'home ranges' because it is debatable whether an animal exhibits a true home range in 43 days. We included four mountain lions in this analysis (three adult females, one adult male; Table 1). We did not have sufficient data to adequately estimate historical space use for other radio-collared mountain lions.

To quantify movements of mountain lions, we defined three periods across the daily cycle: crepuscular (1 h before and after sunset and sunrise), diurnal (1 h after sunrise to 1 h before sunset), and nocturnal (1 h after sunset to 1 h before sunrise). We estimated mountain lion movement as mean step length between sequential telemetry locations separated by 2 h during nocturnal and crepuscular periods, and where possible during diurnal periods, for mountain lions with at least 1 year of tracking data prior to the closure (1–8 years). For 'steps' that spanned both nocturnal and crepuscular periods, we assigned these to the period of greater overlap. We compared mean step lengths (with 95% confidence intervals) of individual mountain lions estimated prior to (with all historical data for that animal) and during the closure to test the prediction that they would move less with reduced human activity. We limited this analysis to three mountain lions (two females, one male) for whom we had sufficient historical movement data (≥1 year). We excluded one animal due to an insufficient number of sequential locations needed to estimate step lengths during the parks closure associated with missing locations that were not recovered by remote upload.

Next, to investigate a potential behavioural mechanism underlying the predicted shorter movement distances, we compared the mean distance between diurnal locations (i.e. locations from 1300 hours; putative rest sites) and the centroid of subsequent nocturnal locations (putative foraging areas) prior to (with all historical data for that individual) and during the closure for the same three individuals used in the step length analysis. Our goal here was to understand whether mountain lions were occupying diurnal locations (putative rest sites) closer to their nocturnal foraging areas, which might allow them to reduce distances travelled per day when human activity was reduced in parks. Finally, we estimated mean step lengths and confidence intervals during diurnal, nocturnal, and crepuscular periods for the three mountain lions (two males, one female) whose collars collected locations separated by 2 h continuously for 14—15 (24–25 April) days during and 30–32 days after (8–10 June 2020) the closures to investigate potential changes in diurnal movement. In total, we analysed movement of five mountain lions (three females, two males) with our movement analyses (Table 1).

We identified parturition events, tagged kittens, and tracked kitten survival using telemetry and remote cameras (Benson et al., 2020; Moriarty et al., 2012). We excluded space use and movement data collected from females < 100 days following parturition events because females restricted space use and movements when travelling with young kittens (J. Benson et al., unpublished data). Specifically, we removed data associated with five reproductive events from two females involved in our space use and movement analyses. We did this to eliminate variation in space use and movement that was the result of maternal behaviour, rather than variation in human activity. One radio-collared female (P54) gave birth to a litter of kittens during the Covid park closure on 25 April. Thus, we truncated the monitoring period for her space use estimate during the park closure to the 29 days before she gave birth (27 March–25 April). For this female, we used 29 days (rather than 43) for all space use estimates (both before and during the

TABLE 1 Mountain lions included in different analyses of space use, movement, resource selection, and road crossing behaviour in greater Los Angeles before, during, and after the park closures associated with the Covid-19 pandemic. Shown are sexes, age classes (adult or subadult [SA]), whether each individual was included in each analysis, and the total number of individuals in each analysis

			Analysis						
				Movement			Resource selection		
ID	Sex	Age	Space use[a]	Step length[b]	Day - night[c]	Step length[d]	Female[e]	Diurnal[f]	Road crossing[g]
P19	F	Adult	Yes	Yes	Yes	No	No	No	No
P54	F	Adult	Yes	Yes	Yes	No	Yes	No	Yes
P62	F	Adult	Yes	No	No	No	Yes	No	Yes
P65	F	Adult	No	No	No	No	Yes	No	Yes
P77	F	Adult	No	No	No	Yes	Yes	Yes	Yes
P80	F	Adult	No	No	No	No	Yes	No	Yes
P67	F	SA	No	No	No	No	Yes	No	Yes
P75	F	SA/Adult	No	No	No	No	Yes	No	Yes
P22	M	Adult	Yes	Yes	Yes	Yes	No	Yes	No
P63	M	Adult	No	No	No	No	No	No	Yes
P81	M	SA	No	No	No	No	Yes	No	Yes
P78	M	SA	No	No	No	Yes	No	No	Yes
			$n = 4$	$n = 3$	$n = 3$	$n = 3$	$n = 7$	$n = 2$	$n = 10$

[a]Comparison of mean area used during sequential 43 (or 29) day periods from historical monitoring (1–8 years) and the park closure.
[b]Comparison of mean (2-h) step length during historical (1–8 years) and park closure periods.
[c]Comparison of mean distances between diurnal and subsequent nocturnal locations during historical and park closure periods.
[d]Comparison of mean (2-h) step length during (14–15 days) and after (30–32 days) the park closure.
[e]Comparison of resource selection of females ($n = 7$) before (76 days) and during (43 days) park closure.
[f]Comparison of resource selection for two individuals (in separate models) during (14–15 days) and after (30–32 days) the park closure.
[g]Comparison of road crossing rates before (43 days), during (43 days), and after (43 days) park closure.

park closure) to make sure our comparisons were between consistent time periods.

2.4 | Resource selection

We investigated resource selection by comparing resource use to availability with an approach similar to Johnson's (1980) third-order (within home range) selection. As noted above, we do not refer to our estimates of space use as home ranges; nonetheless, these estimates reflected the areas used by each individual during the periods of interest and provided appropriate measures of resource availability. Thus, we estimated space use with 100% a-LoCoH using all locations for each animal during periods before, during, or following the park closure as needed for our models (see below). Within these polygons, we estimated availability by systematically sampling 30 m pixels separated by 90 m resulting in 123 pixels/ km^2 for each animal (Benson, 2013). We estimated the Euclidean distance from used and available locations to natural vegetation classes, human land-use classes, and roads and trails (Table S1 in the Supporting Information). Specifically, for vegetation types, we modified two existing vegetation layers (SMMNRA Vegetation Layer, 2007; CALVEG, USDA-Forest Service Pacific Southwest Region 2013) by combining similar vegetation types to produce a layer with five broad classes: chaparral, coastal sage scrub, prairie/meadow, upland woodland, and riparian woodland (Table S1). For areas where natural habitat was developed or otherwise altered for anthropogenic activities, we generalized a digital land-use map (Southern California Association of Governments Open Data) to derive two land-use classes: development and altered-open (Table S1). Development included commercial areas and residential areas with ≥2.5 houses/hectare. Altered-open were areas modified by humans to a lesser extent than developed areas and included golf courses, schools, landscaped areas such as city parks, low-density residential areas (<2.5 houses/hectare), cemeteries, horse ranches, and agricultural areas. We also estimated distances to primary roads (major freeways), secondary roads (intermediate-sized paved roads), tertiary roads (neighbourhood roads), and trails (fire roads, other unpaved roads, and hiking trails; Table S1). However, we excluded primary and secondary roads from resource selection models because they were correlated with other variables such as development and altered-open. We estimated slope and elevation from digital elevation models in ArcGIS and classified all used and available pixels accordingly. We removed variables that were highly correlated ($r > 0.5$) and rescaled values for continuous variables by subtracting their mean and dividing by 2 standard deviations.

