RECREATION, VEGETATION MANAGEMENT, AND DISEASE IMPACT SYMPATRIC CARNIVORE ACTIVITY IN CALIFORNIA'S EAST BAY PARKS

By

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ABSTRACT

RECREATION, VEGETATION MANAGEMENT, AND DISEASE IMPACT SYMPATRIC CARNIVORE ACTIVITY IN CALIFORNIA'S EAST BAY PARKS

Leigh Janet Douglas

East Bay Regional Park District designated over 1000 ha of protected wildland-urban interface habitat in the hills of California's East Bay Area for invasive tree removal to reduce fire risk and restore native habitat over a 10-year period starting in 2016. From June to November 2019, 36 camera traps were deployed using a stratified two-pronged detection approach of surveying recreation and wildlife trails to assess the impact of vegetation management on the spatiotemporal distribution of sympatric carnivore species while accounting for potential impacts of human activity and proximity to development. The sampling effort resulted in 5,191 cumulative trap nights, 2,739 coyote detections, 319 gray fox (*Urocyon cinereoargenteus*) detections, 271 bobcat (*Lynx rufus*) detections, 133 red fox (*Vulpes vulpes*) detections, and 4 mountain lion (*Puma concolor*) detections while recreationists were detected over 13 times more frequently than coyotes, the most detectable carnivore. Nine percent of coyote detections contained individuals with visually identifiable symptoms of parasitic skin disease. Coyote detection probability increased with increasing recreation intensity while their temporal activity was more nocturnal in highly recreated areas. Bobcat detectability conversely decreased with increasing recreation intensity, but recreation didn’t influence either fox species spatially. Only coyote detectability was influenced by development level with coyotes being most detectable in the least developed habitat. Coyotes were less detectable in treatment than control habitat, but this difference was not statistically significant. Coyotes and bobcats were significantly more nocturnal in treatment versus control habitat. Canopy cover was positively correlated with the probability of detecting coyotes, bobcats, and gray foxes, suggesting that reducing canopy cover to the treatment plan’s target of 50% could disturb the activity of these species. Coyotes and bobcats were more detectable and more nocturnal on recreation trails than wildlife trails. Red and gray fox detectability was not influenced by trail type and both species were primarily nocturnal. Bobcat detectability decreased with increased coyote detections, but bobcats overlapped temporally with coyotes significantly more than did red and gray foxes. Temporal activity overlap between recreationists and mangy coyotes on park trails was double that of healthy coyotes. This study seeks to provide land managers with a spatiotemporal activity modeling framework that can be used to develop plans to mitigate human-wildlife conflicts while assessing the efficacy of native habitat restoration.

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INTRODUCTION

Wildland Urban Interface (WUI) habitat comprises 10% of the total land area in the continental United States where human infrastructure abuts remnant undeveloped landscape thereby forcing human and wildlife inhabitants into an often mutually uneasy state of coexistence (Radeloff et al. 2005). Human lives and livelihoods are put at risk by wildfires (Radeloff et al. 2018) and antagonistic interactions with wild animals such as depredation (Bateman and Flemming 2012), vehicle collision (Kreling et al. 2019), and zoonotic disease (Patz et al. 2004) while natural ecosystems are increasingly degraded (Bar-Massada et al. 2014), biotically homogenized (McKinney 2006), and disturbed by the frequent activity of people (Larson et al. 2016). Government agencies that steward WUI public lands are thus uniquely challenged to fulfill obligations of prioritizing public safety and safeguarding ecological resiliency simultaneously.

The 40-km-long eastern ridgeline of California's San Francisco Bay known as the East Bay Hills contains approximately 1200 ha of WUI habitat comprising 30% of the region's protected land managed by East Bay Regional Park District (EBRPD) on behalf of nearly 3 million combined residents of Alameda and Contra Costa counties (CDFW 2015, WPR 2018). The succession of shrublands and woodlands took place in the region by the middle of the 20th century after the suppression of indigenous peoples' fire management and the reduction of cattle grazing pressure (Keeley 2005). The East Bay

Hills are infamously known for fueling what was at that time the most expensive wildfire in United States history. The 1991 East Bay Hills Fire (Aka Tunnel Fire) resulted in 25 human casualties, 150 critical injuries, over 600 ha of land scorched, over 3,000 structures lost, and $1.5 billion in damages (USFA 1991).

The U.S. Fire Administration (USFA) branch of the Federal Emergency Management Agency (FEMA) declared EBRPD’s failure to implement recommended fuel reduction strategies and maintain proper WUI fuel breaks partially responsible for the severity and extent of the East Bay Hills Fire. To mitigate and prevent future WUI fires, EBRPD created the Wildfire Hazard Reduction and Resource Management Plan (WHRRMP) that targeted 83% of WUI habitat in the East Bay Hills for fuel reduction treatment to achieve a target of 50% canopy cover in fuel reduction treatment areas over a 10-year period from 2016 to 2026 (CDFW 2015). Treatment activities would include selective thinning of exotic *Eucalyptus globulus* stands and residential fuel break areas, a two-step process involving both mechanical removal and repeated herbicide applications to stumps and non-native emergent vegetation.

In line with WHRRMP project monitoring and mitigation objectives, EBRPD staff deployed infrared remote cameras in treatment habitat containing exotic trees and control habitat containing native trees to elucidate the spatiotemporal activity patterns of mammalian carnivores within these habitat types. Camera trapping is an increasingly popular and well-established methodology for assessing the impacts of anthropogenic habitat disturbance on terrestrial mammals due to its relatively low cost, stress minimization to study species, and high community engagement potential via online social media platforms (Ordeñana et al. 2010, Erb et al. 2012, Wang 2014). Vegetation treatment occurred on a rolling basis, so continuous survey effort was designed to detect both immediate alterations in species presence associated with the process of treatment and long-term changes as the total area treated in the East Bay Hills reached the WHRRMP target.

While the removal of eucalyptus for wildfire hazard reduction and native habitat restoration has been practiced in the Bay Area since 1973, the impacts of this activity on mammalian wildlife remain enigmatic (Gross 2013, Coats 2014). Eucalyptus forests increase soil hydrophobicity, thereby reducing systemic water retention and increasing the likelihood of fire, while eucalyptus seed dispersal and seedling emergence is enhanced by fire (Ferreira et al. 2000, Calviño-Cancela et al. 2018). These wildfire hazard risk factors were cited by EBRPD and WHRRMP affiliates as justification for attempting to convert eucalypt habitat to native woodlands as both forest types support comparable invertebrate, amphibian, and avian biodiversity in California (Sax 2002, Fork et al. 2015). Wild mammalian carnivores in the families Canidae and Felidae were selected as focal species for assessing WHRRMP impacts because canid and felid species tend to maximize and minimize their use of anthropogenically disturbed habitat, respectively, due to the flexibility and rigidity of their diets and because intraguild competition within and between families for shared environmental resources can be highly antagonistic (Fedriani et al. 2000). Focal species included mountain lions (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), and red foxes (*Vulpes vulpes*).

I conducted two sets of statistical analyses to address the spatial and temporal dimensions of activity separately for each focal carnivore species. This two-pronged camera detection method presents a novel way of evaluating how species use microhabitat features to mediate their interactions with humans and other species by explicitly estimating the difference in detection probabilities between more disturbed humanmade and less disturbed natural travel routes. Increased nocturnal activity to avoid overlapping with primarily diurnal humans in WUI habitat is widespread among mammals and the resulting reduction in niche partitioning between antagonist species may confer fitness costs with evolutionary consequences (Gaynor et al. 2018, Patten et al. 2019). Several studies conducted throughout the extended Bay Area found that the nocturnal temporal overlap of carnivore species increased with amount of human activity at a survey site while this study additionally sought to determine how carnivore activity varies in response to vegetation management (Reilly 2015, Wang et al. 2015, Smith et al. 2018, Nickel et al. 2020).

I expected the detectability of the region's feline apex predator, the mountain lion, to be low in the East Bay Hills because the total area surveyed constituted only 8% of the average mountain lion home-range size in the East Bay Area (Grigione et al. 2002). Mountain lions studied in the WUI of the neighboring Santa Cruz Mountains also tended to avoid human activity spatiotemporally, strongly preferring undeveloped habitat to forage and breed in and even exhibiting sustained fear responses to remote playbacks of human voices (Wilmers et al. 2013, Smith et al. 2017, 2019, Nickel et al. 2020, Yovovich et al. 2020). The consequential release of predation pressure on ungulate prey and smaller bodied carnivores (hereafter: mesocarnivores, including coyote, foxes, and bobcats) when mountain lion activity is low can have cascading effects on regional biodiversity (Prugh et al. 2009, Fischer et al. 2012, Ripple et al. 2014, Patten et al. 2019). Population densities of mesocarnivores tend to increase with proximity to developed areas due to the aggregation of anthropogenic food resources, fragmentation of suitable habitat, and reduced activity or extirpation of large-bodied carnivores that regulate mesocarnivore populations both directly through predation and behaviorally through intimidation (Bateman and Flemming 2012).

In the East Bay Hills, coyotes being the most detectable species likely affects the activity patterns of smaller mesocarnivores such as bobcats and foxes that are known prey to coyotes (Fedriani et al. 2000, Larson et al. 2015, Farmer and Allen 2019). Fine scale spatiotemporal avoidance behaviors (i.e., niche partitioning) and reduced activity of weaker competitors can result from combining strong intraguild antagonism with intense anthropogenic disturbance (Wang et al. 2015, Smith et al. 2018). The competitive edge possessed by coyotes over mountain lions in WUI habitat enabled coyotes to expand their geographic range by 40% while mountain lions have decreased their range by almost the same extent over the past several hundred years (Prugh et al. 2009).

