Title
COVID-19 suppression of human mobility releases mountain lions from a landscape of fear

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Authors
Wilmers, Christopher C
Nisi, Anna C
Ranc, Nathan

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Report

COVID-19 suppression of human mobility releases mountain lions from a landscape of fear

Highlights

- Under normal circumstances, mountain lions strongly avoid urban areas
- Human mobility declined by more than 50% during the COVID-19-associated lockdown
- Mountain lions relaxed their fear of the urban edge during the lockdown
- Pandemics can alter ecological relationships because of changes in human behavior

Authors

Christopher C. Wilmers, Anna C. Nisi, Nathan Ranc

Correspondence

cwilmers@ucsc.edu

In brief

The COVID-19 pandemic altered human behavior, causing a more than 50% reduction in human mobility. This resulted in mountain lions relaxing their aversion to urban areas. Wilmers et al. reveal that pandemic disease can partially mute the ecological effects of humans, resulting in rapid behavioral changes in wildlife.

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Report

COVID-19 suppression of human mobility releases mountain lions from a landscape of fear

Christopher C. Wilmers,[1,2,*] Anna C. Nisi,[1] and Nathan Ranc[1]
[1]Center for Integrated Spatial Research, Environmental Studies Department, University of California, Santa Cruz, Santa Cruz, CA 95064, USA
[2]Lead contact
*Correspondence: cwilmers@ucsc.edu
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SUMMARY

Humans have outsized effects on ecosystems, in part by initiating trophic cascades that impact all levels of the food chain.[1,2] Theory suggests that disease outbreaks can reverse these impacts by modifying human behavior,[3,4] but this has not yet been tested. The COVID-19 pandemic provided a natural experiment to test whether a virus could subordinate humans to an intermediate link in the trophic chain, releasing a top carnivore from a landscape of fear. Shelter-in-place orders in the Bay Area of California led to a 50% decline in human mobility, which resulted in a relaxation of mountain lion aversion to urban areas. Rapid changes in human mobility thus appear to act quickly on food web functions, suggesting an important pathway by which emerging infectious diseases will impact not only human health but ecosystems as well.

RESULTS

Humans present a substantial source of mortality for many taxa and are especially deadly to large carnivores, killing adults at rates 9 times higher than any of their other predators.[5] As such, humans can initiate trophic cascades,[6] whereby their negative impacts on large carnivore density or behavior lead to positive impacts on the carnivore's prey such as increases in density or changes in habitat use.[1,2] These cascades of alternating negative and positive effects, which often continue to lower trophic levels, can impact public health[7] and reshuffle whole ecosystems.[1,8] While there have been many examples of trophic cascades where humans occupy the top level in the food chain, it is unknown whether humans can be subordinated to intermediate links in trophic cascades by other lifeforms, reversing the sequence of positive and negative effects on ecosystem functions. Theory suggests that infectious agents—if powerful enough to cause widespread disruption in human behavior or numbers—could initiate trophic cascades[3,4] with humans relegated to an intermediate link. Despite regional disease outbreaks (e.g., Ebola) and global pandemics (e.g., COVID-19) impacting human behavior over large spatial scales, however, this has not yet been tested. Here we test whether the coronavirus SARS-CoV-2, which causes the disease COVID-19, can subordinate humans to the second level in a trophic cascade, impacting mountain lion habitat use (Figure 1).

In the Santa Cruz Mountains of California, two distinct types of human development impact large carnivores: urban boundaries where dense residential development meets wildlands and lower density exurban and rural residential development where houses and wildland vegetation intermingle. Mountain lions (*Puma concolor*) are the largest carnivore in this system and the majority of their mortality is caused by humans (Table S1). As such, human threat creates a landscape of fear whereby mountain lions generally avoid human voices[9–11] and habitat close to human infrastructure,[12] resulting in increased energy expenditure by mountain lions,[13] reduced vagility, and smaller home ranges.[14] This landscape of fear also has cascading impacts on mountain lion kill rates of deer,[15] plant architecture,[16] and rodent space use.[17]

On March 17, this region initiated a shelter-in-place order (SIPO) in response to the COVID-19 pandemic. This lockdown drastically changed human behavior, resulting in a more than 50% decline in human mobility as people confined themselves to their homes and reduced driving and walking (Figure 2A). This allowed us to test whether changes in human mobility in response to the COVID-19 pandemic resulted in a relaxation of the landscape of fear on mountain lions (Figure 1).

