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RESEARCH

Illuminated landscapes: urbanization's influence on predator and prey behavior

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Abstract
Urban development and habitat fragmentation have reshaped ecosystems across North America, creating heavily modified landscapes characterized by dense human populations, built infrastructure, and widespread artificial light and noise pollution. Yet the specific components of urbanization that alter wildlife spatiotemporal activity remain insufficiently understood, particularly across gradients of human disturbance. Using data from 61 camera trap stations in two contrasting urban landscapes in California, USA, we examined the influence of multiple anthropogenic factors on the diel activity of an apex predator (puma, *Puma concolor*), a mesocarnivore (bobcat, *Lynx rufus*), and an ungulate prey species (mule deer, *Odocoileus hemionus*). We quantified the effects of artificial light at night (ALAN), proximity to noise pollution, moonlight intensity, and co-occurring wildlife on nighttime habitat use. General Linear Mixed Models revealed species-specific responses to these urban stressors. Pumas and bobcats were less active in areas with more ALAN. Pumas also avoided areas of high human use but were more active where mule deer were present. In contrast, mule deer increased nighttime activity in artificially illuminated areas while avoiding noise and bright moonlight, consistent with predictions under the human shield hypothesis. Our findings highlight ALAN as a major driver of wildlife behavior at the urban edge, interacting with sensory conditions and human disturbance to restructure predator-prey dynamics. As human activity increasingly extends into nighttime hours, overlapping with wildlife, targeted management strategies, integrating artificial light mitigation with public education, may help reduce human-wildlife conflicts.

Keywords Artificial light · California · Camera trap · Noise pollution · Puma concolor · Urban edge

Introduction

Urban growth is one of the most pervasive land-use changes globally, reshaping ecosystems and wildlife habitats at an accelerating pace. Although the urban-wildland interface occupies less than 5% of the Earth's surface, it supports nearly half of the world's human population (Schug et al. 2023). Globally, approximately 72% of Earth's land surface is now dedicated for human use (IPCC 2020) with an estimated 32% of all land cover transformed between 1960 and 2019 (Winkler et al. 2021). Projections suggest that urban land cover will reach 1.2 million km² by 2030 (Seto et al. 2012), further intensifying habitat loss, fragmentation, and ecological degradation (Liu et al. 2016; Williams et al. 2020). In the United States, much of this expansion is driven by low-density suburban and exurban growth (Radeloff et al. 2005; World Bank 2024; US Census Bureau 2025), which replaces wildlands with road infrastructure, traffic, and noise (Benítez-López et al. 2010). This encroachment can alter wildlife behavior and habitat use as well as temporal activity patterns (Gallo et al. 2022), though responses may vary with species or guild. Some generalist species may exploit anthropogenic resources (Murray et al. 2016), and small carnivores and mesocarnivores may even do well in fragmented habitat (Tigas et al. 2003; Young et al. 2019). For specialists and large carnivores, some may persist in highly fragmented habitat (e.g., Wang et al. 2024), but many often decline as habitat becomes increasingly fragmented (Gagné et al. 2016; Santini et al. 2019).

Pressures stemming from land-use change are especially pronounced in California, United States, where contrasting

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urbanization trajectories (i.e., urban vs. urban-rural) create distinct ecological contexts for wildlife (Ordenana et al. 2010; Riley et al. 2003). In Southern CA, Orange County's outward sprawl has produced highly fragmented habitat for medium to large-bodied mammals, extensive edge conditions, and widespread light and noise pollution (Barrientos et al. 2023; Vickers et al. 2015). In contrast, the San Francisco Bay Area's emphasis on infill development has constrained outward expansion, preserving larger and connected open-space networks but increasing human presence along their boundaries (Thorne et al. 2013; Greeninfo Network 2022). Orange County is now one of the state's most densely developed landscapes characterized by severely fragmented forest habitat patches, whereas San Mateo County retains lower-density development, lower traffic volumes, and more contiguous networks of forested land in county, state, watershed districts, and National Park Service land (Thorne et al. 2013; Greeninfo Network 2022). These contrasting models of urban growth have generated distinct disturbance dynamics, including variation in human population and building densities and traffic volume that can influence how carnivores and their prey adjust behaviorally across urban-wildland interfaces (Ordeñana et al. 2010).

Despite substantial research on the effects of urbanization on wildlife (e.g., Lewis et al. 2015; Magle et al. 2021; Maurer et al. 2022; Stoner et al. 2023; Granados et al. 2024), the specific mechanisms underlying behavioral shifts such as changes in diurnal-nocturnal activity patterns, modified habitat use, or altered foraging behavior, remain poorly understood, particularly with respect to the sensory pathways through which artificial light at night (ALAN) and noise pollution operate. Sensory pollutants can create predator-free space, allowing prey that may benefit from irrigated vegetation and reduced hunting pressure, to exploit illuminated or noisy environments avoided by predators (Ciach and Fröhlich 2019; Ditmer et al. 2021; Fisher et al. 2023; Shannon et al. 2014; Smith et al. 2017). This is consistent with predictions under the human shield hypothesis where predators avoid human-dominated areas, while prey select those areas to avoid predators (Berger 2007). However, these dynamics vary widely across species and landscapes. Predators may be less able to adapt where fragmentation increases the likelihood of encounters with people in developed areas, elevating the risk of human-wildlife conflict and mortality (Stoner et al. 2023). Even protected areas now experience ALAN levels far above historical baselines (Kyba et al. 2017; Seymoure et al. 2019), contributing to the functional fragmentation of terrestrial mammal ranges across North America (Ditmer et al. 2021). This can lead to changes in animal behavior as ALAN can increase prey detectability by visual predators (Hoffman et al. 2022), altering movement and animal foraging behavior (Beier 2006), or drive selection for darker areas (Sunde et al. 2024). Meanwhile, noise from transportation and recreation can modify animal behavior by increasing prey vigilance and anti-predator responses (Zeller et al. 2024), causing some species to avoid noisy environments (Collins et al. 2022; Fisher et al. 2023). Alternatively, areas with lower traffic volumes and reduced human activity may be perceived as less risky to wildlife, allowing some species to more freely use these habitats (Whittington et al. 2019), particularly at night when human activity is reduced (Kautz et al. 2021). In other cases, species may become habituated to noisy environments, which can increase vehicle collision risk as vigilance or flight responses diminish (Bowles 2013).

Urbanization reshapes species interactions through habitat loss and by altering diel activity patterns and predator-prey overlap (Ditchkoff et al. 2006; Lowry et al. 2013). Although spatial and dietary adjustments are common responses to anthropogenic activity (Rogala et al. 2011; Kays et al. 2017; Larson et al. 2020; Lewis et al. 2021; Granados et al. 2024; Bolas et al. 2025), temporal shifts may be especially important where fragmentation and barriers limit spatial flexibility. For example, many mammal species increase nocturnality to avoid humans (Gaynor et al. 2018; Burton et al. 2024), even when home range size or spatial use shows limited change (Granados et al. 2023). Fragmentation can also promote more diurnal activity (Norris et al. 2010; Barrueto et al. 2014; Gallo et al. 2022), heightening the potential for conflicts with people (Naha et al. 2016).

Comparing wildlife responses across multiple anthropogenic gradients can reveal which aspects of urbanization most strongly influence behavior. This is particularly important for pumas (*Puma concolor*) in California, where they are the only remaining apex predator across much of their range and they increasingly occupy urbanized landscapes due to ongoing habitat fragmentation. Changes in the activity of pumas could have consequences for interacting species, including their prey, mule deer (*Odocoileus hemionus*) and co-occurring mesocarnivores, such as bobcats (*Lynx rufus*) (Pierce et al. 2000; Lewis et al. 2015). While human disturbance is known to affect wildlife across trophic levels (Granados et al. 2023; Burton et al. 2024), our understanding of its influence on diel activity across contrasting development contexts remains limited. We compared the site use and temporal activity of pumas, bobcats, and mule deer between two regions with similar ecosystems but contrasting development intensity: San Mateo County on CA's central coast and Orange County (OC), in Southern CA. Orange County is densely populated (1520 people/km^2), and dominated by suburban development (Vickers et al. 2015), whereas San Mateo County has a lower population density (622 people/km^2; US Census Bureau 2023; World Population Review 2025) and a more connected mosaic network of open space preserves and coastal-montane habitats. We were specifically interested in identifying anthropogenic and habitat-related factors influencing overall site use of our focal species, as well as evaluating whether the effects of human-related variables on nocturnal activity varied between our study regions. Finally, we quantified temporal activity overlap between regions and characterized diel activity patterns for each species to assess whether differences in anthropogenic landscape disturbance explain regional variation in temporal animal behavior.