Urban adapted coyotes differ both genetically and behaviorally from their wildland congeners, the result of anthropogenic filtering of traits selecting for dietary flexibility, fission-fusion sociality, residency in smaller home ranges, and increased boldness (Gehrt et al. 2009, Larson et al. 2015, Poessel et al. 2015, Breck et al. 2019, Adducci et al. 2020). Due to their propensity for eating small commensals (e.g., domestic cats *Felis catus*: Fedriani et al. 2001) and their ability to coalesce into large packs to defend their territories, coyote populations residing in the WUI of 96 cities in the continental United States were deemed nuisances by land managers (Poessel et al. 2016). Public perception of coyotes has also been damaged by notable cases of direct attacks on humans in WUI habitat (Carbyn 1989, Timm et al. 2004), including six recorded coyote bite incidents between 2020 and 2021 in East Bay parks, with one bite to the neck hospitalizing a 5-year-old girl (NBC Bay Area 2020, CDFW 2021).

Disease can increase the risk of human-coyote conflicts as diseased coyotes are significantly more diurnal, select for habitat where human activity is high due to associated food availability, and boldly explore developed areas to find artificial food sources when their ability to capture their natural prey is compromised (Murray et al. 2015, Breck et al. 2019). Diseased coyotes using Canadian WUI habitat consumed 33% more human food and 87% less prey than healthy coyotes (Murray et al. 2015). Mange, a hypersensitive immune response to infestation by ectoparasitic mites in the family Sarcoptidae, is one such disease afflicting mammals that numerous studies have linked to anthropogenic disturbance of natural habitat, including in WUI populations of coyotes, mountain lions, bobcats, foxes, raccoons (*Procyon lotor*), and rodent prey species (Riley et al. 2007, Poessel et al. 2015, Foley et al. 2016, Cypher et al. 2017, Serieys et al. 2018). Secondary poisoning from anticoagulant rodenticides commonly dispensed in commercial and residential areas to limit rodent-caused damage to infrastructure is frequently comorbid with severe mange in carnivores that use WUI habitat (Steinberg et al. 2015, CDPR 2018).

Mange is highly conspicuous because alopecia (i.e., balding), skin thickening, discoloration, and pruritic skin lesions are typical symptoms of advanced pathology that can be observed noninvasively via camera trapping (Oleaga et al. 2011, Murray et al. 2015 and 2016, Carricondo-Sanchez et al. 2017). Sarcoptic mange, mange caused by *S. scabiei*, can cause demographic shifts in coyote populations by sterilizing females and often causing death from secondary infection of open wounds or exposure (Pence and Windeberg 1994). Mange can be transmitted from infected coyotes to conspecifics, sympatric canids and procyonids, domestics, and people via direct interactions and indirectly through contact with mite infested bedding (Daszak et al. 2000, Pisano et al. 2019). As an epizootic, mange can also precipitate population crashes of affected species resulting in sustained local extirpation and genetic bottlenecking (Riley et al. 2007, Serieys et al. 2015). These public health and ecological concerns necessitate the development of predictive models capable of disentangling the effects of different kinds of habitat disturbance.

Hypotheses and Predictions

I hypothesized that recreation intensity and proximity to development would influence the spatiotemporal activity patterns of carnivores more than vegetation treatment status. I predicted that coyotes would be more detectable than bobcats and foxes in habitat disturbed by people and invasive vegetation due to the bobcat’s strict diet and the vulnerability of foxes to intraguild predation (Fedriani et al. 2000). I hypothesized that wildlife trails enabled carnivores to be active during the day near people and predicted all carnivores would be more nocturnal on recreation trails than wildlife trails in order to avoid hikers, dog walkers, bicyclists, and equestrians (hereafter: recreationists) (Hojnowski 2017, Patten et al. 2019). I hypothesized that bobcats and foxes would try to avoid coyotes, but this would be mediated by recreation, development, and habitat characteristics. I predicted that coyote detectability would vary inversely with the detectability of smaller bodied carnivores and that a skew towards nocturnality in recreated, developed, and nonnative habitats would reduce niche partitioning between sympatric carnivores. Lastly, I hypothesized diseased coyotes would be bolder than healthy coyotes so predicted greater temporal overlap between diseased coyotes and recreationists compared to healthy coyotes (Murray et al. 2015, Breck et al. 2019).

MATERIALS AND METHODS

Study Area

Tilden Nature Area, Tilden Regional Park, and Sibley Volcanic Regional Reserve, hereafter referred to as Tilden-Sibley has been protected for recreational use since 1936 and represents 1,176 ha of Pacific coastal habitat, a quarter of which has been designated for WHRRMP's Fuel Reduction Treatment (EBRPD 2018, Fig 1). Tilden-Sibley's heterogeneous landscape is currently comprised generally of 45% woodland, 25% shrubland, 20% grassland, and 10% developed habitat, specifically of 130 unique admixtures of native and non-native plant species, making the study area highly variable across fine spatial extents (EBRPD 2004). A mosaic overstory of native trees include coast live oaks (*Quercus agrifolia*), scrub oaks (*Quercus berberidifolia*), Monterey pines (*Pinus radiata*.), California bays (*Umbellularia californica*), coastal redwoods (*Sequoia sempervirens),* Pacific madrones (*Arbutus menziesii*), and stands of invasive blue gum eucalyptus (*Eucalyptus globulus*) (EBRPD 2018). Understory composition varies by elevation, proximity to water, and level of human disturbance and frequently includes California huckleberry (*Vaccinium ovatum*), California blackberry (*Rubus ursinus*), western poison oak (*Toxicodendron diversilobum*), coyote brush (*Baccharis pilulari*), California sagebrush (*Artemisia californica*), chamise (*Adenostoma fasciculatum*), coastal wood fern (*Dryopteris arguta*), western sword fern (*Polystichum munitum*), Scotch broom (*Cytisus scoparius*), French broom (*Genista monspessulana*), English ivy (*Hedera helix*), black mustard (*Brassica nigra*), fennel (*Foeniculum vulgare*) and both native and invasive grasses and thistles (EBRPD 2018).

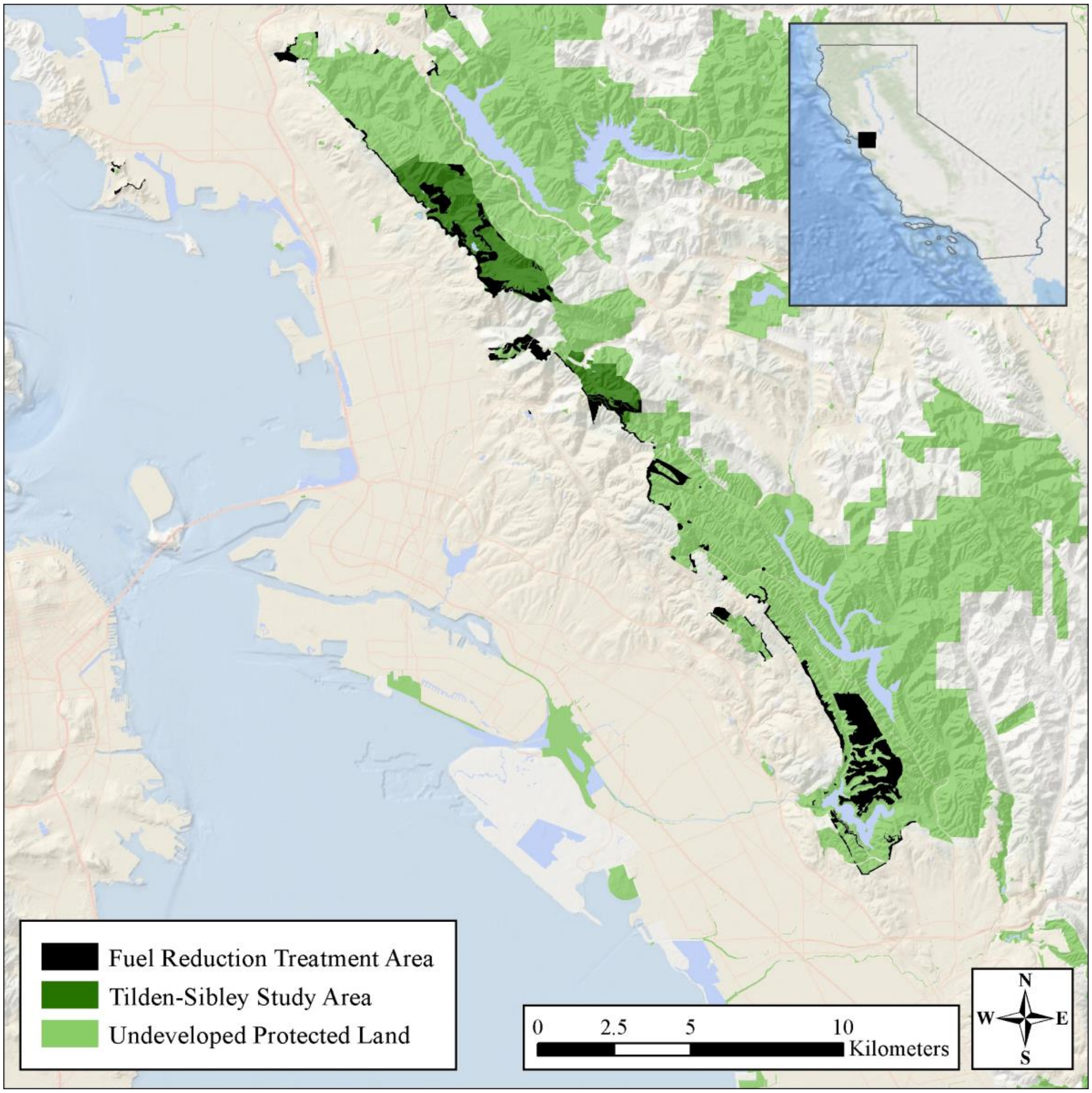

Figure 1. Tilden Regional Park and Sibley Volcanic Regional Preserve (Tilden-Sibley), Fuel Reduction Treatment Area (black), and other undeveloped public land (green) managed by East Bay Regional Park and East Bay Municipal Utilities District adjacent to the cities of El Cerrito, Berkeley, Piedmont, and Orinda, California, USA.