We placed GPS collars on six animals, whose home ranges encompassed a gradient of land uses from the urban boundary to less developed areas. We modeled mountain lion habitat selection in relation to land use to examine if mountain lions' fear of humans was impacted by changes in human mobility due to COVID-19. The collars recorded location data throughout 2019 and the first 9 months of 2020, allowing us to test whether changes in human mobility associated with the pandemic impacted mountain lion responses to human development. The landscape of fear created by humans was represented in our models by the density of houses on the landscape,[12,14] and by the urban boundary line and those areas within it. Housing density captures the localized, fine-grained impacts of the physical structure of a house and associated human activity around that house, while our urban boundary covariate captures the additional impacts of urban areas such as heightened vehicle and pedestrian traffic. We hypothesized that during the COVID-19-associated lockdown, mountain lions would remain averse to housing density as activity by people in and around their homes persisted, but that they would relax their otherwise

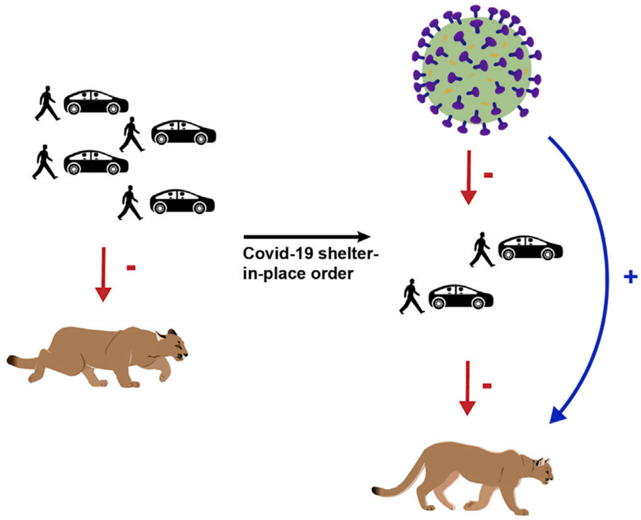

Figure 1. COVID-19 suppression of human mobility releases mountain lions from a landscape of fear

Prior to the COVID-19 pandemic (left half), human mobility elicits a fear response in mountain lions, causing them to strongly avoid urban areas. The emergence of COVID-19 due to the SARS-CoV-2 virus depicted here leads to shelter-in-place orders (SIPOs), which subordinate humans to an intermediate link in this cascade of ecological interactions by reducing human mobility, which in turn relaxes mountain lion aversion to urban areas.

higher aversion to urban areas due to the reduction in people driving and walking.

To test whether changes in human behavior resulting from the COVID-19 pandemic impacted mountain lion habitat selection, we carried out two step-selection analyses[18] (STAR Methods). In the first analysis, we included human mobility (measured as the change in routing requests for driving trips from Apple) as a continuous covariate and asked how human mobility interacted with our housing density and urban boundary covariates to impact mountain lion habitat selection. At pre-SIPO levels of human mobility, mountain lions displayed a strong aversion to the urban edge with their preference for habitat increasing with the distance from the urban edge (Figure 2B). However, at the lowest levels of human mobility during the lockdown, mountain lions' aversion to the urban edge disappeared (Figure 2B). These results were driven by a considerable impact of the interaction between human mobility and the urban edge on mountain lion habitat selection ($\beta = 0.241 \pm 0.165$, $p = 0.008$; Table S2). This effect was greater than that of all natural covariates and surpassed only by the impact of housing density during the daytime ($\beta = -0.504 \pm 0.055$, $p < 0.001$; Table S2).

In order to rule out the possibility of seasonal effects underlying our results, we performed a second analysis in which we divided 2020 into SIPO and non-SIPO periods (Figure 2A) and compared these to results for the same period from 2019. Corroborating our previous analysis, we found that during the SIPO period, mountain lions relaxed their otherwise strong aversion to the urban edge ($\beta = 0.271 \pm 0.201$, $p = 0.038$ during SIPO compared to $\beta = 0.020 \pm 0.292$, $p = 0.917$ outside SIPO; Figures 2C–2E; Table S3). We were also able to rule out seasonal effects as no similar impact was observed over the same temporal window from 2019 ($\beta = 0.211 \pm 0.270$, $p = 0.551$ during SIPO equivalent time period compared to $\beta = 0.022 \pm 0.180$, $p = 0.875$ outside SIPO equivalent time period; Table S3).