We modelled resource selection in a use-availability framework with generalized linear mixed models (GLMMs) implemented in the R (version 3.4.1) package 'lme4' with a binary (0 = available, 1 = used) response variable (family = binomial, link = logistic; Bates et al., 2015).

We constructed a number of models to test our prediction that mountain lions would exhibit greater selection (or lesser avoidance) of anthropogenic landscape features during the closure. Most animals we tracked were resident females (n = 7), so we constructed a model with data from these seven females to investigate potential sources of variation in resource selection during nocturnal and crepuscular periods (daytime data were insufficient; Table 1). We tracked these females from 11 January to 27 March (before closure) and 27 March to 9 May (during closure). We included random intercepts for an individual to account for the unbalanced sample sizes of locations across individuals (Gillies et al., 2006). We included means of 616 used locations (range: 365–756) and 8259 available locations (range: 5992–10,940) per female for this analysis. We considered models with (1) all resource variables and no interactions, (2) interactions between resource variables and a dummy-coded variable for closure (before closure = 0, during closure = 1), and (3) the null model. Interactions with the dummy-coded variable for closure allowed us to evaluate differences in resource selection for these females before and during the Covid-19 parks closure. We calculated the difference in Akaike's Information Criterion (ΔAIC) between these models to evaluate relative support and made inference on models with ΔAIC < 10 (Bolker et al., 2009).

To investigate differences in resource selection during diurnal periods when changes relative to human activity might be strongest, we fit individual-level, diurnal resource selection models for the two adult, resident mountain lions (one male, one female) for whom we had collected locations every 2 h throughout the day during (male = 17, female = 18 days; 24–25 April to 9 May 2020) and after (male = 32 days, female = 30 days; 9 May to 8–10 June 2020) the closure. We included 199 and 194 used locations and 495 and 859 available locations in the male and female diurnal models, respectively. In these models, we fit interactions between resource variables and a dummy-coded variable for closure (after closure = 0, during closure = 1). We did not model resource selection for the third individual for whom we had sufficient diurnal data because he was a subadult male that was dispersing during the monitoring period such that his data were not appropriate for the third-order resource selection (Johnson, 1980). Thus, we were only able to evaluate resource selection during diurnal periods for two individuals (one male, one female; Table 1), which limited our inference about changes in resource selection during the daytime period.

For the three resource selection models, we used the interaction models to evaluate whether there were differences between the periods when the parks were closed and open. When differences were found, we ran separate models for the periods with parks open and closed. These separate models provided cleaner interpretation of selection and avoidance relative to availability without the presence of interactions. We use the terms selection and avoidance throughout to indicate that (1) used locations were significantly closer to (selection) or farther from (avoidance) distance-based resource variables (vegetation types, land-use types, roads, trails) than were available locations, or (2) values of classification-based resource variables (elevation and slope) were significantly greater or lower at used locations relative to available locations. Specifically, we inferred selection or avoidance of resource variables when 95% confidence intervals of fixed-effect beta coefficients did not overlap 0. We present the beta coefficients (effect sizes) from our models so that readers can evaluate the relative strength of selection and avoidance of each resource variable.

2.5 | Road crossing

We used GPS data to investigate the frequency with which mountain lions (n = 10) crossed primary (major freeways) and secondary (other large and intermediate-sized roads) roads, which act as hard or semi-permeable barriers to mountain lion movement in greater LA (Riley et al., 2014). We inspected all instances where straight-line paths between sequential telemetry locations intersected primary or secondary roads. In most cases (92%), it was clear that the animal had crossed the road as there was no other explanation for sequential locations given the configuration of the roads (examples in Figure S1 in the Supporting Information). However, in a few (8%) instances, it was plausible that the mountain lion reached the second location in a sequential pair without crossing the roads by not moving in a straight line (example in Figure S1). To be conservative, we only considered definitive road crossings in our analysis. We estimated road-crossing rates as the number of definitive crossings/number of days monitored for 10 radio-collared mountain lions during 43-day periods before, during, and following the closure (Table 1). An additional radio-collared mountain lion was captured in March and was not monitored sufficiently prior to the pandemic closures so we excluded this individual from the road-crossing analysis. Additionally, the adult male occupying Griffith Park did not cross any primary or secondary roads during the monitoring period and, thus, did not contribute any data to the analysis.

3 | RESULTS

3.1 | Human activity

All three sources of data indicated that human activity was greatly reduced in parks and roadways in our study area during the period of park closures (27 March–9 May 2020; Figure 2).

3.2 | Space use and movement

The mean and median areas used by resident mountain lions prior to the closure were larger than the areas used during the closure (n = 4 individuals; Table 2, Figure 3). Individual resident mountain lions used shorter mean step lengths during the closure than they had used during 1–8 years prior during at least one of the daily periods (n = 3 individuals; Figure 4a). The mean distance between diurnal locations and centre of subsequent nocturnal locations was also shorter for these mountain lions during the closure compared to their movement during the previous 1–8 years; however, variation was high and confidence intervals around means overlapped for two of three individuals (Figure 4b).