Tilden-Sibley's terrain is moderately rugged with Grizzly Peak and Round Top representing the tallest features in Tilden and Sibley, respectively, standing over 535 m above sea level over 200 m above each park's valley floor. Regional climate is Mediterranean with annual rainfall ranging from 300 to 800 mm on dry versus wet years (NOAA 2018). Connectivity between Tilden and Sibley is maintained by the Caldecott Wildlife Corridor, a strip of parkland providing safe passage for human and nonhuman park users over California State Route 24, an 8-lane highway serving as a major thoroughfare between Bay Area suburbs and urban centers. Subsequently, commuter traffic on roads through Tilden-Sibley is common to bypass highway congestion. Tilden-Sibley abuts the cities of El Cerrito, Berkeley, and Piedmont to the west and meets protected land managed by East Bay Municipal Utilities District (EBMUD) on its eastern border. EBRPD and EBMUD lands combine to form 20,934 ha of contiguous undeveloped habitat, roughly half of which is recreated, surrounded by intermediate density housing development (i.e., suburban) (City of Oakland 2018, EBRPD 2019).

Previous Work

Twenty Bushnell Trophy Cam HD Essential E3 Game Cameras were installed in Tilden and Sibley from 23 June to 21 November 2016 by EBRPD personnel to monitor the impacts of invasive vegetation management (e.g., eucalyptus thinning and brush removal) on medium to large sized terrestrial mammals over a 10-year period. Original camera sites were established to collect baseline data on the detectability of focal species in microhabitats that varied with respect to trail type (e.g., service road, single-track, unofficial manmade, and wildlife path), treatment status, and human disturbance intensity. During this preliminary phase, 3 cameras were destroyed and 9 trap locations were selected for continued monitoring while the rest were terminated so 8 cameras could be redistributed to increase the spatial extent of surveillance. Camera placement was opportunistic and stratified such that half of the camera trap locations were placed within areas targeted for eucalyptus thinning (treatment) while the remainder surveyed non-targeted nearby habitat dominated by native tree species (control). During that time cameras recorded more frequent diurnal detections of several focal mammal species on wildlife trails and low use recreation trails than heavily used recreation trails leading to this study’s hypothesis that recreation activity and proximity to human infrastructure may obscure the effects of vegetation type on wildlife detectability.

Data Collection and Management

Camera Placement

Camera locations were finalized for an additional 20 Bushnell Trophy Cam Aggressor Game Cameras by 15 April 2019 that established 9 new camera sites and to ensure that each site was equipped with 2 cameras to survey a recreation trail and nearby wildlife trail at 18 overall trap sites simultaneously (Fig 2). Recreation trails and trails made and maintained by wildlife were surveyed to maximize the detectability of carnivores using these linear features as preferred travel routes (Cusack et al. 2015, Wang et al. 2015, Baker and Leberg 2018, Patten et al. 2019). Geospatial analysis in ArcMap version 10.5.1 was used to locate camera trap sites that would enable stratified systematic sampling of 3 locational strata to establish a gradient of human development intensity: Tilden-Sibley's residential edge, interior, and wildland edge. Site stratification enabled hypothesis testing of whether behavioral changes of focal carnivores were related to human development, human activity, or both forms of disturbance. Nickel et al. (2020) found that recreation intensity peaked at relatively remote ridgeline locations with sought-after viewsheds, such as Tilden-Sibley's wildland edge, compared to locations closest to residences, suggesting that carnivores may face unique spatiotemporal stressors when using highly recreated versus highly developed habitat.

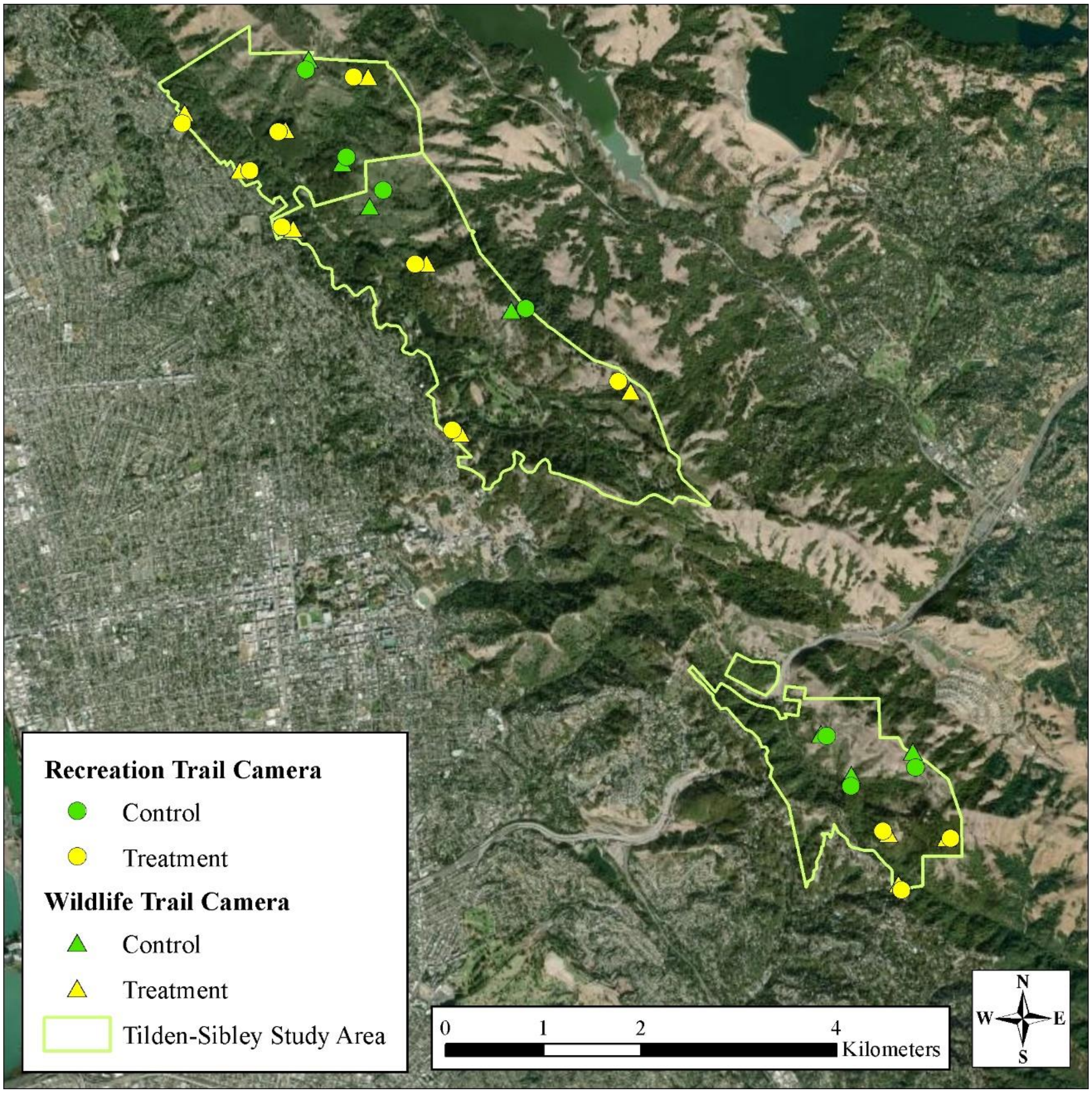

Figure 2. Tilden Regional Park and Sibley Volcanic Regional Preserve (Tilden-Sibley) and paired camera traps (n=36) deployed in 2019 on recreation trails (circles) and trails made by wildlife (triangles) in control (green) and treatment (yellow) habitats.

Recreation trail camera placement were pre-selected and uploaded into a Garmin handheld global positioning system (GPS) prior to conducting fieldwork to ensure a minimum aerial distance of 500 m between camera sites. Once appropriate mounting objects were found, recreation trail camera trap UTM locations were entered into the GPS and used to establish a 250 m radius within which the nearest wildlife trail in the same habitat type could be identified. Paired wildlife trails were selected for camera surveillance only if there was both a clear disturbance of understory vegetation and the presence of deer or mammalian carnivore sign. Recreation trail cameras were placed in Bushnell Trophy Aggressor Series Bear Safe Security Cases to deter vandalism, fastened to trailside trees with bolts and a Python cable lock, and positioned diagonally or perpendicularly to the surveyed trail. Wildlife trail cameras were also positioned along observed paths of animal movement and secured with cable locks to trees or shrubs that were large enough not to be easily damaged by people or perturbed by wind. Camera height was highly variable due to the opportunistic use of trees as mounting objects but camera viewsheds were tested to ensure that all focal species could trigger the traps.

Residential edge camera trap locations were less than 350 aerial m from Tilden-Sibley’s western boundary abutting intermediate density housing while cameras on the wildland edge were placed less than 350 aerial m from the park’s eastern border with non-recreated protected land managed by EBMUD. Trails positioned in each park’s interior between these two buffered edges were considered intermediate. In total, 6 pairs of cameras (2 pairs per park) were deployed within each development stratum. When camera placement was finalized, minimum, maximum, and average distances between paired cameras were systematically smaller than that between unpaired cameras: 38 m, 219 m, and 105 m were the minimum, maximum, and average aerial distances between paired cameras while 473 m, 1,476 m, and 691 m were analogous distances between unpaired recreation trail cameras.

Areas targeted by EBRPD for fire hazard fuel reduction treatment comprised 56% of camera trap sites while the remaining sites would not be treated under the WHRRMP to monitor the impact of mechanical and chemical management of mostly invasive vegetation (i.e., *Eucalyptus globulus, Acacia sp.*, and *Pinus radiata*) on mammalian wildlife activity. Additionally, 22% of camera sites surveyed sparsely covered shrublands dominated by scrub oaks, coyote brush, and chamise; 88% more densely covered woodlands habitat dominated by oaks, bay laurels, redwoods, pines, eucalyptus, or combinations thereof.