DISCUSSION

Our results provide evidence that the drastic change in human behavior due to the COVID-19 pandemic had cascading effects on mountain lion habitat selection. Our results show that humans have been subordinated to the second rather than top level in a trophic cascade or set of behaviorally mediated indirect interactions. Anecdotal evidence of wildlife appearing in cities globally during the COVID-19 pandemic, such as reports of mountain lions walking into downtown Santiago, Chile, or golden jackals foraging in broad daylight in urban Tel Aviv, Israel,[19] provide support for the possible widespread nature of this phenomenon. The indirect effects of COVID-19 on mountain lion habitat selection happened within a time period of days to weeks, indicating rapid behavioral plasticity in both humans and mountain lions. We did not test whether such modifications to landscapes of fear by a virus cascade to trophic levels below mountain lions, but such an impact is likely to depend on the duration of time over which human behavior is altered and whether the impacts at lower trophic levels require a behavioral (faster) or demographic (slower) response.

By taking advantage of the natural experiment provided by the SIPO, this study also highlights the importance of human mobility on the habitat preferences of a large carnivore. The SIPO allowed us to separate the influence of human mobility (e.g., vehicle and pedestrian traffic) from the human footprint (e.g., the locations of houses and roads) on mountain lions, revealing that aside from, and in addition to, humans' static impacts, human mobility itself strongly drives wildlife behavior. Human mobility has increased dramatically over the last century with improvements in vehicle technology, infrastructure, and accessibility. This rise in mobility is likely correlated with an increasing human footprint but has its own unique impacts on animal ecology[20] and requires more research to fully appreciate how it impacts ecosystems independently and in conjunction with the other impacts of humans. As this study reveals, human mobility can change rapidly whereas other types of human impacts on the environment, such as those of the built environment, usually change over much longer timescales. As such, we expect future rapid reversals of human-driven trophic cascades to operate primarily through changes in human mobility.

Subordination of humans to intermediate links in trophic cascades may occur in circumstances other than global pandemics[19,21] such as during regional disease outbreaks that impact human behavior or numbers on a large scale such as occurred in response to the Ebola or Zika viruses in West Africa and Brazil, respectively. As such, our results indicate that regional or global disease outbreaks in humans have the potential to impact not only human health but the ecology of the affected region as well. The timescale of such trophic cascade reversals may be short in many cases as disease outbreaks are controlled by public health measures, but could also persist when such actions fail to control disease spread (e.g., malaria). As emerging infectious diseases such as COVID-19 are expected to increase in the future,[22] the subordination of humans

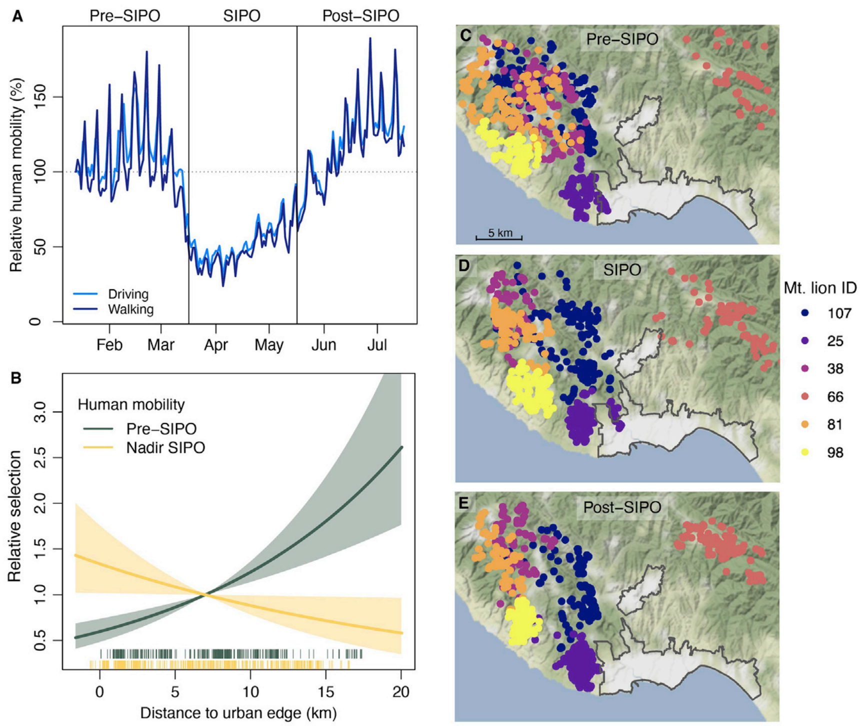

Figure 2. COVID-19 impacts human mobility and mountain lion habitat selection

(A) Human mobility (walking and driving) prior to, during, and after the shelter-in-place order (SIPO). Mobility values are expressed in percentages relative to the values from January 13, 2020.