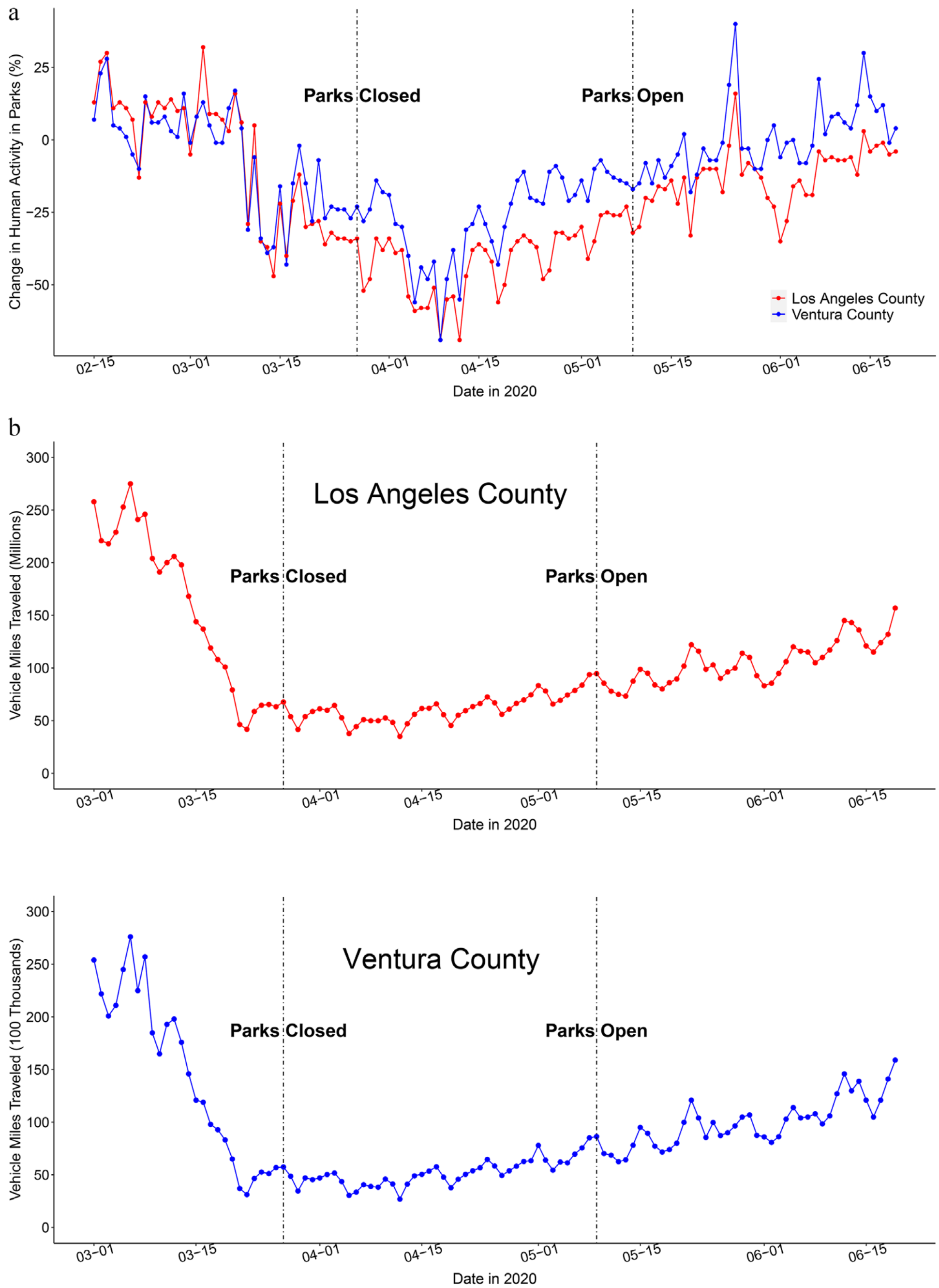

FIGURE 2 Data on human activity in our study area from Los Angeles and Ventura Counties: human mobility (number of visits and length of stay in parks; data from Google, https://www.google.com/covid19/mobility/) 2a), estimates of vehicle miles travelled (2b; data from StreetLight Data, Inc, https://www.streetlightdata.com/), and estimates of visitors to SMMNRA, January–August 2010–2020 (2c; data from National Park Service, https://irma.nps.gov/Portal/)

Mountain lions with 2-h fix schedules during diurnal periods ($n = 3$) exhibited variable patterns that appeared to be influenced by local environmental conditions and behavioural state (resident vs. dispersal). The resident adult male in Griffith Park, LA used smaller diurnal step lengths during the closure compared to after parks reopened (Figure S2 in the Supporting Information). A resident adult female in the Simi Hills used similar step lengths during and after the closure during crepuscular and diurnal periods, but had smaller nocturnal step lengths during the closure (Figure S2). A dispersing subadult male in the Santa Susana Mountains exhibited similar step lengths during diurnal and crepuscular periods during and after the closure, but greater step lengths during the closures at night (Figure S2).

3.3 | Resource selection

For resident adult females ($n = 7$ individuals) during crepuscular and nocturnal hours, there was strong empirical support for differences

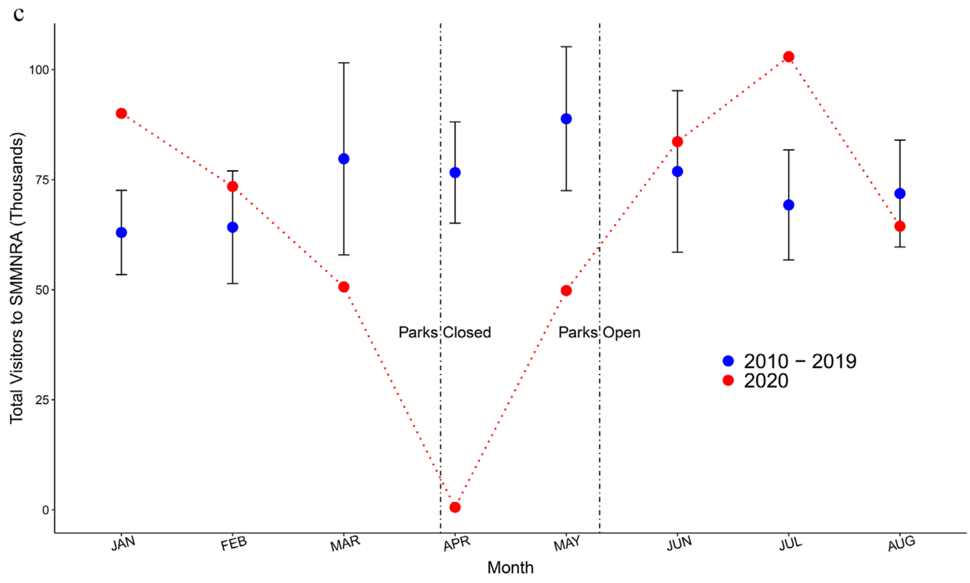

FIGURE 2 Continued

TABLE 2 Space use of resident adult mountain lions in greater Los Angeles, 2012–2020. Shown are animal ID, Sex, general location (Area; SMM = Santa Monica Mountains, SH = Simi Hills, GP = Griffith Park), area of space used during the Covid closure, mean and median area used during historical monitoring (1–8 years), lower (LCL) and upper (UCL) 95% confidence limits of historical space use, and number of space use estimates (over 43 or 29 days) generated with historical data

			Covid space use	Historical space use				
ID	Sex	Area	Value (km^2)	Mean (km^2)	Median (km^2)	95% LCL	95% UCL	*n*
P19	F	SMM	17.6	46.8	42.5	40.1	53.0	40
P54	F	SMM	5.2	35.2	28.2	23.8	47.0	12
P62	F	SH	30.7	40.3	45.8	31.0	50.0	7
P22	M	GP	9.9	13.7	13.4	13.0	14.3	54