Felid vision is highly adapted to low-light conditions, supporting a predominantly nocturnal hunting strategy (Tamura et al. 1989; Olliver et al. 2004). Given this sensitivity to light, we predicted that puma detections would be particularly responsive to sensory pollutants (i.e., noise and light), especially ALAN (Ditmer et al. 2021), and that responses to moonlight would vary with the degree of urbanization (Wereszczuk and Zalewski 2023). We further expected pumas to avoid brighter and more heavily disturbed areas, and anticipated greater overall nocturnality in Orange County due to higher human density (Gaynor et al. 2018; Burton et al. 2024). Bobcats are typically crepuscular hunters that also rely on low-light conditions, so we anticipated reduced detections in brightly illuminated habitats within more urbanized areas (Lombardi et al. 2017). For mule deer, we expected higher detections in moderately illuminated areas where predator presence may be relatively lower, but reduced deer use of the brightest zones, which are often associated with greater human disturbance, despite offering high-quality irrigated or cultivated forage (Ditmer et al. 2021, 2023).

Methods

Study area

Wildlife data for this study came from two long-term monitoring projects in San Mateo County (1,178.4 km^2 land area) and Orange County (OC, 2,053.31 km^2), California, United States. San Mateo County (centroid: 37.381238°; −122.334825°) lies along the central California coast within the greater San Francisco Bay Area whereas OC (centroid: 33.783139°; −117.859018°) is approximately 550 km to the south in coastal Southern California (Fig. 1). Vegetation in San Mateo is dominated by grasslands, evergreen and deciduous woodlands, conifers, and shrubland; Orange County is characterized by grasslands, coastal sage scrub, chaparral, and oak woodland (Buck-Diaz and Evens 2015).

Both counties are similar in climate and mammal assemblages (Jameson and Peeters 2004), but vary in the extent of anthropogenic disturbance (Table S1, Figs. S1, S2). OC has experienced rapid, high density suburban development within an arid, coastal landscape, creating irrigated neighborhoods within an extensive urban matrix. In contrast, San Mateo County on California's Central Coast has patchier development interspersed with protected open spaces (Greeninfo Network 2022). Together, these counties provide a natural experiment for understanding how different types of urban growth affect wide-ranging carnivores at the urban edge. Approximately 59% of OC land is classified as developed, and is dominated by residential, commercial-industrial zones, transportation corridors, and other urban infrastructure (Rice et al. 2017) compared to 32% urbanized land in San Mateo County (Sustainable San Mateo County 2016; US Geological Survey 2024). Our sampling areas in OC, OC Parks and Irvine Ranch Open Space Conservancy open spaces, cover roughly 250 km^2 and exist within a highly urbanized landscape (OC Parks 2025). Protected habitat patches of ≥ 3 km^2 or more, the minimum area of habitat patch more likely to be used by pumas (Stoner et al. 2023) are more extensive in OC (OC: 25.8% of land, 531.4 km^2) than in San Mateo (372.8 km^2, 31.6%) (Greeninfo Network 2022). Road density is comparable across regions (OC: 0.90 km/km^2; San Mateo: 0.95 km/km^2; U.S. Census Bureau 2021; Table S1). While both regions share similar growing-season lengths, San Mateo County receives substantially more annual precipitation (Redwood City: averages 438 mm/year) than Orange County (Irvine, OC: 332 mm/year; US Climate Data 2025).

Data collection

We used camera traps to monitor spatial and temporal puma, bobcat, and mule deer activity across 61 sampling points in Orange and San Mateo counties from January 1, 2022 through December 31, 2024. Sampling focused on two biologically relevant seasons as defined by seasonal differences in rainfall patterns: winter (December to March) and summer months (June to September). Camera deployments spanned a range of public jurisdictions, including California State Parks, federal lands (Golden Gate National Recreation Area managed by the National Park Service), municipal land and watersheds, and county park systems (Table 1).

San Mateo County cameras were part of the Bay Area Puma Project's (bapp.org) long-term monitoring network, initiated in 2007 to collect wild felid data across the multiple counties in the San Francisco Bay Area (Santa Clara, Alameda, Contra Costa, Solano, Sonoma, Marin, Santa Cruz, and San Mateo) (Stoner et al. 2023). In OC, we used data from 22 cameras, deployed and maintained by the Irvine Ranch Conservancy (IRC) and OC Parks as part of ongoing efforts to monitor wildlife and human activity in IRC open spaces (i.e., Fremont Canyon, Black Star Ranch, Whiting