(B) The impacts of human mobility (measured by driving trips) on mountain lion response to the urban edge (± SE) at pre-SIPO levels of mobility (calculated as mean change in driving trips over the 6 weeks from January 13 to March 1) and at the nadir of mobility during the SIPO (the minimum driving mobility during the SIPO period). Rug plots show housing density at used locations from two 4-week periods corresponding to these pre- and during-SIPO mobility levels: January 13–February 13 and March 17–April 17, 2020.

(C–E) GPS locations of mountain lions during the pre-, during, and post-SIPO periods in relation to urban areas (delineated by the black line).

to intermediate links in trophic cascades and their consequent environmental impacts may become more commonplace.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.06.050.

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AUTHOR CONTRIBUTIONS

C.C.W. conceived of the idea and wrote the paper. A.C.N. performed the analysis and contributed to drafts of the paper. N.R. contributed to the analysis and drafts of the paper.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Data and code	Zenodo: https://zenodo.org/record/4940189#.YMa0bjZKiCg	Zeonodo: https://doi.org/10.5281/zenodo.4940189
Software and algorithms		
Rstudio	R Code Team	https://www.r-project.org/
Survival package	CRAN	https://cran.r-project.org/web/packages/survival/index.html
Raster package	CRAN	https://cran.r-project.org/web/packages/raster/index.html

RESOURCE AVAILABILITY

Lead contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the lead contact, Christopher Wilmers (cwilmers@ucsc.edu)

Materials Availability

This study did not generate new unique reagents.

Data and code availability

The data and code generated during this study are available at Zenodo: https://doi.org/10.5281/zenodo.4940189

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We conducted our study on 6 adult wild pumas (*Puma concolor*) consisting of 4 females and 2 males. We captured pumas using trained hounds or box traps and anaesthetized them with Telazol following Animal Use Protocol WilmC1612 issued by UC Santa Cruz to C. C. Wilmers. Pumas were fitted with GPS Vertex collars produced by Vectronics Aerospace (Vectronics Aerospace GPS Plus, Berlin, Germany) equipped with a remote drop off and were released at the capture site.

METHOD DETAILS

Study Area

We conducted our study in the Santa Cruz Mountains of California. The study area is roughly 2800 km^2 and is bounded to the north by Silicon Valley and the cities of San Francisco and San Jose, to the east and south by farmland, residential development, a major interstate highway, and the city of Santa Cruz, and to the west by the Pacific Ocean. The Santa Cruz Mountains is a fragmented and variegated mosaic containing different levels of human influence, ranging from urban to heterogeneous levels of exurban and rural residential development intermixed with tracts of relatively intact habitat in open space preserves, state and county parks, and undeveloped privately held properties. The study area is comprised of coastal mountains ranging from sea level to 1154 m. Dominant vegetation types consist of coastal chaparral and grassland, oak woodland and redwood. Mountain lions (*Puma concolor*) are the largest carnivore in this system and the majority of their mortality is caused by humans (Table S1). Black-tailed deer (*Odocoileus hemionus columbianus*) are the preferred food item of pumas in this area.[23] For further detail about the study system see Wilmers et al.[12]

Data collection

GPS collars recorded locations every 4 h. Data were retrieved via either an Iridium satellite uplink or direct download from the collar.

QUANTIFICATION AND STATISTICAL ANALYSIS

Resource Selection Analysis

We used step selection functions (SSFs) to quantify puma habitat selection.[18] We used SSFs, a type of resource selection function (RSF) where availability is defined based on observed animal movement behavior,[24] so that we could properly sample available locations from the movement paths of each animal.[25] Specifically, we generated available locations from simulated steps, and contrasted these with observed used points in a conditional logistic regression model.[18] In our analysis, we first excluded non-movement points by filtering out all 4 h GPS locations that were < 20 m from the previous location. With this dataset of movement locations, we generated 20 available locations for each used movement location using the following equations,

$$x_t = x_{t-1} + D_{t,} * \cos(\theta t)$$

$$y_t = y_{t-1} + D_t * \sin(\theta t)$$

where ($\boldsymbol{x_t}$, $\boldsymbol{y_t}$) are the longitude and latitude locations of each point at time t, $\boldsymbol{D}$ is a vector of step distances, and θ is a vector of turning angles. For each puma, step distances were randomly drawn from empirical distributions of the step lengths of other individuals of the same sex,[18] and turning angles were drawn from a $[0, 2\pi]$ circular uniform distribution.[25] The relative probability of use, $w(\boldsymbol{x})$, takes the exponential form, $w(\boldsymbol{x}) = \exp(\beta \boldsymbol{x})$. In this equation, $\boldsymbol{x}$ is a vector of covariates associated with each GPS location. We estimated covariate effects (β) using conditional logistic regression through the *clogit* function from the *survival* package[26] in R.