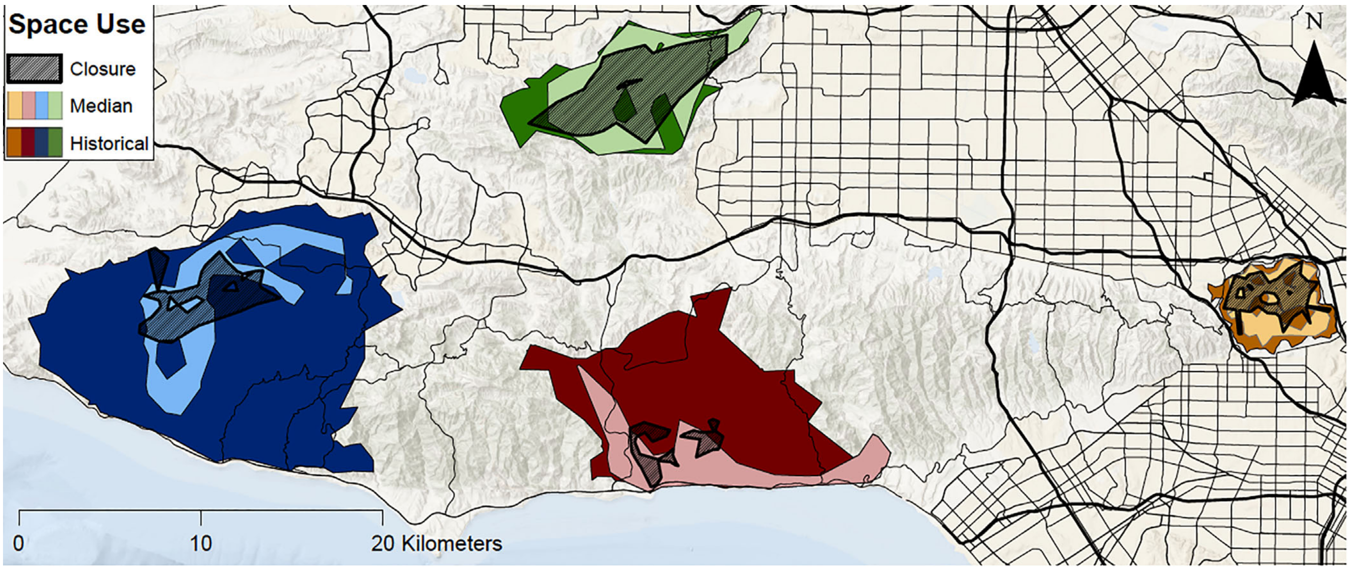

FIGURE 3 Space use by four mountain lions in greater Los Angeles. Shown are polygons representing area used during Covid park closure, median area used during the historical tracking period, and area used during the entire historical tracking period

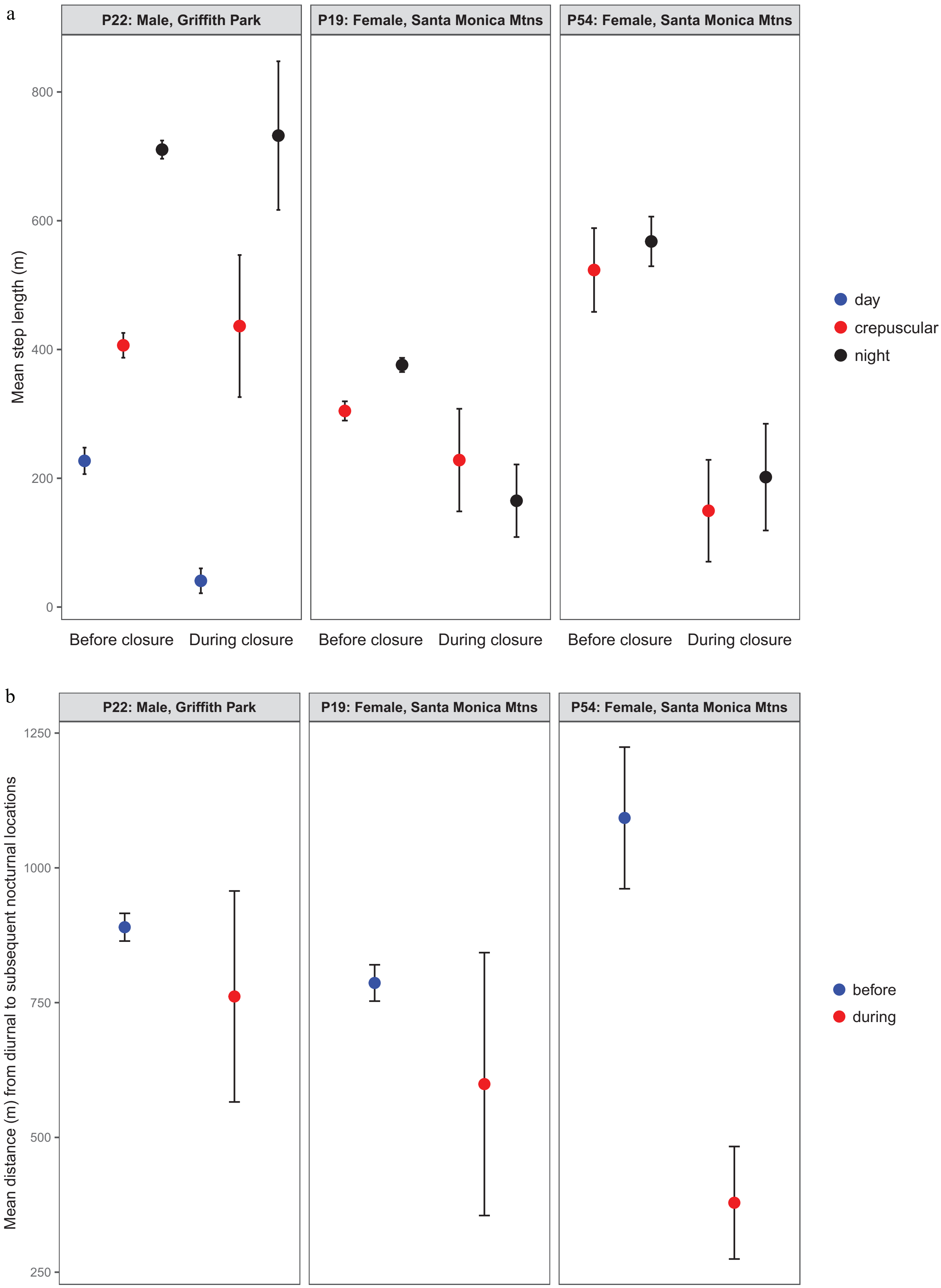

FIGURE 4 Mean step length by mountain lions before (1-8 years) and during the Covid park closure (43 days) with 95% confidence intervals for diurnal, crepuscular, and nocturnal periods (4a); and mean distance moved between diurnal locations (putative rest sites) and centre of nocturnal locations (putative foraging areas) visited the subsequent night before and during the park closures (4b)