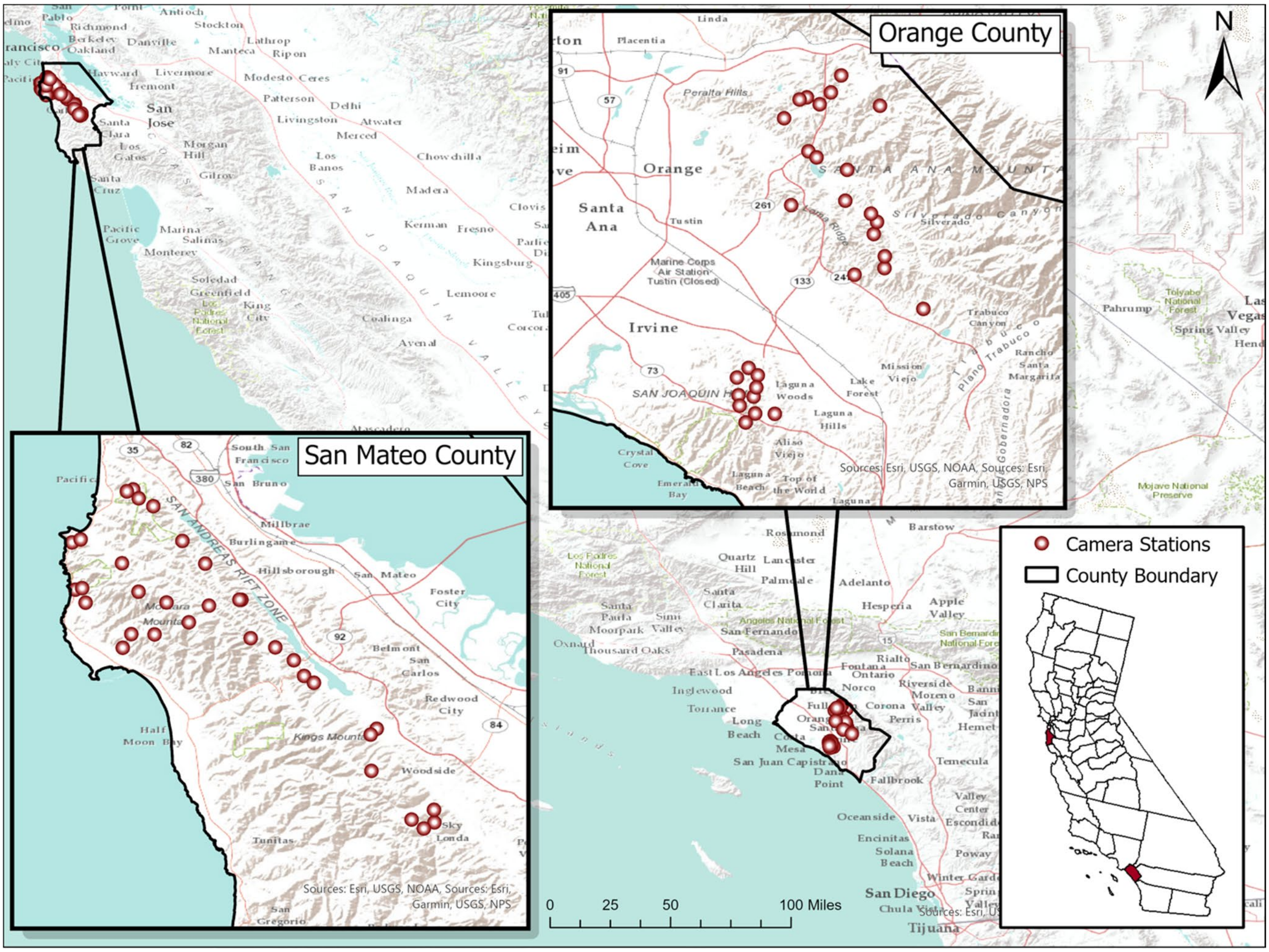

Fig. 1 Camera trap stations used in this study in San Mateo County and Orange County, California, USA 2022 to 2024

Table 1 Camera trap sampling effort in protected areas and open spaces in San Mateo and Orange counties

County	Open space/protected area	Land agency	Open space size (km^2)	Types of human activity permitted	Number of camera stations	Camera days
Orange	Irvine Ranch Conservancy	Irvine Ranch Conservancy	6.07	hiking	19	14,301
	Laguna Coast Wilderness Park	OC Parks	28.33	hiking	10	905
San Mateo	Sweeney Ridge	Golden Gate National Recreation Area (GGNRA)	11.09	Hiking, cycling	2	1,236
	Rancho Corral de Tierra	GGNRA	15.61	Hiking, cycling	4	2,920
	Huddart County Park	San Mateo County Parks	3.80	Hiking, horseback	1	183
	SFPUC	San Francisco Public Utilities Commission	80.8	Hiking	14	9,330
	Pedro Point Headlands	Pacifica Land Trust	0.96	Hiking, cycling	2	990
	Wunderlich County Park	San Mateo County Parks	3.81	Hiking	4	1,826
	Montara State Beach	CA State Parks	37.55	Hiking, cycling	2	1,246
	San Pedro Valley County Park	San Mateo County Parks	4.62	Hiking, horseback	1	1,141
	SF Archer Range	San Francisco Archers	1.65	Archery	2	1,338

Ranch, Santiago Oaks, Laguna Coast Wilderness Park). In late 2023, the Bay Area Puma Project added six cameras to sample additional locations in OC Parks and IRC.

Cameras (Reconyx Hyperfire HF2 and Bushnell Trophy brands) were deployed at approximately 1 m height above the ground along wildlife and designated multi-use trails in county, federal, and state park lands. Each camera station consisted of a single camera, and no visual or olfactory attractants were used. Stations were spaced at least 500 m apart, and locations were selected based on habitat suitability, evidence of prey species, and prior puma detection history (Coon et al. 2020; Stoner et al. 2023; Granados et al. 2024). Sampling effort ranged from 61 to 366 days per camera, totaling 35,416 trap days (Table 1).

Camera trap images were annotated by IRC and Felidae Conservation Fund personnel and volunteers. For Felidae cameras, images were processed using WildePod (wildepod.org), a cloud-based image platform that incorporates MegaDetector, an AI model that identifies humans, animals, and vehicles, while removing images from false triggers (Beery et al. 2019; Microsoft 2020; Fennell et al. 2022). All AI-generated classifications were reviewed and confirmed by trained volunteers. Images containing people were deleted immediately after being processed.

Data analysis

We first processed raw species detection histories for pumas, bobcats, mule deer, and humans to determine independent events using a 30-minute independence threshold, minimizing double-counting of individuals (O'Brien et al. 2003; Gerber et al. 2010). Wildlife detections were used to model species responses to our covariates of interest, whereas human detections were incorporated as predictor variables, as described below.

Influence of anthropogenic and environmental covariates on overall site use

We sought to characterize broad patterns in species detections across our study area and assess how anthropogenic and environmental predictors influenced monthly detections using Bayesian Generalized Linear Mixed Models (GLMMs). Species were modeled separately, with the response variable defined as the number of independent detections per month at each station. Thus, for each camera station, each month was treated as a separate data point in our models. Covariates included in data analyses are listed in Table 2. Anthropogenic covariates included human activity (detections per 100 camera days), mean ALAN within 500 m of each station (nW/cm^2/sr, Elvidge et al. 2021) distance to the nearest urban area (km, Caltrans 2020; US Geological Survey 2024), and distance to noise-polluted areas (km), defined as locations ≥ 45 dBA threshold (Bureau of Transportation Statistics 2025). Environmental covariates included habitat type (hardwood woodland, herbaceous ground cover, forest, shrub; California Department of Forestry and Fire Protection 2025), terrain ruggedness index (TRI), and mean monthly moonlight intensity (lux) (Śmielak 2023). To examine trophic relationships, mule deer detection rate (per 100 camera days) was included as a predictor in puma models. For bobcats, puma detection rate was included instead of mule deer to test whether bobcats avoided areas frequented by pumas. Pumas are known to prey on bobcats, and bobcat avoidance of pumas has been documented (Hass 2009; LaBarge et al. 2022). In mule deer models, puma detection rate was included to test for potential predator avoidance responses (Pierce et al. 2004).

Table 2 Covariates tested in our Generalized Linear Mixed Models (GLMMs) to explore the influence on wildlife site use

Category	Covariate	Details	Data source
Small-scale human activity	Detections of human activity	Pooled detection rate of hikers, cyclists, or people on horseback based on independent detections per month.	Camera trap data
Landscape disturbance	Urban	Distance to nearest urban center (km)	Caltrans 2020; US Geological Survey 2024
	Light pollution	Mean light pollution per year within a 500 m buffer around each camera station (nW/cm^2/sr)	Elvidge et al. 2021
	Noise Pollution	Distance (km) to noise pollution (dBA) zone from each camera trap station	Bureau of Transportation Statistics
Habitat & Environment	Vegetation/ Habitat type	Categorical variable describing California Vegetation by Wildlife Habitat Relationship at each camera station (hardwood woodland, herbaceous ground cover. Forest, or shrub)	California Dept of Forestry and Fire Protection 2025
	Terrain ruggedness Index (TRI)	An Index of topographic heterogeneity from Digital Elevation raster layer at each camera trap station	Digital Elevation Model, ArcGIS Pro v 2.5
	Moonlight intensity (lux)	Mean predicted lunar intensity (lux) for each camera trap station relative to an average full moon based on the coordinates and date and time, and lunar phase in that location.	Śmielak 2023
Sampling effort	Camera days	Number of days each camera trap station was active	Camera trap data

Continuous covariates (species detection rates, moonlight intensity, distance to urban areas) were standardized to have a mean of 0 and standard deviation of 1. A negative binomial error structure was used for improved model convergence relative to a Poisson distribution and to account for overdispersion in GLMMs. Sampling effort (camera days) was accounted for by including the number of sampling days per station as a log offset. Camera station ID and year were included as random intercepts. To reduce influence from extreme predictor values, outliers were removed using boxplot visualization and the *rstatix* package in R, prior to analysis (Kassambara 2023). Specifically, three outliers for species detections were excluded for the mule deer model and two were excluded from the puma model.

Models were fit in R using *brms* with 3 chains, a burn-in length of 5,000, 30,000 iterations, and a thinning interval of 5 (Bürkner m2017; R Core Team 2024). We used non-informative priors with a uniform distribution for covariates. Collinearity was evaluated using the Variance Inflation Factor (VIF) (VIF < 5 considered acceptable; Lüdecke et al. 2020; Kuhn et al. 2022). Model convergence was assessed using R-hat values of 1.1 (Gelman and Hill 2006) and by visual inspection of posterior distributions using the *bayesplot* package (Gabry and Mahr 2025). Model estimate plots were also generated with *bayesplot* (Gabry and Mahr 2025).