Camera Settings and Maintenance

All cameras were programmed to record a burst of 3 images separated by 3 sec intervals between successive triggers 24 hours per day with camera shutter speed set to high and sensor levels set to auto-adapt to ambient temperature. White flash was disabled to increase the crypsis of cameras to deter vandalism. Memory cards used in recreation trail cameras were 32 GB to accommodate the expected high volume of camera triggers from recreationists and wildlife trail cameras were equipped with 16 GB memory cards. Cameras were serviced once or twice monthly to replace memory cards, change batteries if sensors indicated less than full charge.

Sampling Period

Analyses were limited to camera data generated between 1 June and 1 November 2019 due to asymmetric survey effort between wet and dry seasons biased in favor of the dry season. In California, precipitation is absent or sparse between the months of June and November, which represents a time of increased wildfire risk and biological stress on terrestrial mammals forced to aggregate around limited available water resources (NOAA 2019). Increased sampling effort was allocated during the dry season because of the reasonable assumption that recreation would intensify during the summer months due to low precipitation, thus enabling enhanced hypothesis testing concerning mammalian carnivore response to park use patterns. I also hypothesized that effects of vegetation treatment status would be enhanced during the dry because habitat dominated by eucalypt species tends to be drier on average than native California woodlands, potentially making treatment areas less suitable for carnivores use (Ferreira et al. 2000).

Data Processing

Images were downloaded onto a portable hard drive after each survey and sorted hierarchically by site then by trail type then by species, including recreationists. I then used RECONYX opensource image tagging software MapView Professional (https://reconyx.com/software/MapView) to automate the transfer of image metadata including custom tags into tabular form as a .csv document. Correct species identification was verified by confirming correct assignment of images to species folders prior to import into MapView Professional and translation into tabular format. Image metadata recorded by MapView Professional based on the imported folder structure included date, time, location, trail set type, and species. I used R statistical programming software version 4.0.2 to convert MapView Professional's output into a sequence of independent events with 10 minutes specified as the threshold for independence (R Development Core Team 2020). I then used the package camtrapR to automatically generate species detection histories, detection maps, and summary tables (Niedballa et al. 2020).

Coyote Mange Identification

I inspected coyote detections for the presence or absence of visible symptoms compatible with a hypersensitive immunological response to *Sarcoptes scabiei* infestation including pruritic skin lesions, hyperkeratosis, alopecia, and emaciation (Pence and Windberg 1994, Oleaga et al. 2011, Murray et al. 2015, Carricondo-Sanchez et al. 2017, Niedringhaus et al. 2019). I classified coyote detections as mange-positive if ≥ 1 coyote exhibited clear patterns of hair loss and visibly irritated (e.g., dark, scaly, and wounded) skin approximately exceeding 25% of its total body surface area as is diagnostic of severe infections (Beigh et al. 2016, Fig 3). Coyote detections containing potential symptoms not meeting this severity criterion were classified as mange-negative due to the possibility that alopecic regions could indicate external wounds unrelated to infestation (Carricondo-Sanchez et al. 2017).

Figure 3. Mange positive coyote detections displaying moderate (top) to severe (bottom) disease symptoms under variable ambient light conditions captured in Tilden-Sibley in 2019.

Detection events lacking the resolution to identify severe mange including images that were blurred, overexposed, or that only captured a small portion of a detected coyote were excluded from analyses comparing healthy and diseased coyotes but were retained for analyses that pooled all coyote detections. Mange-negative detections featured coyotes that appeared completely asymptomatic. Lesions compatible with sarcoptic mange are more difficult to detect nocturnally with infrared sensors than with white flash (Carricondo-Sanchez et al. 2017). Thus, for nocturnal events defined as such by appearing in gray scale with black backgrounds coupled with a timestamp occurring between the hours of sunset and sunrise, I had to rely on cues relating to body shape, apparent texture, and color when I could not confirm the presence of diurnally detectable lesions. Mange-positive events displayed variably severe symptoms ranging from moderately severe cases featuring conspicuous mange-compatible balding not approaching total body surface area to extreme cases where 100% of a coyote's body surface appeared affected. Typical body locations where alopecia could be consistently identified included the anogenital region, abdomen, tail, paws, and pinnae (Oleaga et al. 2011, Murray et al. 2015, Beigh et al. 2016, Carricondo Sanchez et al. 2017).

Statistical Analyses

Occupancy Modeling

Statistical models predicting wildlife spatial occurrence based on presence data generated from imperfect survey methods, such as camera trapping, produce biased parameter estimates if the possibility of observing false absences is not explicitly accounted for. Occupancy modeling's hierarchical approach combines two logistic regression equations that respectively represent distinct probabilities that 1) a surveyed area was occupied by a species and 2) the species was detected during a survey given that it was present and therefore able to be detected (MacKenzie et al. 2002). Occupancy, therefore, measures the proportion of sample sites where a species was truly present regardless of how detectable it was, while detection probability reflects trapping success rate influenced by both camera placement and a species' activity levels or local abundance at a site (MacKenzie et al. 2002). These models outperform traditional relative abundance indices (e.g., number of detections/number of surveys) by addressing the heterogeneity in the observed presence of a species in a study area with a joint probability statement and assessing the effects of covariates on species' detection probability (p) and occupancy (psi) (Sollmann et al. 2013). Detection histories that serve as the foundation for occupancy models are matrices of 1s, 0s, and NAs representing detections, non-detections, and missing data, respectively.

Occupancy models assume that each sample site is closed to changes in occupancy status of a species during a sampling season, that detectability and occupancy are either constant across all units or vary with site covariates, that detections of a species are spatially independent, and that no species are misidentified. Violation of these assumptions can cause models to produce erroneous parameter estimates. The first assumption of site closure can be relaxed, however, if changes in occupancy status reflect the random movement of a species in and out of a site. This study violated the closure assumption because the distance between cameras was much smaller than typical home-range sizes of focal species. Occupancy parameters must be interpreted as the probability that a species used a site during a survey if the closure assumption was violated. Estimates of instantaneous occupancy (i.e., habitat use) are usually greater than true occupancy estimates as the former reflect probability of movement detected rather than stable residency of a species within a given site (MacKenzie 2005).

Single-season single-species occupancy models were fit using the unmarked R package and Akaike's Information Criterion corrected for small sample sizes (AICc) was used to select the top models within the candidate sets for each focal species (Chandler et al. 2020). Quasi AICc was used in cases where models could only be fit while correcting for overdispersion (Chandler et al. 2020). Every day that all recreation camera traps operated simultaneously throughout the sampling period was used as a survey occasion resulting in 58 total occasions between 1 June and 15 September 2019. This subset of the sampling period contained the maximum number of paired cameras (n=32) simultaneously operating and collecting human activity data for modeling carnivores' spatial response to daily fluctuations in recreation intensity. Four cameras in two camera sites with the most missing data due to recreation trail camera failures were excluded from analysis because their inclusion prevented model convergence. I used a stepwise approach for model selection in which I first determined the optimal occupancy model while holding the detection model constant with all detection covariates before repeating the process to determine the best detection model while holding the occupancy model constant with the covariates identified as the best in the first step. Parameter estimates from competitive models were not averaged to reduce bias in interpreting covariate effects (Cade 2015).

The site-level categorical covariates I explored included development level and treatment status while continuous covariates included slope, elevation, average percent canopy cover within a 50 m radius of each camera, and distance to water. Elevation and slope were extracted from the United States Geological Survey's (USGS) 2016 digital elevation model using the raster package in R while percent canopy cover was extracted from LANDFIRE's 2016 database. Time-varying survey covariates used for all species included daily recreation events and trail type. Trail could not be used as a site covariate because the paired survey design placed cameras on both trail types at each site. Daily coyote events were used as a survey covariate in the models of smaller-bodied focal species. All continuous covariates were standardized to improve model performance and covariate comparisons. All covariates were used in the detection portion of the model unless the inclusion of covariates caused model convergence issues.

Temporal Overlap

The R package overlap was used to calculate coefficients of overlap $\hat{\Delta}_1$ and $\hat{\Delta}_4$ representing the extent of shared area under probability density curves for two species' diel activity patterns for sample sizes less than 50 and greater than 50, respectively (Ridout and Linkie 2009, Ridout and Meredith 2020). This method employed non-parametric kernel density estimation using the times of species detections converted into radians to generate overlap estimates between 0 and 1, corresponding to no overlap and completely overlapping activity. Coefficients of overlap were calculated for focal carnivores and recreationists and grouped by trail type, development level, and vegetation treatment to assess the effects of these factors on the temporal behavior of focal carnivores.

Overlap analyses were conducted for all coyotes combined and also separately for apparently diseased and healthy coyotes. Recreation level was considered high if recreation detections per site were greater than or equal to 20 events per day on average, medium if between 20 and 10 events per day, and low if there were fewer than 10 events per day. Bootstrapping with 999 samples was used to generate normalized 95%

confidence intervals while the coefficients of overlap derived from the original sampling were taken as mean overlap estimates. In this analytical context, diel activity was defined as activity observed over a 24-hr period, nocturnal activity referred to activity observed between 2100 and 0500 hours, corresponding to an hour after sunset and an hour before sunrise, respectively. Diurnal activity was defined as occurring between 0700 and 1900 hours and crepuscular activity occurred within an hour of sunrise and sunset.

RESULTS

Camera traps in Tilden-Sibley surveyed the study area for 5,191 cumulative trap nights (144 ± 12 trap nights per camera trap) from 1 June to 1 November 2019 and generated 13,512 photos of focal carnivore species and 814,280 photos of recreationists. Mountain lions were the least detectable carnivore species and were detected only 4 times throughout the sampling period exclusively and nocturnally on recreation trails. Coyotes were the most detectable carnivores (n=2,739 detections), captured on all recreation trail cameras and 89% of wildlife trail cameras, and were detected on recreation trails over 7 times more frequently than on wildlife trails (Table 1).