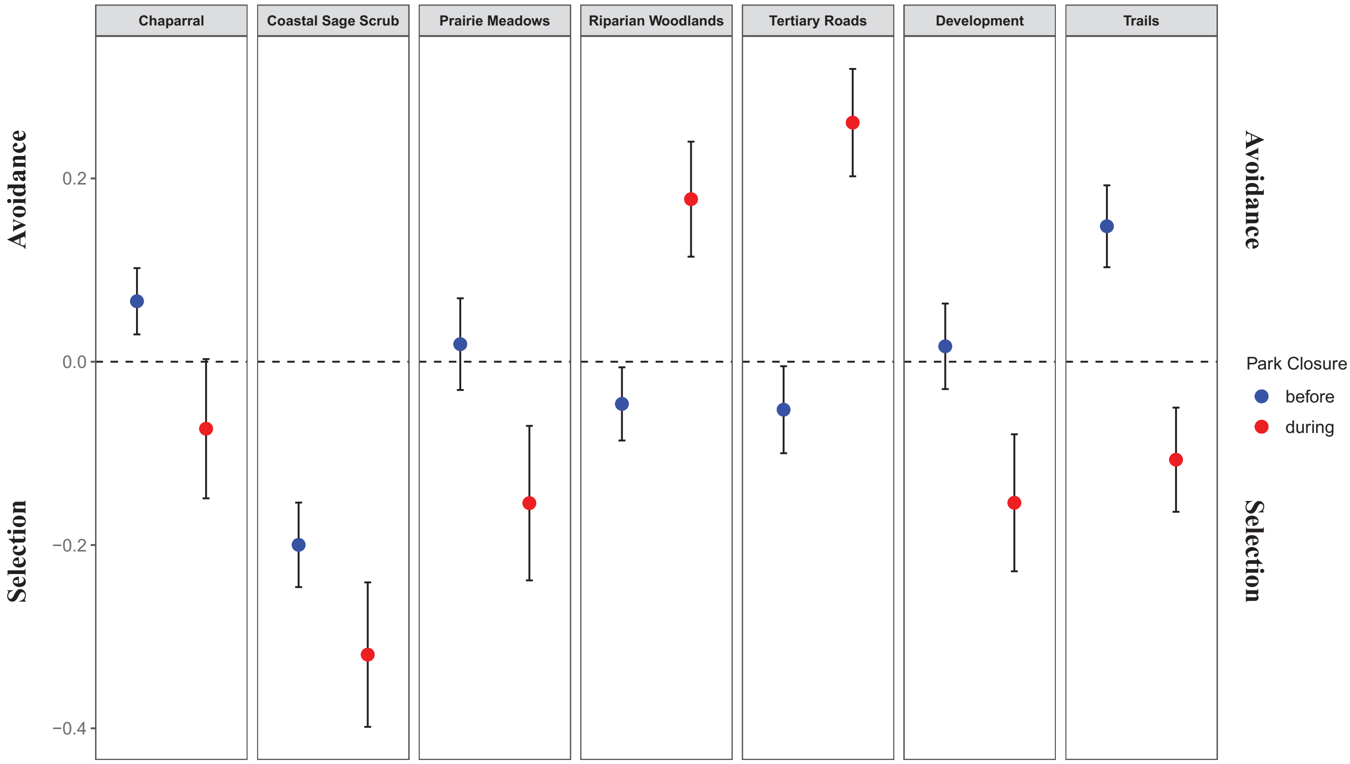

FIGURE 5 Coefficients from resource selection model for resident, female mountain lions ($n = 7$) before and during the Covid parks closure in greater Los Angeles, 2020. All variables are distance-based meaning that coefficients < 0 indicate selection, > 0 indicate avoidance

in resource selection before and during the closure as the model with interactions was superior to both the model without interactions (ΔAIC = 262) and the null model (ΔAIC = 866). Our prediction regarding anthropogenic features was supported as females selected development and trails during the closure, whereas they avoided trails and did not select or avoid development prior to the closure (Figure 5, Table S2 in the Supporting Information). However, contrary to our prediction, they avoided tertiary roads more during the closure (Figure 5, Table S2). Females also selected prairie-meadow more and avoided riparian woodlands more during the closure (Figure 5, Table S2).

Resident mountain lions for whom we had sufficient diurnal data ($n = 2$ individuals) also altered selection of anthropogenic landscape features during the day (Figure S3; Tables S3 and S4 in the Supporting Information). An adult female in the Simi Hills avoided trails and development after the parks reopened but neither avoided or selected these features during the closure (Figure S3). This female also selected prairie-meadow during the closure but neither selected or avoided it once parks reopened (Figure S3). She also exhibited reduced selection of shrub vegetation (chaparral and coastal sage scrub), selected lower elevations, and avoided altered open more during the closure (Figure S3). The adult male in Griffith Park, LA, selected development diurnally during the closure, whereas he did not select or avoid development after parks reopened (Figure S3). This male showed strong avoidance of trails both during and following the closure, whereas he increased selection of riparian woodlands once parks reopened (Figure S3, Table S4).

3.4 | Road crossing

Only a single mountain lion (dispersing subadult male) crossed primary roads during our study period. He crossed one primary road a single time prior to the parks closure and one primary road three times during the closure. We documented 144 total crossings of secondary roads by 10 radio-collared mountain lions (seven females, three males) from 12 February to 21 June 2020. Mountain lions crossed secondary roads at very similar daily rates before (mean = 0.12, range 0–0.47, $n = 10$ mountain lions), during (mean = 0.11, range = 0–0.40, $n = 10$), and after (mean = 0.11, range = 0–0.39, $n = 10$) the closure, providing no support for the prediction that road crossing would increase during the closure.

4 | DISCUSSION

Contrary to widespread perceptions of expanded home ranges and movement of wildlife during Covid-19 shutdowns in urban areas (e.g. Sahagun, 2020), resident mountain lions in greater LA responded by using smaller areas and moving shorter distances. Thus, our results support the theoretical prediction that animals should use the smallest areas within which they can obtain sufficient resources (Mitchell & Powell, 2007; Wilson, 1975). However, mountain lions relaxed avoidance of trails and development during the Covid closure, which may have facilitated shorter step lengths and reduced space use. Energetic costs of travelling for animals in general and mountain lions specifically are a function of body weight and speed (distance per unit time; Taylor & Heglund, 1982; Wang et al., 2017). Our results indicate that mountain lions reduced distances travelled during 2-h intervals during the Covid park closures, suggesting that they were able to travel in a more energetically efficient manner with reduced human activity on the landscape. Previous work has shown that carnivores select trails to facilitate efficient movement (Dickie et al., 2017; Kays et al., 2017). Specifically, mountain lions in Alberta responded to seasonal variation in human activity by selecting areas farther from trails during summer when activity was higher (Morrison et al., 2014). Our findings indicate that mountain lions sacrifice travelling efficiency while navigating 'normal' levels of disturbance in greater Los Angeles. Despite our relatively limited sample sizes, our work shows that mountain lions appear capable of responding quickly to reduced human activity to increase movement and space use efficiency, even in landscapes with an extremely large human footprint.

Previous work has documented disparate responses of wildlife to human disturbance. Animals may move less in human-altered landscapes due to barriers to movement or anthropogenic subsidies (Tucker et al., 2018). Alternatively, animals may move farther and use larger areas as they travel between fragmented patches and avoid human disturbance (Gehrt et al., 2009; Riley et al., 2003). A resident male mountain lion in our study occupied an extremely small home range (24 km^2 during 5 years; Riley et al., 2021) surrounded by three of the busiest freeways in California and high-density urban development within the city of LA (Figure 3). To our knowledge, this is the smallest home range reported for an adult male mountain lion. However, here we show that he used an even smaller area within this home range and moved shorter distances (diurnally) during the period of reduced human activity. Thus, human disturbance can influence animal movement differently at different scales and considering the hierarchical nature in which animals make decisions about space use and movement is important. When selecting a home range from the larger landscape (second-order resource selection; Johnson, 1980) animals may use smaller areas and move shorter distances relative to human footprint and hard barriers to movement (Riley et al., 2021). Within that home range (third-order resource selection; Johnson, 1980), animals may need to traverse longer distances and use larger areas when avoiding humans, consistent with our current results.