Model structure is shown below:

Puma

$$\begin{gathered}
Overall\ detections = \beta_1 * TRI_1 \beta_2 * LightPollution_i \\
+\beta_3 * NoisePollution_i + \beta_4 * MuleDeerDetRate + \beta_5 * County \\
+\beta_6 * HabitatType + \beta_7 * HumanActivityDetRate \\
+\beta_8 * MoonIntensity + \beta_9 * Dis\tan ceUrban + \varepsilon cameraStationj_j + \varepsilon year_j
\end{gathered}$$

Bobcat

$$\begin{gathered}
Overall\ detections = \beta_1 * TRI + \beta_2 * LightPollution_i + \beta_3 * NoisePollution_i \\
+\beta_5 * County + \beta_6 * HabitatType + \beta_7 * HumanActivityDetRate \\
+\beta_8 * MoonIntensity + \beta_9 * Dis\tan ceUrban \\
+\beta_{10} * PumaDetRate + \varepsilon cameraStationj_j + \varepsilon year_j
\end{gathered}$$

Mule deer

$$\begin{gathered}
Overall\ detections = \beta_1 * TRI_i + \beta_2 * LightPollution_i \\
+\beta_3 * NoisePollution_i + \beta_5 * County + \beta_6 * HabitatType \\
+\beta_7 * HumanActivityDetRate + \beta_8 * MoonIntensity \\
+\beta_9 * Dis\tan ceUrban + \beta_{10} * PumaDetRate + \varepsilon cameraStationj_j + \varepsilon year_j
\end{gathered}$$

where β represents the beta coefficient for each predictor variable and $\mathcal{E}$ denotes the random effect for camera array.

Influence of anthropogenic and environmental covariates on nocturnal detections

Human disturbance can drive some species to shift their activity toward nighttime hours as a strategy to reduce predation risk from people or predators (Gaynor et al. 2018; Burton et al. 2024). To evaluate wildlife responses to varying degrees of disturbance across study areas and the influence of human disturbance on activity during this diel period, we classified independent detections as diurnal, crepuscular, or nocturnal, based on trigger timestamps relative to sunrise and sunset, accounting for seasonal variation in daylight (Theuerkauf et al. 2003; Ross et al. 2013; Caravaggi et al. 2018). This classification allowed us to assess how anthropogenic factors influenced nighttime activity and how these effects varied between counties. Diurnal detections occurred between 1 h after sunrise and 1 h before sunset. Crepuscular detections were defined as the hour before sunrise and the hour after sunset (Theuerkauf et al. 2003; Ross et al. 2013; Caravaggi et al. 2018). Finally, nocturnal detections took place between 1 h after sunset and 1 h before sunrise (Theuerkauf et al. 2003; Ross et al. 2013; Caravaggi et al. 2018).

We tested the influence of several covariates listed in Table 2. As our site use models indicated that artificial light could have an important influence on overall activity, we dove deeper into this to see how light (moonlight and artificial) affected detections at night. Unlike models for overall site use, here, we included interaction terms between County and Light Pollution, as well as between Moonlight and Distance to Urban Areas, to better assess context-dependent effects of natural and artificial illumination on nocturnal activity. These interaction terms allowed us to test for differences in species responses to ALAN between counties and whether the effects of moonlight varied with proximity to urban areas. For nocturnal models, habitat type was simplified to binary covariate: open (herbaceous or shrubland) vs. closed habitat (woodland or forest) to capture broad structural differences relevant to visibility and predator-prey dynamics.

Model structure is shown below:

Puma

$$\begin{gathered}
Nocturnal\ detections = \beta_2 * LightPollution_i \times \beta_5 * County \\
+\beta_3 * NoisePollution_i + \beta_4 * MuleDeerDetRate \\
+\beta_6 * HabitatType + \beta_7 * HumanActivityDetRate \\
+\beta_8 * MoonIntensity \times \beta_9 * Dis\tan ceUrban + \varepsilon cameraStationj_j + \varepsilon year
\end{gathered}$$

Bobcat

$$\begin{gathered}
Nocturnal\ detections = \beta_2 * LightPollution_i \times \beta_5 * County \\
+\beta_3 * NoisePollution_i + \beta_4 * MuleDeerDetRate + \beta_6 * HabitatType \\
+\beta_7 * HumanActivityDetRate + \beta_8 * MoonIntensity \times \beta_9 * Dis\tan ceUrban \\
+\beta_{10} * PumaDetRate + \varepsilon cameraStationj_j + \varepsilon year_j
\end{gathered}$$

Mule deer

$$\begin{gathered}
Nocturnal\ detections = \beta_2 * LightPollution_i \times \beta_5 * County \\
+\beta_3 * NoisePollution_i + \beta_6 * HabitatType \\
+\beta_7 * HumanActivityDetRate + \beta_8 * MoonIntensity \\
\times \beta_9 * Dis\tan ceUrban + \beta_{10} * PumaDetRate + \varepsilon cameraStationj_j + \varepsilon year_i
\end{gathered}$$

As with the site use models, camera station and year were included as random intercepts. For the nocturnal models, we excluded outliers to minimize the influence of extreme predictor values, using boxplot visualization and the *rstatix* package in R (Kassambara 2023). This resulted in the exclusion of four outliers for species detections from the mule deer model, three from the bobcat model, and five from the puma model. In both model categories (i.e., site use and nocturnal models), we interpreted 80% credible intervals (CI) as indicators of weaker evidence of an effect on the response variable, whereas 95% CIs that did not overlap zero were interpreted as strong evidence of an effect (Kéry and Royle 2020).

Diel activity patterns between study areas

We used trigger timestamps from independent detections to compare temporal activity curves for each species, as well as for humans, between counties. Date and time stamps were converted to radians to generate kernel density curves from all independent detections for each species (Ridout and Linkie 2009). Because many camera stations recorded > 75 puma detections, we used the overlap estimator Δ_4 for wildlife activity overlap (Lashley et al. 2018). We used the Mardia Watson-Wheeler (MWW) two-sample test (Batschelet 1981) to identify significant differences in activity distributions between counties using the R package *circular* (Indestege et al. 2025; Lund et al. 2017). Activity curves and overlap coefficients were generated using the *overlap* package in R (Meredith and Ridout 2016).

All statistical analyses were conducted in R v. 2024. 4.3.3 (R Core Team 2024).

Results

Species detections within counties

Most puma detections (64.5%) occurred in San Mateo County. Within each county, pumas were mainly detected at night (OC: 55.8%, San Mateo: 47.8%, Table 3). Bobcat detections were distributed across nocturnal and diurnal periods in both counties (> 33% in each period), similar to mule deer, although nocturnal mule deer detections were lower in OC (25.4%) (Table 3). As expected, human activity was mainly diurnal in both regions (Fig. 2).

Influence of anthropogenic and environmental covariates on overall site use

Pumas and bobcats showed stronger negative responses to anthropogenic factors than mule deer did (Fig. 3; Table S2). For pumas, detections decreased with ALAN (estimate: −1.10, 95% credible interval (CI): −2.06, −0.17) and showed a weak positive association with moonlight intensity (estimate: 0.09, 80% CI: 0.01, 0.17). Habitat effects were modest as detections were greater in hardwood woodland relative to forest (estimate: 1.09, 80% CI: 0.04, 2.13) and lower in herbaceous habitat (estimate: −2.03, 80% CI: −3.96, −0.15).