Coyotes with conspicuous mange symptoms comprised 9% of coyote detections and were detected on 61% of surveyed recreation trails compared to 28% of wildlife trails. Bobcats accounted for 252 recreation trail and 19 wildlife trail events. Gray foxes were the only carnivores whose use of the different trail types was roughly equivalent, appearing 172 times on recreation trails and 147 times on wildlife trails. Red foxes, like coyotes and bobcats were much less detectable on wildlife trails (n=12 events) than recreation trails (n=127 events). In total, 49,635 independent detection events of recreationists were recorded, making park visitors 13 times more detectable than Tilden-Sibley’s most commonly detected wild carnivore.

Table 1. Summary of independent detection events and number of camera sites (n=18 per trail type) each focal carnivore species was detected in surveys (n=5,191 trap nights) conducted in Tilden-Sibley from June to November 2019.

	Recreation Trail		Wildlife Trail	
Species	Detections	Cameras	Detections	Cameras
Mountain Lion	4	3	0	0
Coyote (Total)	2406	18	333	16
Mange (–)	2108	18	258	16
Mange (+)	222	11	36	5
Bobcat	252	17	19	4
Gray Fox	172	15	147	13
Red Fox	126	9	7	3

Occupancy Modeling

Coyote

In total, 32 cameras over 58 survey occasions resulted in 1834 functional surveys, 25% of which detected coyotes. The naïve occupancy estimate, or the proportion of cameras that captured coyotes was 0.97; as a result, no covariates influenced their use of Tilden-Sibley. The top model for coyote detection probability included trail type, recreation, treatment, stratum, slope, elevation, and canopy cover as covariates and carried 47% of the explanatory weight of the 190 models considered in the candidate set (Table 2). There was one competitive model carrying 25% of the explanatory weight including trail type, recreation, stratum, slope, elevation, distance to water, and canopy cover as predictors.

Table 2. Top single-season single-species occupancy models for mesocarnivore species detected in Tilden-Sibley from 1 June to 15 September 2019 ranked using AIC corrected for small sample size (AIC_c). K represents the number of model parameters and w each model's weight. Covariate abbreviations are T = trail, R = daily recreation, C = daily coyote, D = development stratum, V= vegetation treatment, CC = canopy cover, W = distance to water, E = elevation, S = slope.

Species	Top Model(s)	K	AIC_c	ΔAIC_c	w
Coyote	p(T + R + V + D + S + E + CC) ψ(1)	10	1586.5	0.00	0.47
	p(T + R + D + S + E + W + CC) ψ(1)	10	1587.7	1.26	0.25
Bobcat	p(T + S + W) ψ(1)	5	576.3	0.00	0.11
	p(T + R + W) ψ(1)	5	576.4	0.08	0.11
	p(T + R + W + CC) ψ(1)	6	577.1	0.76	0.08
	p(T + S + W + CC) ψ(1)	6	577.3	0.97	0.07
	p(T + W + CC) ψ(1)	5	577.4	1.08	0.05
	p(T + R + C + W) ψ(1)	6	577.8	1.45	0.04

Species	Top Model(s)	K	AIC_c	ΔAIC_c	w
Gray Fox	p(E + W) ψ(1)	5	222.4	0.00	0.13
	p(E + W + CC) ψ(1)	6	222.7	0.38	0.10
	p(S + E + W) ψ(1)	6	222.8	0.48	0.10
	p(W + CC) ψ(1)	5	223.6	1.19	0.07
Red Fox	p(T + S + W) ψ(1)	5	285.6	0.00	0.45

According to the top model, coyote detection probability was 0.63 (95% CI 0.59, 0.67) on recreation trails compared to 0.07 (95% CI 0.05, 0.10) on wildlife trails, marking significantly higher detectability on trails frequented by people (Fig 4). Additionally, coyote detectability was greater in control (p=0.63, 95% CI 0.59, 0.67) compared to treatment habitat (p=0.58, 95% CI 0.48, 0.67) but the difference between the habitat types was not significant (Fig 4). Mean detectability estimates of coyotes using Tilden-Sibley's interior and residential edge were 0.63 (95% CI 0.59, 0.67) and 0.73 (0.61, 0.83), respectively, lower than the 0.78 (95% CI 0.68, 0.86) detection probability estimate at wildland edge sites (Fig 4). Coyote detectability was positively correlated with recreation intensity, slope, elevation, and canopy cover, and negatively correlated with distance from water (Figs 4 and 5). In the competitive model, coyote detectability negatively correlated with distance from water (Fig 5).

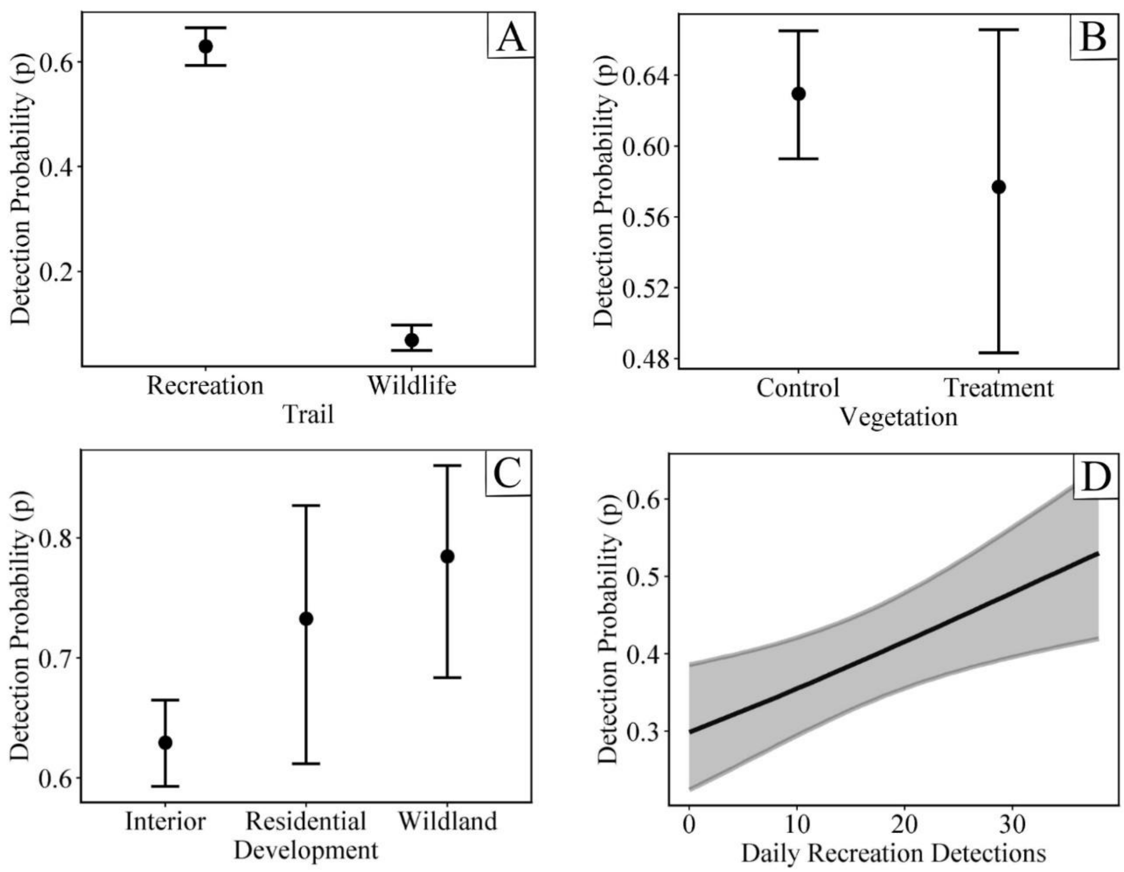

Figure 4. The effect of model variables associated with anthropogenic disturbance on detection probability from the top single-season single-species occupancy model for coyotes in Tilden-Sibley from 1 June to 15 September 2019 containing trail type (A), vegetation treatment (B), development stratum (C), and daily recreation detections (D) as covariates.