Humans kill mountain lions intentionally and unintentionally in greater LA through vehicle collisions, poaching, shooting following livestock depredation, and rodenticide poisoning (Benson et al., 2020; Vickers et al., 2015). Temporal shifts in behaviour between day and night can reduce mortality of carnivores (Benson et al., 2015) and may promote coexistence in human-dominated landscapes (Carter et al., 2012; Nickel et al., 2020). However, avoiding human activity might also have indirect consequences for fitness and population dynamics of large carnivores, similar to behaviourally mediated costs incurred by prey as they avoid predators in time and space (Frid & Dill, 2002). Indeed, previous work has documented increased movement rates and energy expenditure for mountain lions in developed areas (Wang et al., 2017). Thus, in the small, isolated populations in southern California, which are threatened with local extinction by demographic and genetic risk factors (Benson et al., 2016a, 2019), increased energy expended as mountain lions avoid human activity could further reduce fitness of individuals and increase extinction risk. Large carnivores may compensate for increased energy expenditure in anthropogenic landscapes with increased kill rates on ungulates (Smith et al., 2015), which could have cascading effects on prey populations and community structure (Wang et al., 2017). Additionally, mountain lions and other large carnivores with nutritional deficiencies may be more likely to enter anthropogenic areas and exhibit risk-sensitive foraging on wild prey or domestic animals (Blecha et al., 2018; Lance et al., 2010), such that reduced energy efficiency of predators in fragmented landscapes could potentially exacerbate human–wildlife conflict. If true, this would complicate the assumption that avoidance of humans promotes coexistence (e.g. Carter et al., 2012; Nickel et al., 2020).

Wildlife managers in human-dominated landscapes occupied by top predators of conservation concern should attempt to maintain sufficient densities of large prey to withstand potentially higher kill rates. If large carnivores are more likely to enter developed areas and become involved in conflicts with humans when energetically stressed (Blecha et al., 2018; Lance et al., 2010), providing an adequate wild prey base could also help to mitigate human–wildlife conflict. Indeed, maintaining sufficient densities of wild ungulate prey has been identified as a key strategy for reducing wolf–human conflict involving livestock in Europe's human-dominated landscapes (Kuijper et al., 2019). Additionally, educating residents in the Santa Monica Mountains and adjacent areas about the importance of protecting domestic animals (livestock and pets) by confining them in secured and covered enclosures at night or using properly trained guard dogs can help to reduce losses and human-mountain lion conflict (Wyckoff et al., 2016; J. Sikich and S. Riley, unpublished data). Unfortunately, there is little ecological information regarding mule deer (*Odocoileus hemionus*) in the Santa Monica Mountains and adjacent areas, which is the main prey for mountain lions (Benson et al., 2016b). Thus, quantifying density, behaviour, and population dynamics of mule deer in the Santa Monica Mountains and across greater Los Angeles is an important research priority to facilitate a sound conservation strategy for mountain lions in this population threatened with local extinction (Benson et al., 2016a, 2019).

Mountain lions moved shorter mean distances between diurnal locations (putative rest sites) and centres of nocturnal activity (putative foraging areas) during the closure. However, our results were not conclusive as variation was high and sample sizes were low for these day–night distances during the closure given the relatively short duration (range 22–37 distance measurements per animal). Despite this uncertainty, it is plausible that reduced human activity allows large carnivores to select daytime rest sites more freely on the landscape and in closer proximity to nocturnal foraging areas. In human-dominated landscapes, cover is an important diurnal resource for large carnivores as they seek to avoid human activity (Boydston et al., 2003). Selection of daytime rest sites farther from humans may have energetic consequences if the most profitable foraging patches are closer to humans (Suraci et al., 2019). In greater Los Angeles, mountain lions kill and consume their primary prey (mule deer) closer to development, whereas they may avoid development more during the day (Benson et al., 2016b;

Riley et al., 2021). Thus, diurnal avoidance of human activity and increased distance between areas containing critical resources (e.g. food and cover) may prevent large carnivores from maximizing energy efficiency in anthropogenic landscapes. We encourage researchers to build on these results with larger sample sizes, which could allow researchers and managers in urban and suburban areas to work with city planners to strategically design and enhance greenspaces to facilitate efficient movement of wildlife between areas containing critical diurnal and nocturnal resources. It is worth noting that mountain lions are primarily crepuscular and nocturnal (e.g. Beier et al., 1995); thus, the behaviour of diurnal species might be even more strongly influenced by changes in human activity.

LA area freeways represent major barriers to animal movement resulting in substantial differences in genetic structure and diversity of mountain lions in isolated habitat patches in southern California (Riley et al., 2014; Ernest et al., 2014). Contrary to predictions, mountain lions did not increase crossing of major roads despite the reduction in traffic volume, and they actually avoided tertiary roads during the closure. Carnivores in greater LA are highly conditioned to avoid crossing major roads such that their home range boundaries often run parallel to freeways (Riley et al., 2006, 2014). Thus, the relatively short duration of the reduced traffic during our study may not have been sufficient to result in changes in behaviour. Additionally, although traffic volume was reduced, LA area roads were still relatively busy. Thus, research investigating pandemic-related changes in road crossing behaviour in other areas where park closures may have resulted in almost no traffic (e.g. remote national parks) might yield different results.

We expect there will be an explosion of research investigating behavioural responses by wildlife to changes in human activity associated with Covid-19 in the coming years. Many intrinsic and extrinsic factors influence animal behaviour in human-altered landscapes across sexes, age classes, individuals, behavioural states, reproductive condition, and environmental context. Thus, rather than pooling all radio-collared animals in our analyses, we were careful to select animals for each analysis based upon important intrinsic and environmental considerations. For instance, when investigating space use within home ranges, we limited the analysis to resident adults and excluded dispersing subadults that were probably not exhibiting home ranging behaviour. Additionally, it was important to ensure that we had adequate data prior to the pandemic (≥1 year) so we could characterize historical movement behaviour to facilitate meaningful comparisons. Thus, our work demonstrates the importance of considering biological and environmental context when investigating pandemic-induced behavioural shifts, which may help future studies avoid confusing or spurious results.