Our central question was whether changes in human behavior during the COVID-19 pandemic impacted how pumas responded to human landscape features. As such we fit models that included interactions between anthropogenic covariates and two metrics of human behavior - human travel behavior (continuous covariate) and shelter-in-place order periods (SIPO; categorical covariate). We first considered human travel behavior, which changed drastically over January-August 2020 with the onset of the COVID-19 pandemic and the SIPO order. Continuous travel data for Santa Cruz County were obtained from Apple mobility trends data[27] Jan 16 2020 – July 17 2020, which shows the percent relative daily routing requests of people driving compared to January 13th 2020. Both driving and walking data were available but were tightly correlated (shown in Figure 2A), so only driving data was modeled for our analysis. We then fit models with defined discrete periods of time based on public health policy for Santa Cruz County – pre-SIPO (January 16- March 16), during SIPO (March 17 - May 17), and post-SIPO (May 18 - August 17). Note that severe wildfires burned in Santa Cruz and San Mateo Counties in August 2020, so we truncated the post-SIPO data to before the fires started.

The anthropogenic covariates considered were (i) housing density and (ii) distance to urban edge. Housing density has been shown to be an important driver of puma movement in our study system,[12,14] and impacts movement differently between the day and night (unpublished data). We calculated housing density using Epanechnikov kernels with a 150 m radius [in houses per sq.km], which is the scale at which housing most strongly impacts puma movement.[12] Housing density was cube root transformed to improve normality and was always interacted with day/night to account for diel behavioral differences. The urban edge was defined by urban service area boundaries for Santa Clara,[28] and Santa Cruz Counties,[29] and city boundaries for San Mateo County.[30] Distance to the urban edge was calculated by computing the Euclidian distance [in m] between each GPS location to the nearest urban edge, with locations inside of urban areas assigned negative distances from the urban edge.

We analyzed the data in two steps. First, we considered whether any changes observed across SIPO periods could be explained by human travel behavior. Using the travel data described above, we fit models that contained interactions between our two anthropogenic covariates, housing density and urban edge, with change in driving trips. For these models only data in 2020 were considered, as travel data from Apple was only available after 1/13/2020. The models we considered were: 1) housing density; 2) housing density and distance to urban edge; 3) housing density and distance to urban edge interacted with travel; and 4) housing density interacted with travel and distance to urban edge interacted with travel, and we performed model selection using Quasi Information Criteria (QIC). We report all models (Tables S2 and S3) and based our inferences in the main text on the best fitting model. In all models, we also included topographic and landscape covariates that previous analyses have shown to be important for puma habitat selection in the Santa Cruz Mountains.[12,14,31,32] Specifically, we included topographic slope, topographic position index (TPI, indicating whether a point is mid-slope or on a valley or ridge), the interaction between slope and TPI, distance to nearest perennial river or stream (National Hydrography Dataset, USGS available at https://www.usgs.gov/core-science-systems/ngp/national-hydrography), and percent vegetation cover. Percent cover was calculated from California GAP data (Gap Analysis Project, USGS available at https://www.usgs.gov/core-science-systems/science-analytics-and-synthesis/gap) using a focal analysis over a 90 m x 90 m window using the *raster* package in R available at https://CRAN.R-project.org/package=raster.

We also included step distance (log transformed) and directional persistence ($\cos[\theta_t - \theta_{t-1}]$, with $\theta_t - \theta_{t-1}$ representing the change in cardinal direction across the two previous steps), as has been recommended in previous studies.[25,33] All covariates were standardized, and we used generalized estimating equations (GEE) for robust standard error estimation.[34] For GEE, each puma was treated as a separate cluster. We checked for potential collinearity using Pearson's correlations, and all pairs of covariates had $|r| < 0.4$.

Second, we considered a discrete characterization of the SIPO to control for potential seasonal variation in puma movement behavior. We fit separate models for 2019 and 2020 that included housing density and distance to urban edge. We chose to compare 2020 with 2019, rather than all previous years for which we have mountain lion monitoring data, because we wanted to restrict our analysis to a consistent sample of individuals (i.e., the same cats monitored in 2019-2020). This analysis design controls for the confounding effects linked to sample composition (individual identity, age, sex). We then used model selection to see whether interactions with distance to urban edge and the SIPO periods (non-SIPO and during SIPO) improved model fit in each year, by fitting two models: 1) with no interaction between distance to urban edge and SIPO period and 2) including that interaction. If puma response to the urban edge was a result of the SIPO and not a result of seasonal change, we would expect to see significant differences between SIPO periods during 2020, but not for the corresponding periods in 2019.