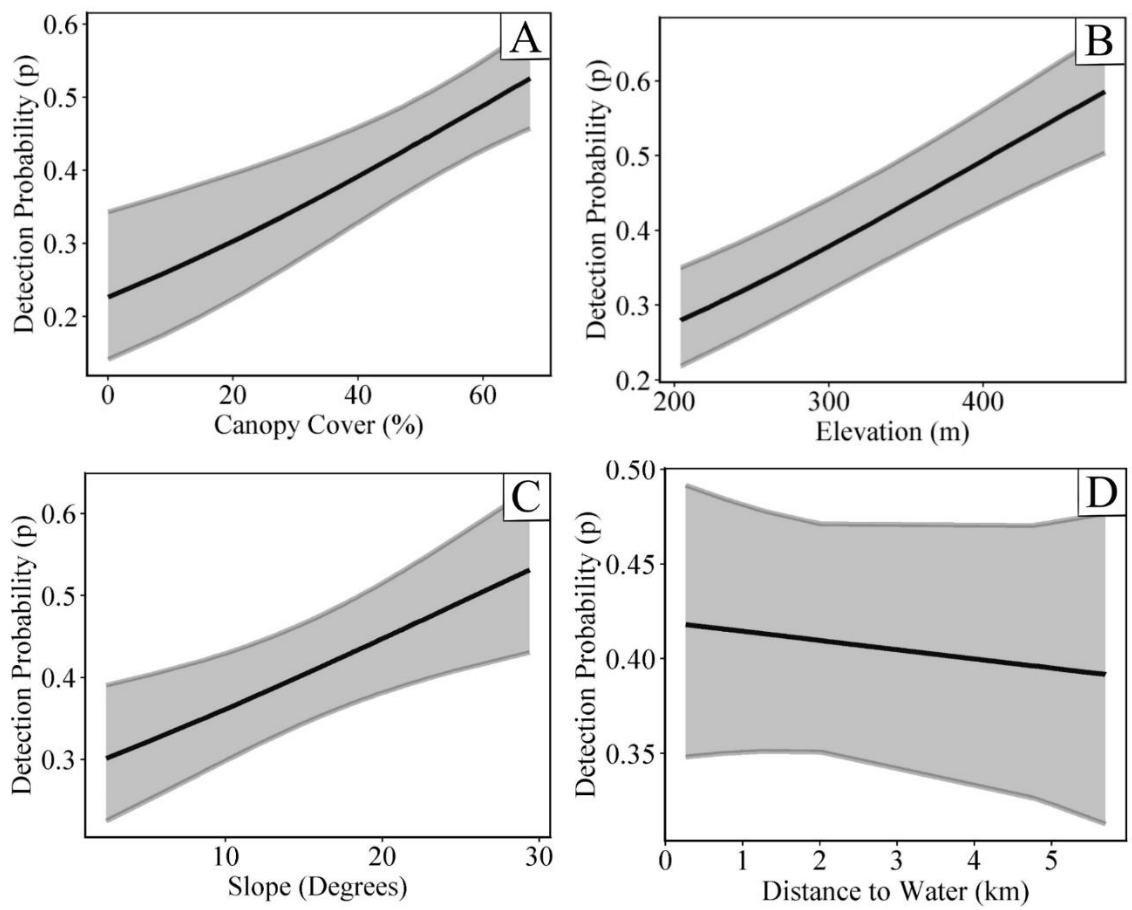

Figure 5. The effect of model variables associated with natural habitat characteristics on detection probability from the top two competitive single-season single-species occupancy model for coyotes in Tilden-Sibley from 1 June to 15 September 2019 containing percent canopy cover (A), elevation (B), slope (C) and distance to water (D) as covariates.

Bobcat

In total, 32 cameras over 58 survey occasions resulted in 1,834 functional surveys, 5% of which detected bobcats. Naïve occupancy for bobcats was 0.46 and no covariates were identified as influential on bobcat use of Tilden-Sibley. The top model for bobcat detection probability included trail type, slope, and distance to water as covariates but carried only 11% of the explanatory weight of the 390 models considered in the candidate set due to model uncertainty between the top 6 models (Table 2). According to the top model, bobcat detection probability was 1 (95% CI 0.99, 1.00) on recreation trails and 0.73 (95% CI 0.24, 0.95) on wildlife trails (Fig 6). Bobcat detectability negatively correlated with slope, and positively correlated with distance to water (Fig 6).

The next best model, which also carried 11% of explanatory weight, identified a negative relationship between bobcat detectability and daily recreation (Fig 6). Canopy cover was also identified as a significant covariate within the third best model carrying 8% of all models' weight that increased bobcat detectability (Fig 6). Daily coyote events acted as a significant covariate in the fifth competitive model carrying only 4% of the explanatory weight decreasing the detectability of bobcats (Fig 6). The cumulative weight of the top 6 models was 0.41 and all of these models contained different combinations of trail type, slope, recreation, coyote, distance to water, and canopy cover as covariates (Table 2). Vegetation treatment and developmental did not affect the bobcat detectability.

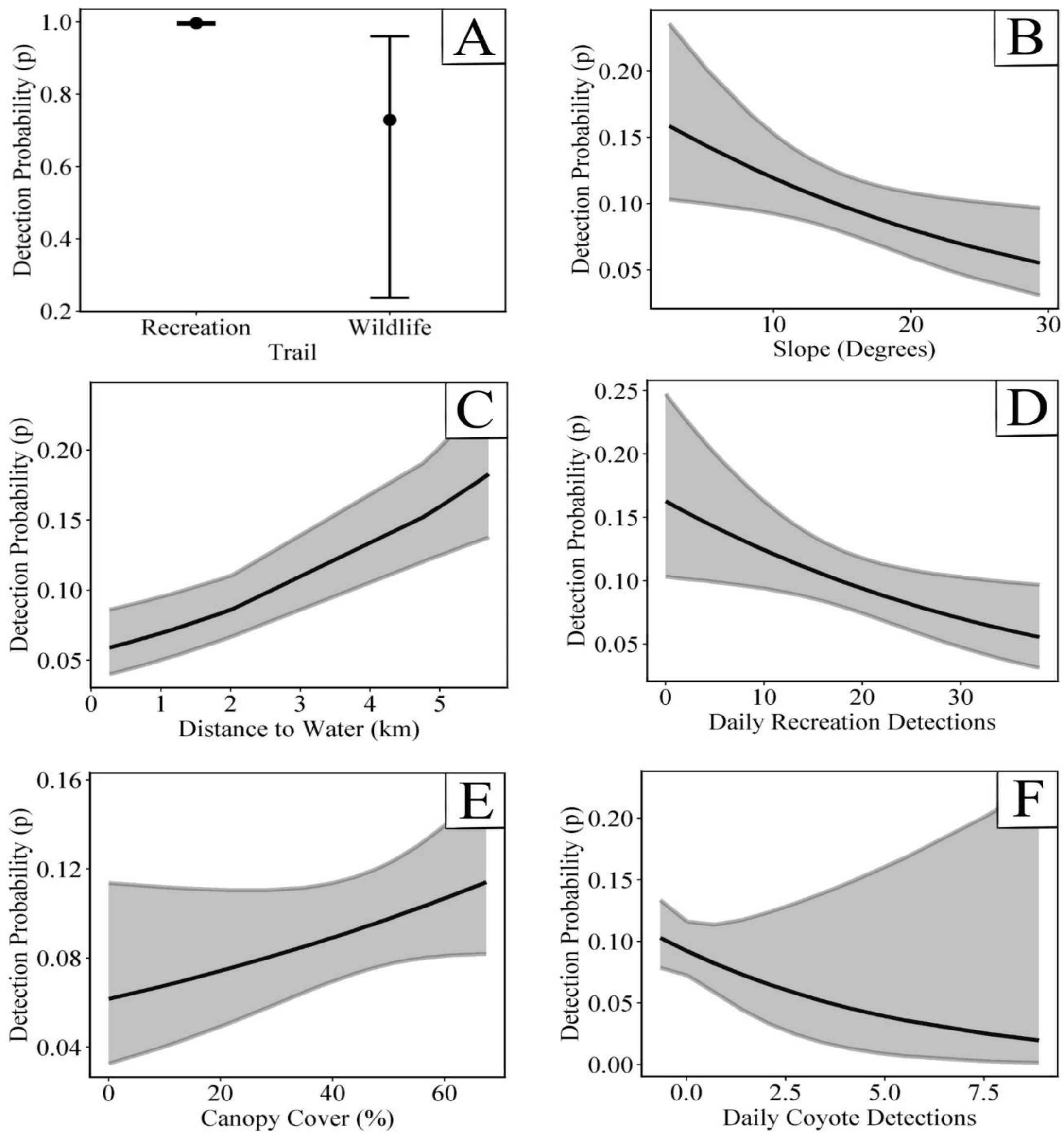

Figure 6. The effect of model variables associated with natural habitat characteristics on detection probability from the top six competitive single-season single-species occupancy model for bobcats in Tilden-Sibley from 1 June to 15 September 2019 containing trail type (A), slope (B), distance to water (C), daily recreation detections (D), canopy cover (E), and daily coyote detections (F) as covariates.

Gray Fox

In total, 32 cameras over 58 survey occasions resulted in 1,834 functional surveys, 3% of which detected gray foxes. Naïve occupancy for gray foxes was 0.38 and no covariates were identified as influential on gray fox use of Tilden-Sibley. The top model for gray fox detection probability included elevation and distance to water as covariates but carried only 13% of the explanatory weight of the 195 models considered in the candidate set due to model uncertainty between the top 4 models (Table 2). According to the top model, gray fox detection probability was negatively correlated with elevation and distance to water but positively correlated with percent canopy cover (Fig 7).

The next best model, which carried 10% of explanatory weight, identified a positive relationship between gray fox detectability and canopy cover (Fig 7). The third best model, which carried 10% of explanatory weight, identified a negative relationship between gray fox detectability and slope (Fig 7). The cumulative weight of the top 4 models was 0.40 and all of these models contained different combinations of trail type, slope, elevation, distance to water, and percent canopy cover as covariates. The effect of development stratum on gray foxes could not be modeled because inclusion of the covariate caused model convergence failures. Anthropogenic disturbance covariates trail type, treatment, recreation, and coyote detection events were not identified as significantly influential to gray fox detectability.