Table 3 Number and percentage of detections in each county for species of interest occurring in different time periods. OC = Orange County

Species	Time period	Number of detections		Percent of detections	
		San Mateo County	OC	San Mateo County	OC
Puma	Crepuscular	156	123	17.5	25.1
	Diurnal	308	97	34.6	19
	Nocturnal	425	269	47.8	55.8
	Total	889	489		
Bobcat	Crepuscular	175	64	16.7	16.9
	Diurnal	519	154	49.7	40.8
	Nocturnal	351	159	33.5	42.1
	Total	1045	377		
Mule deer	Crepuscular	156	377	14.5	18.5
	Diurnal	472	1143	43.9	56.1
	Nocturnal	447	517	41.6	25.4
	Total	1075	2037		
Human activity	Crepuscular	2284	1342	14.5	18.5
	Diurnal	8329	6917	43.9	56.1
	Nocturnal	4359	1815	41.6	25.4
	Total	14,972	10,074		

For bobcats, detections were negatively associated with artificially illuminated areas (estimate: −1.11, 95% CI: −1.98, −0.28), and with distance to urban areas (estimate: −1.19, 95% CI: −2.03, −0.42). Bobcat detections also showed a positive association with human activity at camera stations (estimate: 0.31, 95% CI: 0.12, 0.50).

For mule deer, detections increased with distance from urban areas (estimate: 0.83, 95% CI: 0.16, 1.54) and decreased with brighter moonlight (estimate: −0.19, 95% CI: −0.34, −0.04). Mule deer also showed a weak positive association with both human activity (estimate: 0.11, 80% CI: 0.01, 0.22) and puma detection rates (estimate: 0.13, 80% CI: 0.02, 0.23).

Influence of anthropogenic and environmental covariates on nocturnal detections

We next examined how ALAN and moonlight influenced nocturnal activity across species and between counties. For pumas, nighttime detections decreased with ALAN (estimate: −1.45, 95% CI: −2.85, −0.08; Table S3), mirroring patterns observed in overall site use. Nocturnal puma detections did not strongly differ between counties (estimate: 0.46, 95% CI: −0.82, 1.79; Fig. 4). Although detections in San Mateo County appeared to increase at higher

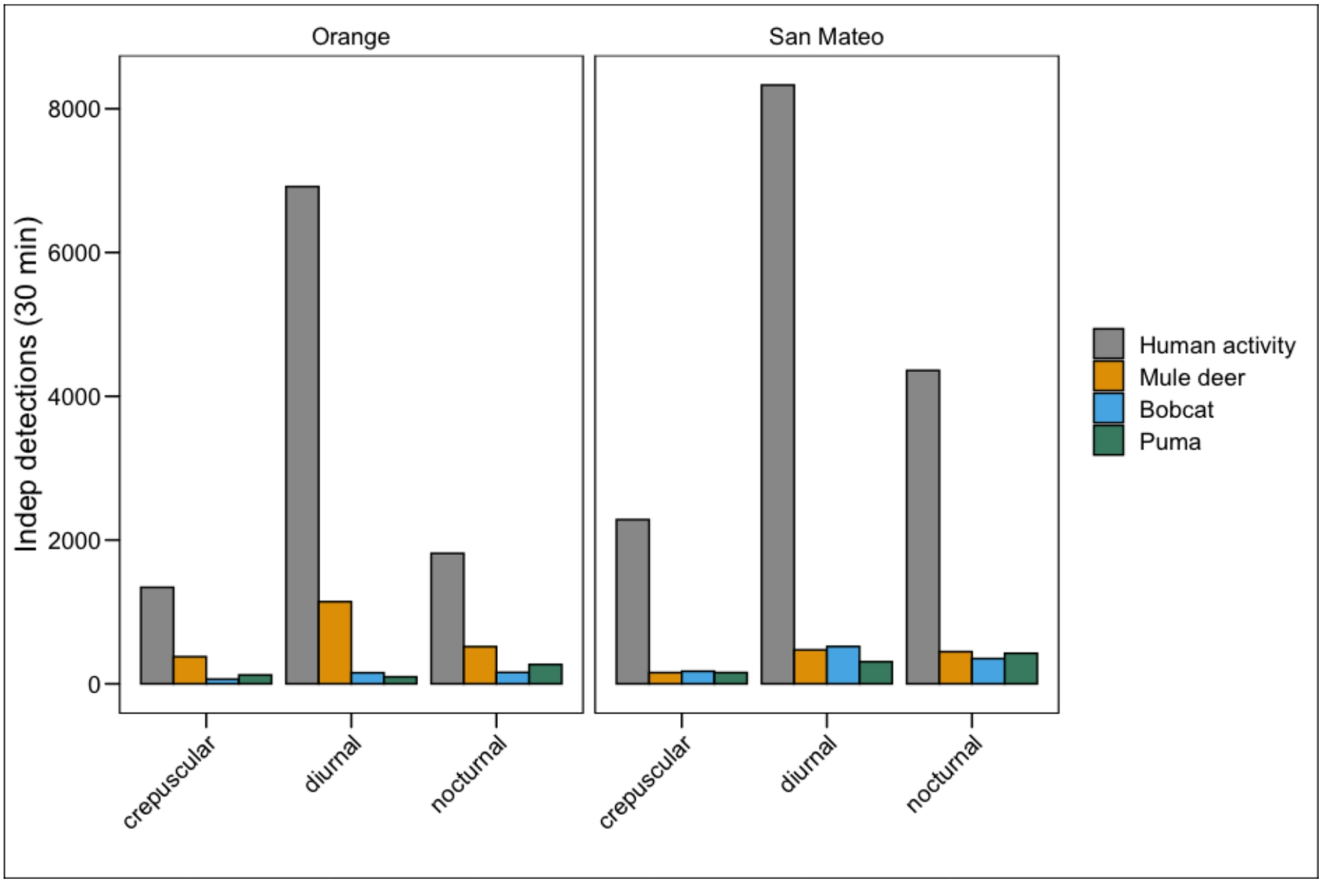

Fig. 2 Independent detections by species and time of day for human activity, mule deer (*Odocoileus hemionus*), bobcat (*Lynx rufus*), and puma (*Puma concolor*) in Orange and San Mateo Counties, California USA, 2022–2024

ALAN levels, this effect was not statistically strong (estimate: 1.51, 80% CI: 0.29, 2.73; Fig. 4). Moonlight intensity showed a weak positive association with nocturnal puma activity (estimate: 0.20, 90% CI: 0.02, 0.38). As with overall detections, distance to areas with noise pollution did not meaningfully influence nighttime activity (estimate: 0.20, 80% CI: −0.47, 0.91). Pumas were more likely to be detected at camera stations where mule deer were present (estimate: 0.36, 95% CI: 0.10, 0.64) and less likely at stations with more human activity (estimate: −0.81, 95% CI: −1.63, −0.12). Nocturnal detections were similar between open vs. closed habitat types (estimate$_{\text{open}}$: −1.22, 95% CI: −3.96, 1.24).

For bobcats, nighttime detections did not vary strongly with ALAN (estimate: 0.71; 95% CI: −0.60, 2.13; Fig. 4) despite overall detections being negatively associated with ALAN. Moonlight had a strong negative effect on nocturnal activity (estimate: −0.44, 95% CI: −0.69, −0.19). Bobcat detections increased with distance from urban areas (estimate: 1.26; 95% CI: 0.37, 2.24) and were positively associated with puma activity (estimate: 0.77, 95% CI: 0.12, 1.45), suggesting overlapping fine-scale habitat use. Although ALAN did not influence nighttime bobcat detections, there were fewer detections closer to noise polluted areas (estimate: −1.06, 95% CI: −2.05, −0.12). Nocturnal activity did not differ between counties (estimate: −0.69, 95% CI: −2.15, 0.67) or between habitat types (estimate$_{\text{open}}$: 0.79, 95% CI: −1.95, 1.89).

For mule deer, ALAN had the opposite effect: nocturnal detections increased with ALAN (estimate: 0.80, 95% CI: 0.01, 1.65). Deer were less active under brighter moonlight intensity (estimate: −0.42, 95% CI: −0.64, −0.19) and more active away from urban areas (estimate: 1.00, 95% CI: 0.20, 1.87). Nocturnal detections were positively associated with puma activity (estimate: 1.40, 95% CI: 0.71, 2.17) and were reduced closer to noise polluted areas (estimate: −0.96, 95% CI: −1.85, −0.12). Deer activity did not strongly differ between counties (estimate: −0.46, 95% CI: −1.70, 0.75), between open and closed habitats (estimate$_{\text{open}}$: −0.02, 95% CI: −1.42, 3.04), or strongly with human activity (estimate: 0.12, 95% CI: −0.45, 0.70; Fig. 4).