Although we had relatively small sample sizes across our different analyses, the animals we tracked represented a high proportion of the mountain lions using this urban landscape during the study. For example, in the Santa Monica Mountains, there are an estimated one to two (males) and five to six (females) breeding adult mountain lions within this small population (Benson et al., 2016a, 2019). Thus, our sample sizes were numerically small but should have provided representative samples for understanding mountain lion behaviour during the relatively short duration (43 days) of the Spring 2020 Covid-19 park closures in the Los Angeles area. Given that our study area is the largest metropolitan area occupied by a large carnivore in North America, these data provided a unique opportunity to increase understanding of behavioural responses of mountain lions to reduced human activity in a landscape dominated by humans. We note that the data we used to document changes in human activity were relatively coarse temporally (daily) and spatially (county level). However, these publicly available data were important to ensure that our assumptions about reduced human activity in parks during the closures were valid. Another limitation of our study was that we did not have information about space use, movements, and resource selection of the main prey for mountain lions in our study area, mule deer. It would be interesting and relevant to know how deer responded behaviourally to the reduction in human activity during park closures, which may have influenced the behavioural patterns we documented for mountain lions. We hope that other researchers were tracking both predators and prey species in the same areas simultaneously during Covid-19 related changes in human activity to build on our results and evaluate potential changes in predator–prey interactions.

Our findings indicate that mountain lions can use fragmented landscapes in a more energetically efficient manner when human activity declines, implying that there are energetic costs for coexistence with humans. Understanding how carnivores compensate for these energetic costs will be an integral component of clarifying the ecological roles of top predators in human-dominated landscapes, a major knowledge gap for ecology and management (e.g. Kuijper et al., 2016). Although many previous studies have shown strong behavioural avoidance of human infrastructure, our results suggest that large carnivores avoid human activity more than the infrastructure itself. Conservation of large carnivores in human-dominated landscapes is challenging given threats posed by habitat loss, direct mortality, lack of connectivity, and human–wildlife conflict (e.g. Chapron et al., 2014; Vickers et al., 2015; Benson et al., 2016a, 2019, 2020). Our results highlight that ecologists and managers must also begin to consider cryptic, indirect costs associated with reduced movement efficiency in anthropogenic landscapes.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

All authors designed the study. J.A.S. and S.P.D.R collected the data. H.N.A. and J.F.B. analysed the data. J.F.B. wrote the manuscript. All authors contributed to revising the manuscript and gave final approval for publication.

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Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.hmgqnk9h8 (Benson et al., 2021)

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REFERENCES

Bates D., Mächler M., Bolker B., & Walker S. (2015). Fitting Linear Mixed-Effects Models Usinglme4. *Journal of Statistical Software*, *67*(1), http://doi.org/10.18637/jss.v067.i01.

Bauer, S., & Hoye, B. J. (2014). Migratory animals couple biodiversity and ecosystem functioning worldwide. *Science*, *344*, 6179.

Beier, P., Choate, D., & Barrett, R. H. (1995). Movement patterns of mountain lions during different behaviors. *Journal of Mammalogy*, *76*, 1056–1070.

Benson, J. F. (2013). Improving rigour and efficiency of use-availability habitat selection analyses with systematic estimation of availability. *Methods in Ecology Evolution*, *4*, 244–251.

Benson, J. F., Mahoney, P. J., & Patterson, B. R. (2015). Spatiotemporal variation in selection of roads influences mortality risk for canids in an unprotected landscape. *Oikos*, *124*, 1664–1673.

Benson, J. F., Mahoney, P. J., Sikich, J. A., Serieys, L. E. K., Pollinger, J. P., Ernest, H. B., & Riley, S. P. D. (2016a). Interactions between demography, genetics, and landscape connectivity increase extinction probability for a small population of large carnivores in a major metropolitan area. *Proceedings of the Royal Society, B Biological Sciences*, *283*(1837), https://royalsocietypublishing.org/doi/full/10.1098/rspb.2016.0957.

Benson, J. F., Sikich, J. A., & Riley, S. P. D. (2016b). Individual and population level resource selection patterns of mountain lions preying on mule deer along an urban-wildland gradient. *PLoS ONE*, *11*, e0158006. https://doi.org/10.1371/journal.pone.0158006.

Benson, J. F., Mahoney, P. J., Vickers, T. W., Sikich, J. A., Beier, P., Riley, S. P. D., Ernest, H. B., & Boyce, W. M. (2019). Extinction vortex dynamics of top predators isolated by urbanization. *Ecological Applications*, *29*, e01868.

Benson John F., Sikich Jeff A., Riley Seth P.D. (2020). Survival and competing mortality risks of mountain lions in a major metropolitan area. *Biological Conservation*, *241*, 108294. http://doi.org/10.1016/j.biocon.2019.108294

Benson, J. F., Abernathy, H. N., Sikich, J. A., & Riley, S. P. D. (2021). Mountain lions reduce movement, increase efficiency during the Covid-19 shutdown. *Dryad Digital Repository*. https://doi.org/10.5061/dryad.hmgqnk9h8

Blecha, K. A., Boone, R. B., & Alldredge, M. W. (2018). Hunger mediates apex predator's risk avoidance response in wildland–urban interface. *Journal Animal Ecology*, *87*, 609–622.

Bolker B. M., Brooks M. E., Clark C. J., Geange S. W., Poulsen J. R., Stevens M. H. H., & White J. S. S. (2009). Generalized linear mixed models: a practical guide for ecology and evolution. *Trends in Ecology & Evolution*, *24*, 127–135.

Boydston, E. E., Kapheim, K. M., Watts, H. E., Szykman, M., & Holekamp, K. E. (2003). Altered behavior in spotted hyenas associated with increased human activity. *Animal Behavior*, *6*, 207–219.

Carter, N. H., Shrestha, B. K., Karki, J. B., Pradhan, N. M. B., & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *PNAS*, *109*, 15360–15365.

Chapron, G., Kaczensky, P., Linnell, J. D. C., Von Arx, M., Huber, D., Andrén, H., López-Bao, J. V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J. C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., … Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. *Science*, *346*, 1517–1519.

Creel, S., & Christianson, D. (2008). Relationships between direct predation and risk effects. *Trends in Ecology and Evolution*, *23*, 194–201.

Dickie, M., Serrouya, R., McNay, R. S., & Boutin, S. (2017). Faster and farther: wolf movement on linear features and implications for hunting behaviour. *Journal of Applied Ecology*, *54*, 253–263.

Ernest, H. B., Vickers, T. W., Morrison, S. A., Buchalski, M. R., & Boyce, W. M. (2014). Fractured genetic connectivity threatens a southern California puma (*Puma concolor*) population. *PLoS ONE*, *9*, e107985.

Frid, A., & Dill, L. (2002). Human-caused disturbance stimuli as a form of predation risk. *Conservation Ecology*, *6*(1), https://www.jstor.org/stable/26271862.

Gaynor, K. M., Hojnowski, C. E., Carter, N. H., & Brashares, J. S. (2018). The influence of human disturbance on wildlife nocturnality. *Science*, *360*, 1232–1235.

Gehrt, S. D., Anchor, C., & White, L. A. (2009). Home range and landscape use of coyotes in a metropolitan landscape: conflict or coexistence? *Journal of Mammalogy*, *90*, 1045–1057.