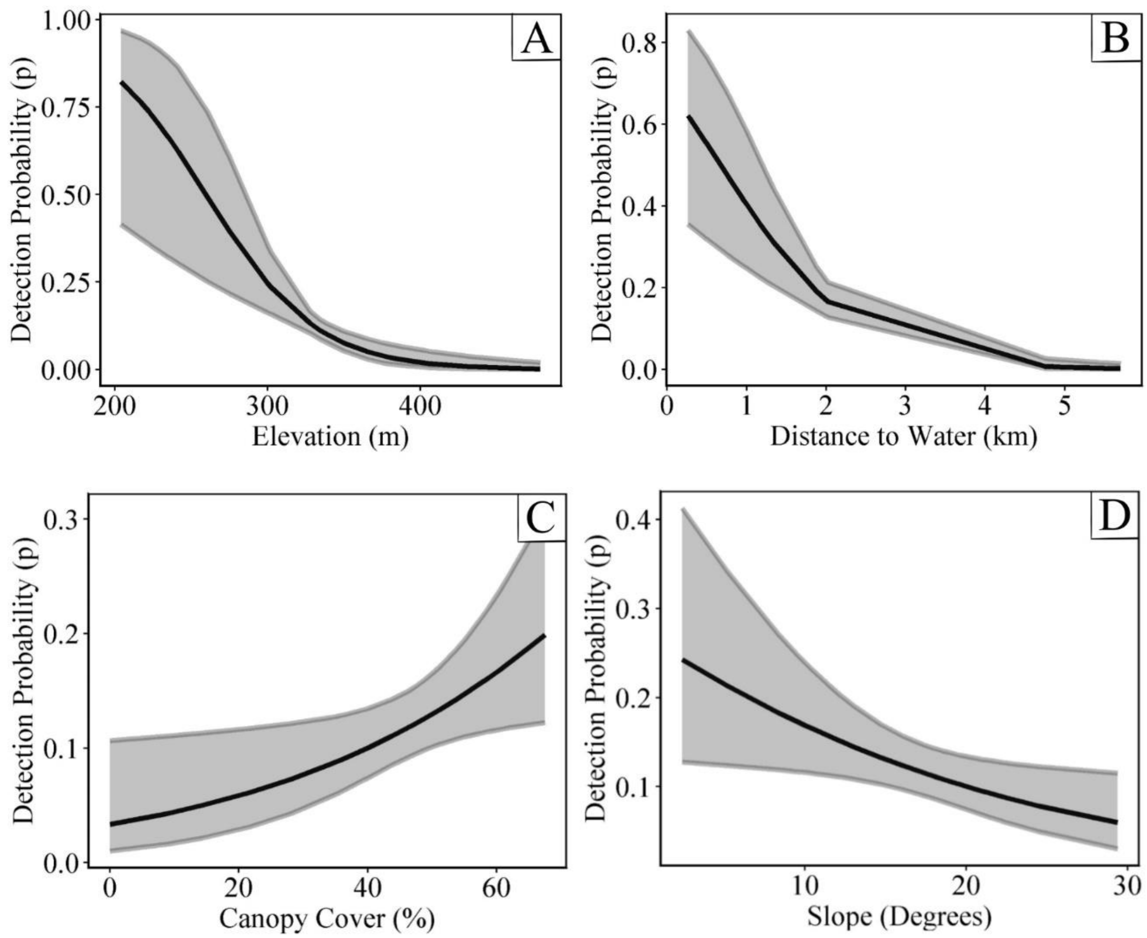

Figure 7. The effect of model variables associated with natural habitat characteristics on detection probability from the top four competitive single-season single-species occupancy model for gray foxes in Tilden-Sibley from 1 June to 15 September 2019 containing elevation (A), distance to water (B), percent canopy cover (C), and slope (D) as covariates.

<u>Red Fox</u>

In total, 32 cameras over 58 survey occasions resulted in 1,834 functional surveys, 3% of which detected red foxes. Naïve occupancy for red foxes was 0.22 and no covariates were identified as influential on red fox use of Tilden-Sibley. The top model for red fox detection probability included trail type, slope, and distance to water as cover as covariates and carried 45% of the explanatory weight of the 195 models considered in the candidate set (Table 2). According to the top model, red fox detection probability was 1 (95% CI 0.99, 1.00) on both recreation trails and wildlife trails, making the parameter estimate uninformative. Red fox detectability was positively correlated with slope and distance to water (Fig 8). The effect of development stratum on red foxes could not be modelled because inclusion of the covariate caused model convergence failures. Anthropogenic disturbance covariates treatment and recreation along with coyote detection events were not identified as significantly influential to red fox detectability.

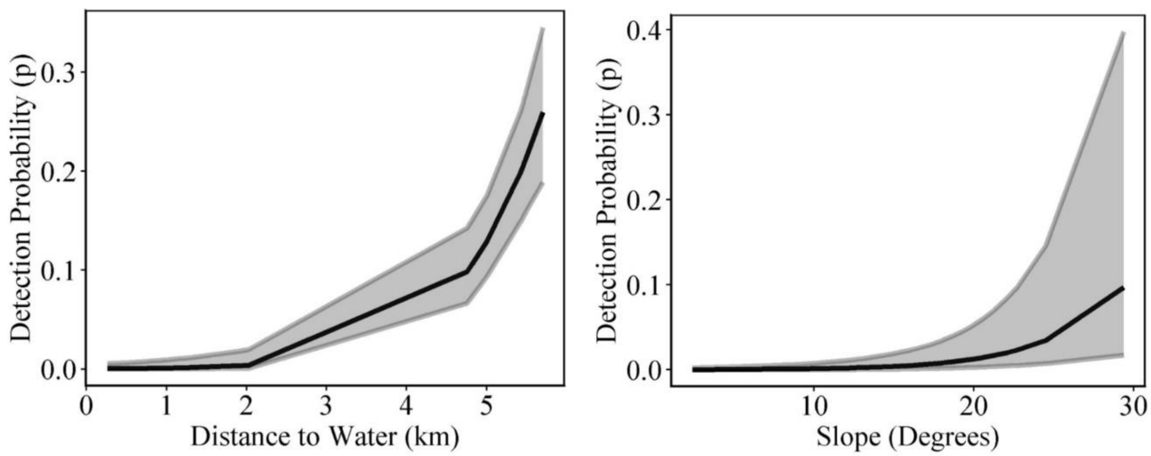

Figure 8. The effect of model variables associated with anthropogenic disturbance on detection probability from the top single-season single-species occupancy model for red foxes in Tilden-Sibley from 1 June to 15 September 2019 containing distance to water (left) and slope (right) as covariates. Trail type was also included in this model but the parameter was uninformative.

Temporal Overlap

Recreation and Wildlife Trails

Coyotes were significantly more nocturnal on recreation trails ($\hat{\Delta}_4$=0.26, 95% CI 0.24, 0.27) than wildlife trails ($\hat{\Delta}_4$=0.49, 95% CI 0.44, 0.53) and coyotes with visible disease symptoms overlapped twice as much with recreationists on park trails than apparently healthy coyotes ($\hat{\Delta}_4$= 0.23, 95% CI 0.21, 0.24; Fig 9). Coyotes were the only carnivore species observed interacting with recreationists on designated park trails and interactions sometimes took place diurnally (Fig 10). Bobcats also overlapped temporally with recreationists more on wildlife trails ($\hat{\Delta}_1$ = 0.47, 95% CI 0.28, 0.65) than recreation trails ($\hat{\Delta}_4$ = 0.25, 95% CI 0.20, 0.29, Fig 9). Both gray and red foxes were primarily nocturnal so their temporal overlap with recreationists was approximately equivalent on recreation trails (gray fox $\hat{\Delta}_4$= 0.13, 95% CI 0.10, 0.17; red fox $\hat{\Delta}_4$ = 0.14, 95% CI 0.09, 0.18) and wildlife trails (gray fox $\hat{\Delta}_4$= 0.16, 95% CI 0.12, 0.20; red fox $\hat{\Delta}_1$ = 0.12, 95% CI 0.00, 0.25; Fig 9).

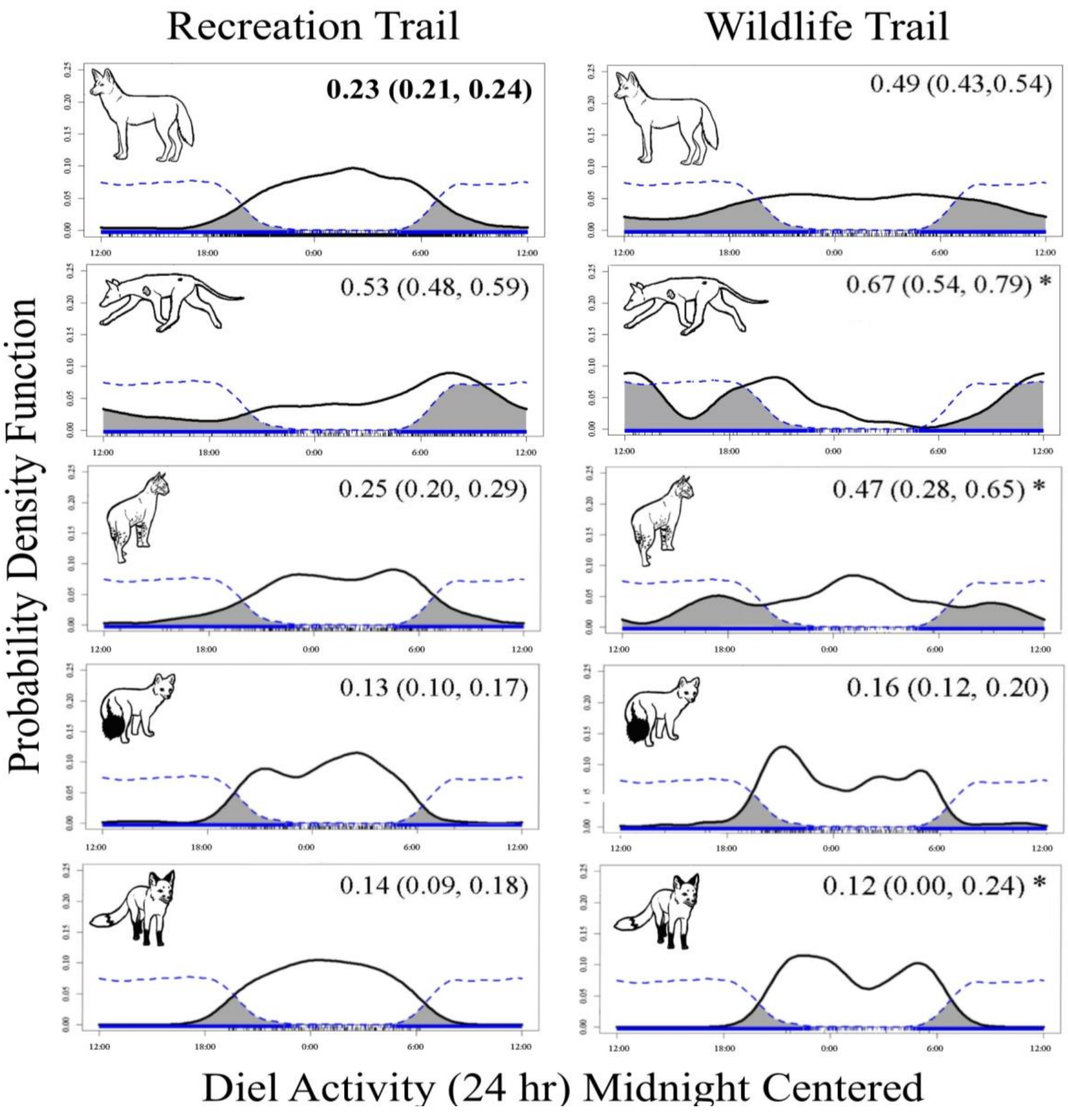

Figure 9. Overlapping 24 hr diel activity patterns (dark gray) between carnivore species (black solid line) and recreationists (blue dashed line) observed on recreation and wildlife trails in Tilden-Sibley from 1 June to 1 November 2019. The activity of healthy coyotes, diseased coyotes, bobcats, gray foxes, and red foxes are shown in

descending order. Overlap coefficients are reported with 95% confidence intervals. Bolded text denotes when a species was significantly more nocturnal on recreation or wildlife trails. Asterisks denote low sample size.