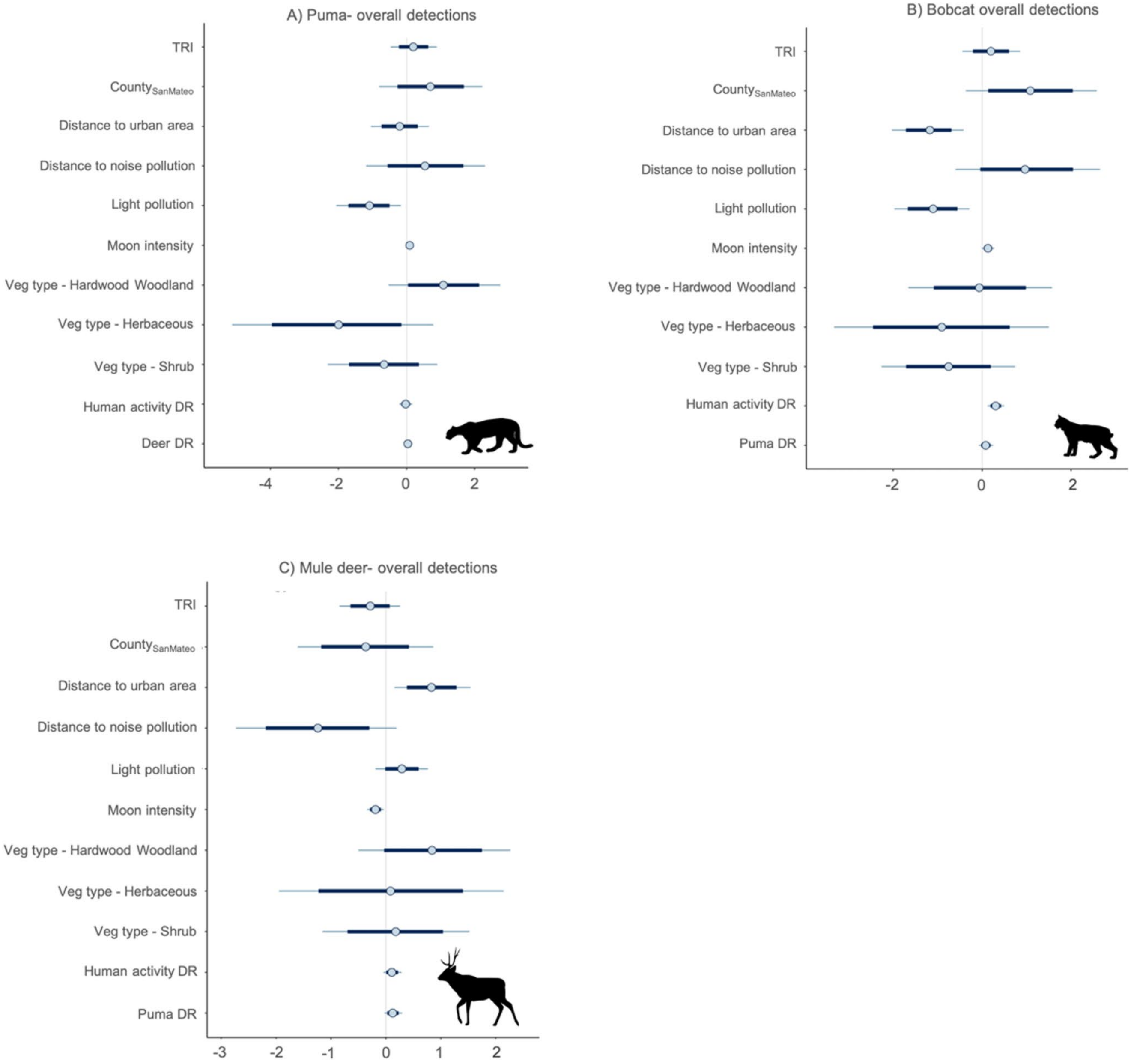

Fig. 3 Posterior estimates from GLMMs testing the influence of anthropogenic and habitat variables on puma (*Puma concolor)*, bobcat (*Lynx rufus*), and mule deer (*Odocoileus hemionus*), detections at camera trap stations in Orange and San Mateo counties, California, USA. The thin lines are the 95% credible intervals (CIs) and the thick lines for each estimate are the 80% CIs

Temporal activity - within-species differences between counties

Activity curves showed county-level differences in peak activity times for each species (Fig. 5, Table S4). As expected, human activity peaked during the daylight hours, with recreational use extending slightly later into the afternoon in San Mateo County compared to OC (Fig. 5). Wildlife activity also varied between regions. In OC, puma activity peaked around dusk, whereas in San Mateo County, it shifted earlier, peaking near 6:00 am (Δ_4: 0.67, MWW: 103.72, 95% confidence interval: 0.62, 0.73).

Mule deer activity showed moderate overlap between counties (Δ_4: 0.67, MWW: 203.22, 95% confidence interval: 0.66, 0.73), but showed opposite patterns relative to pumas. In OC, mule deer activity peaked early in the morning, whereas in San Mateo County, it increased during evening hours. Bobcats showed the greatest overlap in activity patterns between counties (Δ_4: 0.88, MWW: 24.104, 95% confidence interval: 0.83, 0.92). In OC, activity peaked in