Getz, W. M., Fortmann-Roe, S., Cross, P. C., Lyons, A. J., Ryan, S. J., & Wilmers, C. C. (2007). LoCoH: Nonparametric kernel methods for constructing home ranges and utilization distributions. *PLoS ONE*, *2*, e207.

Gillies, C. S., Hebblewhite, M., Nielsen, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E., & Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology*, *75*, 887–898.

Johnson, D. H. (1980). The comparison of usage and availability measurements for evaluating resource preference. *Ecology*, *61*, 65–71.

Kays, R., Parsons, A. W., & Baker, M. C., Kalies, E. L., Forrester, T., Costello, R., Rota, C. T., Millspaugh, J. J., & McShea, W. J. (2017). Does hunting or hiking affect wildlife communities in protected areas? *Journal of Applied Ecology*, *54*, 242–252.

Kuijper, D. P. J., Chamaillé-Jammes, S., Sand, H., Lone, K., & Cromsigt, J. P. G. M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. *Proceedings of the Royal Society B: Biological Sciences*, *283*, 20161625.

Kuijper, D. P. J., Churski, M., Trouwborst, A., Heurich, M., Smit, C., Kerley, G. I. H., & Cromsigt, J. P. G. M. (2019). Keep the wolf from the door: How to conserve wolves in Europe's human-dominated landscapes? *Biological Conservation*, *235*, 102–111.

Lance, N. J., Breck, S. W., Sime, C., Callahan, P., & Shivik, J. A. (2010). Biological, technical, and social aspects of applying electrified fladry for livestock protection from wolves (Canis lupus). *Wildlife Research*, *37*, 708–714.

Manenti, R., Mori, E., Di Canio, V., Mercurio, S., Picone, M., Caffi, M., Brambilla, M., Ficetola, G. F., & Rubolini, D. (2020). The good, the bad and the ugly of COVID-19 lockdown effects on wildlife conservation: insights from the first European locked down country. *Biological Conservation*, *249*, 108728.

Mitchell, M. S., & Powell, R. A. (2007). Optimal use of resources structures home ranges and spatial distribution of black bears. *Animal Behavior*, *74*, 219–230.

Moriarty, J. G., Whited, L., Sikich, J. A., & Riley, S. P. D. (2012). Use of intraperitoneal radiotransmitters to study mountain lion (*Puma concolor*) kittens. *Wildlife Society Bulletin*, *36*, 161–166.

Morrison, C. D., Boyce, M. S., Nielsen, S. E., & Bacon, M. M. (2014). Habitat selection of a re-colonized cougar population in response to seasonal fluctuations of human activity. *Journal of Wildlife Management*, *78*, 1394–1403. https://doi.org/10.1002/jwmg.799.

Nickel, B. A., Suraci, J. P., Allen, M. L., & Wilmers, C. C. (2020). Human presence and human footprint have non-equivalent effects on wildlife spatiotemporal habitat use. *Biological Conservation*, *241*, 108383.

Riley, S. P. D., Sauvajot, R. M., Fuller, T. K., York, E. C., Kamradt, D. A., Bromley, C., & Wayne, R. K. (2003). Effects of urbanization and habitat fragmentation on bobcats and coyotes in southern California. *Conservation Biology*, *17*, 566–576.

Riley, S. P. D., Pollinger, J. P., Sauvajot, R. M., York, E. C., Bromley, C., Fuller, T. K., & Wayne, R. K. (2006). A southern California freeway is a physical and social barrier to gene flow in carnivores. *Molecular Ecology*, *15*, 1733–1741.

Riley, S. P. D., Serieys, L. E. K., Pollinger, J. P., Sikich, J. A., Dalbeck, L., Wayne, R. K., & Ernest, H. B. (2014). Individual behaviors dominate the dynamics of an urban mountain lion population isolated by roads. *Current Biology*, *24*, 1989–1994.

Riley, S. P. D., Sikich, J. A., & Benson, J. F. (2021). Big cats in the big city: Spatial ecology of mountain lions in greater Los Angeles. *Journal of Wildlife Management*, In press.

Rutz, C., Loretto, M. C., Bates, A. E., Davidson, S. C., Duarte, C. M., Jetz, W., Johnson, M., Kato, A., Kays, R., Mueller, T., Primack, R. B., Ropert-Coudert, Y., Tucker, M. A., Wikelski, M., & Cagnacci, F. (2020). COVID-19 lockdown allows researchers to quantify the effects of human activity on wildlife. *Nature Ecology and Evolution*, *4*, 1156–1159.

Sahagun, L. (2020). Coyotes, falcons, deer, and other wildlife are reclaiming L.A. territory as humans stay home. *Los Angeles Times*. https://www.latimes.com/environment/story/2020-04-21/wildlife-thrives-amid-coronavirus-lockdown

Smith, J. A., Wang, Y., & Wilmers, C. C. (2015). Top carnivores increase their kill rates on prey as a response to human-induced fear. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142711.

Suraci, J. P., Frank, L. G., Oriol-Cotterill, A., Ekwanga, S., Williams, T. M., & Wilmers, C. C. (2019). Behavior-specific habitat selection by African lions may promote their persistence in a human-dominated landscape. *Ecology 100*.

Tablado, Z., & Jenni, L. (2017). Determinants of uncertainty in wildlife responses to human disturbance. *Biological Reviews*, *92*, 216–233.

Taylor, C. R., & Heglund, N. C. (1982) Energetics and mechanics of terrestrial locomotion. *Annual Review of Physiology*, *44*, 97–107.

Tucker, M. A., Böhning-Gaese, K., Fagan, W. F., Fryxell, J. M., Van Moorter, B., Alberts, S. C., Ali, A. H., Allen, A. M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J. L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F. M., Blake, S., Blaum, N., … Mueller, T. (2018). Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science*, *359*, 466–469.

Vickers, T. W., Sanchez, J. N., Johnson, C. K., Morrison, S. A., Botta, R., Smith, T., Cohen, B. S., Huber, P. R., Ernest, H. B., & Boyce, W. M. (2015). Survival and mortality of pumas (*Puma concolor*) in a fragmented, urbanizing landscape. *PLos ONE*, *10*, e0131490.

Wang, Y., Smith, J. A., & Wilmers, C. C. (2017). Residential development alters behavior, movement, and energetics in an apex predator, the puma. *PLoS ONE*, *12*, e0184687.

Wilson, E. O. 1975. *Sociobiology: The new synthesis*. Cambridge, Massachusetts, USA: Harvard University Press.

Wyckoff C., Hauser C., Dorrance L., & Fischer C. (2016). Protecting Small Livestock and Predators Alike: Early Successes. *Proceedings of the Vertebrate Pest Conference*, *27*, http://doi.org/10.5070/v427110446.

Zellmer, A. J., Wood, E. M., Surasinghe, T., Putman, B. J., Pauly, G. B., Magle, S. B., Lewis, J. S., Kay, C. A. M., & Fidino, M. (2020). What can we learn from wildlife sightings during the COVID-19 global shutdown? *Ecosphere*, *11*, e03215.

SUPPORTING INFORMATION

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