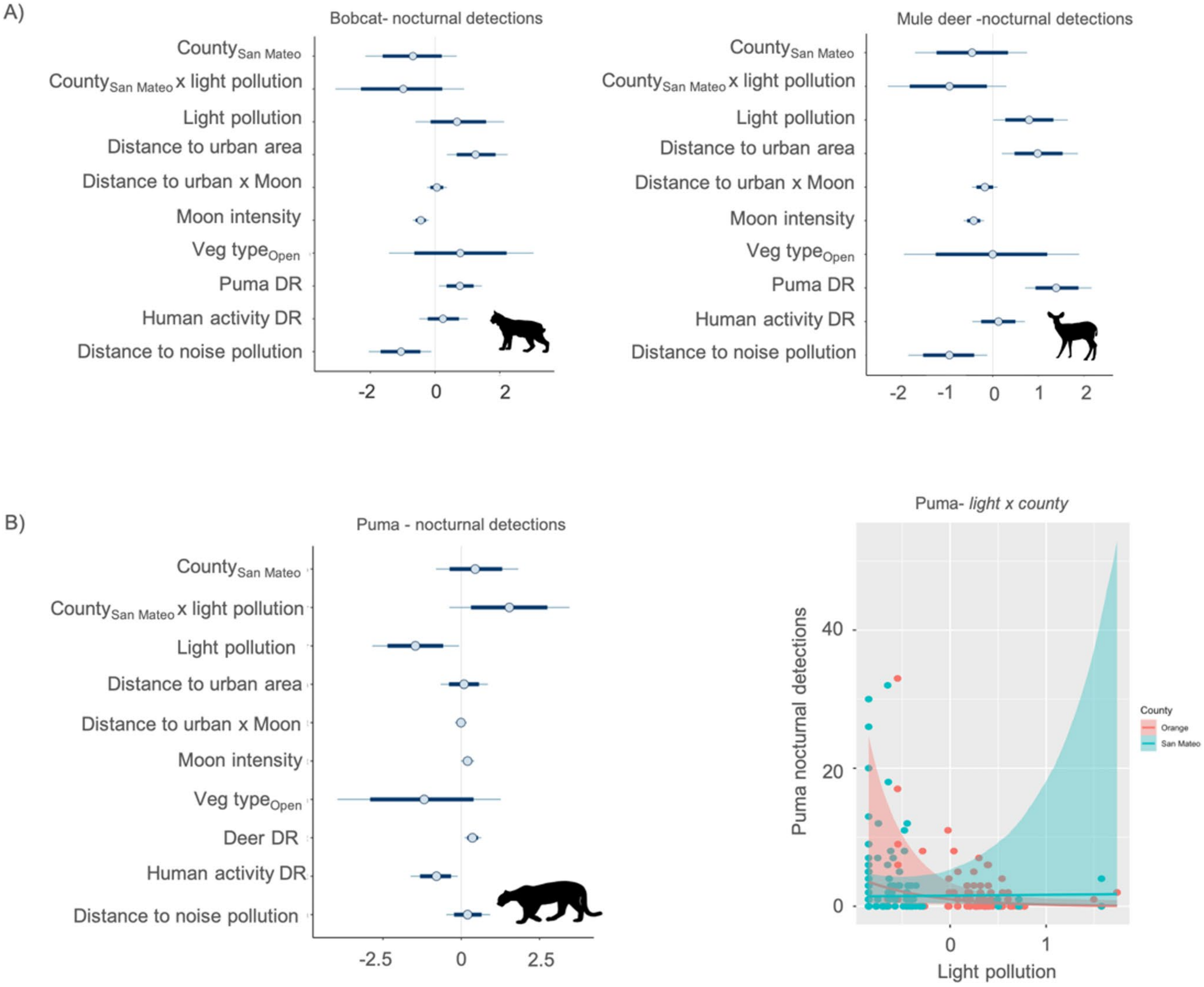

Fig. 4 **A**) Posterior estimates from GLMMs testing the influence of anthropogenic and environmental variables on nocturnal (**A**) bobcat (*Lynx rufus*), mule deer (*Odocoileus hemionus*), and (**B**) puma (*Puma concolor*) detections in Orange and San Mateo Counties, California, USA. Also shown in **B**) is the influence of light pollution on nocturnal puma detections in each county. The thin lines are the 95% credible intervals (CIs) and the thick lines for each estimate are the 80% CIs

the early morning, while in San Mateo County, it was more evenly distributed across the full 24-hour cycle (Fig. 5).

Discussion

While reduced wildlife activity near urban development is well documented (e.g., Merkle et al. 2013; Blecha et al. 2018; Leighton et al. 2022; Granados et al. 2024), our results show that specific drivers of disturbance may be context-dependent and mediated by local human land-use patterns. Specifically, among anthropogenic disturbances, artificial light at night (ALAN) can be an important driver of wildlife temporal activity at the urban-wildland interface (Barrientos et al. 2023). By comparing two coastal California counties with clear differences in habitat fragmentation, human disturbance, and nighttime illumination, we show that wildlife responses to sensory disturbance are not uniform across species or across the urbanization gradient. Overall, puma and bobcat detections declined with increasing ALAN, and the same pattern held for nocturnal puma detections, underscoring their greater sensitivity to nocturnal illumination (Ditmer et al. 2021), consistent with findings for other wild felids (Hickley et al. 2026). In contrast, mule deer detections increased in more illuminated areas but decreased under brighter moonlight. Both ALAN and moonlight are sources of nighttime brightness, but our findings suggest they may exert distinct effects on wildlife,

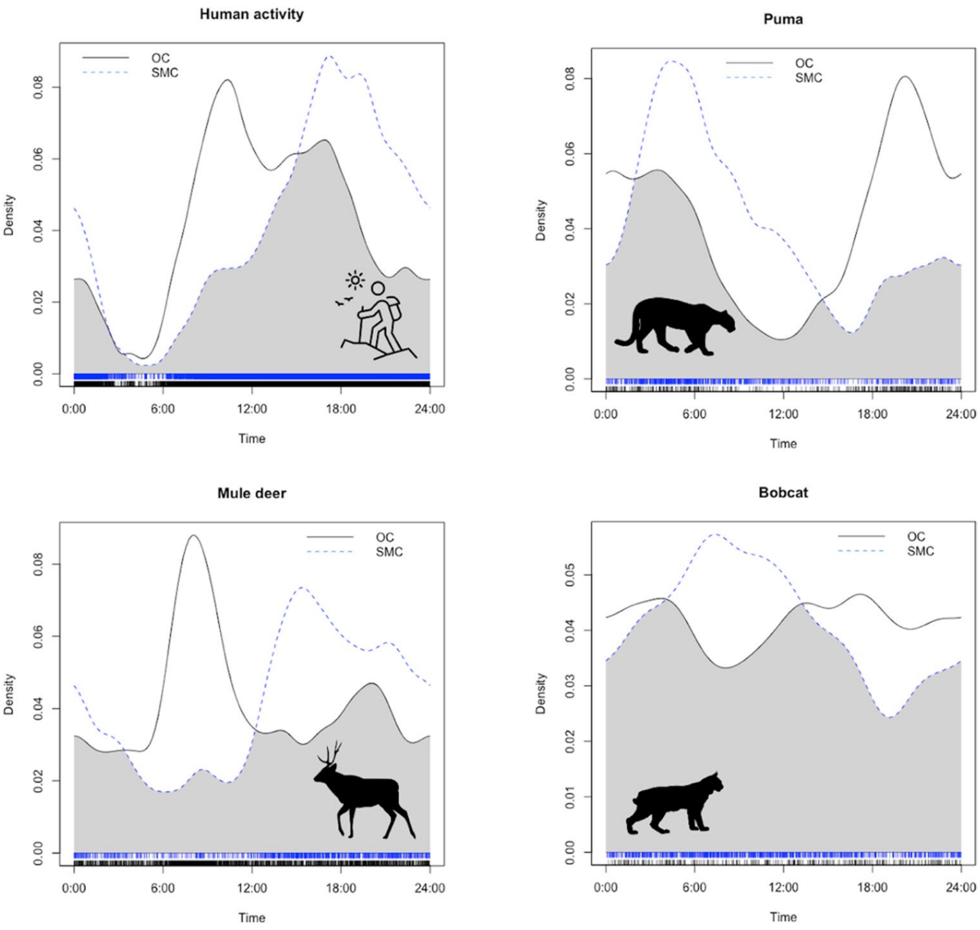

Fig. 5 Kernel density curves for the daily activity patterns for humans, pumas, bobcats, and mule deer in Orange (OC, solid line) and San Mateo (SMC, dashed blue line) counites, 2022 to 2024. The shaded area represents time periods of activity overlap between areas for each species

depending on trophic level, sensory adaptations, and perceived predation risk.

Both of our study areas are urbanized, though San Mateo County has a greater proportion of open space and landscape connectivity, with ecological benefits for wildlife. These landscape features likely reduce nocturnal skyglow, lower overall human disturbance, and maintain darker conditions that support more natural circadian rhythms for carnivores such as pumas (Barrientos et al. 2023). In Orange County (OC), where human activity and artificial light extend later into the evening, there were fewer puma nighttime detections in areas with greater light pollution, suggesting that pumas may delay movement until human presence and illumination decline. In contrast, puma activity in San Mateo County varied less across illumination levels. This pattern may be consistent with a threshold response, where avoidance becomes more pronounced once disturbance exceeds a threshold (e.g., Suraci et al. 2021; Dertien et al. 2021). The darker, less densely populated landscape of San Mateo County allows puma activity to peak earlier, before dawn, indicating that even within metropolitan regions, preserving large, connected, low-illumination open spaces can meaningfully buffer wildlife from sensory pressures (Barrientos et al. 2023).

Conversely, responses to noise were generally weaker for pumas, whereas bobcat and mule deer nighttime detections were greater closer to noisy areas, potentially using anthropogenic noise as a “human shield” or acoustic refuge (Collins et al. 2022; Muhly et al. 2011). Deer detections were also positively associated with puma detections, consistent with patterns observed for overall site use (Granados et al. 2024), highlighting the influence of prey availability on puma movement, given that deer are the primary prey of pumas in California (Stoner et al. 2021). Thus, the positive association between pumas and nocturnal activity near noisy areas likely reflects prey-mediated responses rather than direct attraction to noise. In acoustically saturated environments such as OC, avoiding noise may be infeasible, potentially promoting habituation or masking effects that could even benefit predators by reducing their detectability to prey (Tilgar et al. 2022; Chou et al. 2023).

Moonlight can influence nocturnal predator-prey dynamics, though empirical results across systems are mixed, potentially reflecting differences in how lunar illumination is quantified, environmental context, and interacting anthropogenic factors (Prugh and Golden 2014; Pratas-Santiago et al. 2016). We did not detect increased overall or nighttime puma detections in areas of greater lunar illumination, consistent with patterns seen in cheetahs (Broekhuis et al. 2014), but contrasting with studies of other African carnivores finding greater activity under brighter moonlight, potentially to enhance hunting success (Cozzi et al. 2012). We observed fewer bobcat detections during brighter moonlit periods, whereas ocelot activity in Brazil was largely unaffected by lunar cycles, despite documented behavioral flexibility in hunting (Pratas-Santiago et al. 2016). Similarly, mule deer detections declined under brighter moonlight, contrary to ungulate studies showing no detectable response (Pagon et al. 2013) or increased activity during solunar periods (Sullivan et al. 2016). For mule deer and bobcats, reduced activity under brighter moonlight may reflect efforts to reduce detectability by pumas which can prey upon both species in this system. More broadly, responses to moonlight are highly context-dependent, and can vary across ecosystems (Ladine and Settles 2020; Sergeyev et al. 2023), be masked by cloud cover (Cerri et al. 2023), or be modified by human disturbance (Wereszczuk and Zalewski 2023; Smyth et al. 2025). In California's forested and semi-urban environments, ALAN may further obscure the ecological effects of lunar illumination by saturating nighttime light levels (Falchi et al. 2011). Under such conditions, prey may increasingly use brightly lit, human-dominated areas to reduce predation risk (Lamichhane et al. 2023), increasing the likelihood of human-wildlife conflict in highly lit landscapes (Bombieri et al. 2018).

Species also differed in their responses to human presence associated with outdoor recreation. Our kernel density curves illustrate that pumas may temporally avoid people, consistent with temporal partitioning to minimize encounter risk, whereas bobcats were more frequently detected near human-active sites during the day. This apparent tolerance aligns with observations of urban bobcats exploiting higher prey availability (e.g., rodents, rabbits) in developed or semi-developed areas (Tigas et al. 2002), although avoidance of urban areas has also been reported (Lombardi et al. 2017; Hubbard et al. 2022). Recent work further suggests that bobcats respond to urban extent as well as to the anthropogenic configuration of woody vegetation, which can mediate bobcat movement, concealment, and prey access within developed landscapes (Branney et al. 2024). Thus, the positive association between bobcat detections and distance from urban areas in our study, together with their positive association with puma activity, suggests sensitivity to habitat structure rather than simple avoidance of urban environments. Such variation may arise from differences in irrigation regimes, vegetation structure, or prey distributions between urban and wildland settings (Bateman and Fleming 2012; Chamberlain et al. 2020). Mule deer detections showed relatively weak responses to human activity, providing only limited support for the human shield hypothesis (Berger 2007; Muhly et al. 2011; Granados et al. 2023). Their positive spatial association with pumas, as previously documented (Granados et al. 2024), could reflect shared habitat preferences and the importance of deer as primary prey (Pierce et al. 2000), while temporal segregation may reduce predation risk.

Fine-scale temporal patterns also differed between counties. Pumas are typically crepuscular and nocturnal (e.g., Sweanor et al. 2008; Granados et al. 2024; Bolas et al. 2025; Guzmán-Aguayo et al. 2025) and exhibited distinct peak activity patterns: in OC, activity peaked in the evening, whereas in San Mateo County, peak activity occurred before dawn. These divergences may reflect differences in human use patterns, traffic volume, and nighttime illumination. In OC, where human activity and ALAN remain elevated late into the night, pumas may delay movement until disturbance levels decline (Wang et al. 2017), whereas in San Mateo, darker landscapes may permit earlier activity peaks. Similar behavioral plasticity has been documented in carnivores exposed to human disturbance (Moll et al. 2018). Such shifts in diel activity can have important ecological and fitness consequences. For example, delayed or compressed activity windows may constrain hunting opportunities, alter predator-prey encounter rates, and increase energetic costs if individuals must travel further or make additional kills to meet energetic demands (Smith et al. 2015; Wang et al. 2017). Over time, these costs could influence body condition, reproductive success, or survival, particularly in more heavily urban environments. Mule deer spatially overlapped with pumas but showed reduced temporal overlap (Kautz et al. 2022), consistent with predator-prey temporal partitioning (Botts et al. 2020; Green et al. 2022). Bobcats showed the greatest temporal consistency between counties, suggesting greater behavioral flexibility and tolerance of anthropogenic disturbance in urban environments (Gorman et al. 2024).

Conclusion and applications

As urban expansion continues, understanding how light, noise, and human presence interact to structure predator-prey dynamics will be critical for designing cities that sustain both ecological function and coexistence. Our findings indicate that among urban-edge disturbances, ALAN is a particularly important driver of wildlife temporal activity. Although noise and development have long been recognized as major barriers to wildlife movement and behavior

(Benítez-López et al. 2010; Blecha et al. 2018), we found that light pollution exerted a stronger influence on species detections, particularly for carnivores. Species-specific responses further highlight differences in sensory tolerance and behavioral strategies across urbanization gradients (Sordello et al. 2019; Ditmer et al. 2021).

Our findings have implications for urban planning and management. Even within metropolitan regions, maintaining connected, low-illumination landscapes may buffer sensitive carnivores from increasing sensory disturbance. From a management perspective, ALAN should be explicitly incorporated into wildlife conservation and land-use planning. Reducing skyglow and limiting light spillover into adjacent habitats can help maintain natural nocturnal rhythms and mitigate disruption to light-sensitive species (Falchi et al. 2011; Jackson et al. 2025). Global efforts, including the "Dark Sky Places" initiative, demonstrate that adaptive lighting, shielding, and curfews can effectively reduce ALAN. To date, more than 230 sites have been certified worldwide, including 165 in the United States, (Barentine 2022; Dark Sky International 2025). Similar initiatives are emerging in California, with several Bay Area municipalities developing dark sky ordinances (Sheyner 2025), though implementation and enforcement remain variable. No such ordinances currently exist in OC (Dark Sky International 2025).

As human activity increasingly extends into nighttime hours, temporal overlap between people and carnivores may elevate conflict risk (Aditya and Ganesh 2022). Consequently, shifts in diel behavior and nighttime activity shaped by fragmentation, light pollution, and human presence carry direct implications for conservation and public safety. Management actions such as targeted nighttime access restrictions in key movement corridors, seasonal closures during sensitive periods (e.g., ungulate breeding or birthing seasons), and public education can reduce encounter rates (Shively et al. 2005; Salazar et al. 2024). These measures are particularly important as expanding development and predictable prey resources draw carnivores toward urban edges, increasing conflicts, including interactions with humans and pets (Soulsbury and White 2015; Murray et al. 2016; Bombieri et al. 2018). Coordinated efforts to reduce light pollution, integrate sensory ecology into policy, and to align recreation management with wildlife activity patterns offer cost-effective, evidence-based strategies to sustain biodiversity in rapidly urbanizing landscapes. Together, our findings underscore that sensory disturbance is not uniform in its ecological effects, and that light pollution, in particular, warrants greater attention in urban wildlife research and policy.

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Author contributions A.G., Z.M., and D.S. conceived the study and wrote the main text. A.G. performed the data analysis. A.G., B.C., and C.L. collected and processed data for this study. All authors reviewed the manuscript.

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Data availability Data are available for download at https://doi.org/10.6084/m9.figshare.31562164.v1.

Declarations

Competing interests The authors declare no competing interests.

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