Figure 10. Coyote and recreationist captured midday using the same recreation trail in Tilden Regional Park in September 2019.

Vegetation Treatment

Coyotes overlapped with recreationists significantly more in control ($\hat{\Delta}_4$= 0.34, 95% CI 0.30, 0.35) than treatment ($\hat{\Delta}_4$ = 0.27, 95% CI 0.24, 0.28) habitat but the difference in overlap between habitat types was greatest for coyotes with mange (Fig 11). Bobcats were significantly more nocturnal in treatment ($\hat{\Delta}_4$= 0.17, 95% CI 0.11, 0.22) versus control habitat ($\hat{\Delta}_4$= 0.35, 95% CI 0.28, 0.42, Fig 11). Gray foxes were almost exclusively nocturnal in both treatment ($\hat{\Delta}_4$= 0.14, 95% CI 0.11, 0.17) and control habitat ($\hat{\Delta}_4$= 0.16, 95% CI 0.10, 0.23, Fig 11). Red foxes were similarly nocturnal in treatment ($\hat{\Delta}_4$= 0.15, 95% CI 0.10, 0.20) and to control habitat ($\hat{\Delta}_1$ = 0.13, 95% CI 0.06, 0.19, Fig 11).

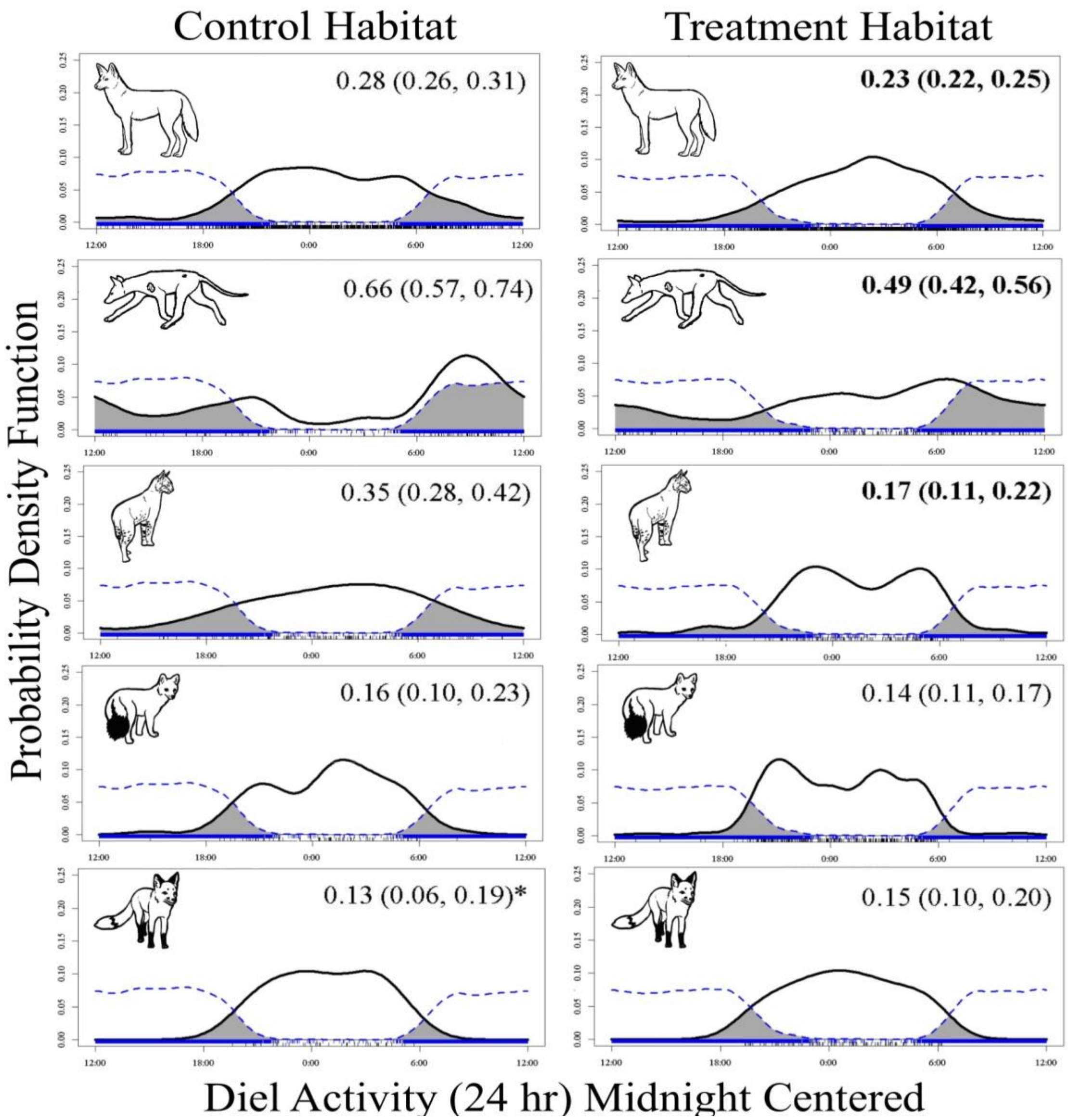

Figure 11. Overlapping 24 hr diel activity patterns (dark gray) between carnivore species (black solid line) and recreationists (blue dashed line) observed in control and treatment habitats in Tilden-Sibley from 1 June to 1 November 2019. The activity of healthy coyotes, diseased coyotes, bobcats, gray foxes, and red foxes are shown

in descending order. Overlap coefficients are reported with 95% confidence intervals. Bolded text denotes when a species was significantly more nocturnal in control or treatment habitat. Asterisks denote low sample size.

Development and Recreation Intensity

Coyotes that appeared healthy overlapped with recreationists significantly less on Tilden-Sibley's wildland edge ($\hat{\Delta}_4$ = 0.20, 95% CI 0.18, 0.22) than its interior ($\hat{\Delta}_4$ = 0.32, 95% CI 0.29, 0.36) or residential edge ($\hat{\Delta}_4$= 0.28, 95% CI 0.26, 0.31) while mangy coyotes overlapped with recreationists the least on the residential edge ($\hat{\Delta}_4$= 0.44, 95% CI 0.33, 0.55) and the most on the wildland edge ($\hat{\Delta}_4$= 0.69, 95% CI 0.61, 0.77, Fig 12). Overall, coyotes were significantly more nocturnal when recreation intensity was high ($\hat{\Delta}_4$ = 0.25, 95% CI 0.23, 0.26) than when it was medium ($\hat{\Delta}_4$ = 0.35, 95% CI 0.32, 0.39) or low ($\hat{\Delta}_4$ = 0.35, 95% CI 0.31, 0.40) but when coyote detections were divided into mange negative and positive categories this trend was apparent but not statistically significant (Fig 13). Bobcats overlapped with recreationists less in residential ($\hat{\Delta}_4$= 0.16, 95% CI 0.09,0.24) habitat compared to interior ($\hat{\Delta}_4$ = 0.29, 95% CI 0.22, 0.37) and wildland ($\hat{\Delta}_4$ = 0.29, 95% CI 0.22, 0.36) habitat but the difference was not significant (Fig 12). Bobcats were most nocturnal in sites where the recreation level was high ($\hat{\Delta}_4$ = 0.16, 95% CI 0.11, 0.22) versus medium ($\hat{\Delta}_4$= 0.26, 95% CI 0.18, 0.33) or low ($\hat{\Delta}_4$= 0.31, 95% CI 0.22, 0.41, Fig 13).

Gray fox activity also did not vary significantly between residential ($\hat{\Delta}_4$= 0.16, 95% CI 0.13, 0.19), interior ($\hat{\Delta}_4$= 0.14, 95% CI 0.08, 0.27), and wildland habitat ($\hat{\Delta}_1$= 0.15, 95% CI 0.06, 0.24, Fig 12). Gray fox overlap with recreationists did not vary significantly between high ($\hat{\Delta}_4$= 0.16, 95% CI 0.13, 0.20), medium ($\hat{\Delta}_1$ = 0.11, 95% CI 0.05, 0.18), and low ($\hat{\Delta}_1$= 0.12, 95% CI 0.05, 0.19) level recreation sites (Fig 13). Red foxes were mostly nocturnal and overlapped the least with recreationists in wildland ($\hat{\Delta}_4$ = 0.10, 95% CI 0.05, 0.20) habitat versus residential ($\hat{\Delta}_4$= 0.20, 95% CI 0.13, 0.27) or interior ($\hat{\Delta}_1$ = 0.13, 95% CI 0.00, 0.27) but the difference in overlap between the strata was not significant (Fig 12). Red fox overlap with recreationists did not vary significantly between high ($\hat{\Delta}_4$ = 0.11, 95% CI 0.06, 0.16), medium ($\hat{\Delta}_1$ = 0.16, 95% CI 0.09, 0.24), and low ($\hat{\Delta}_1$ = 0.08, 95% CI 0.00, 0.20) level recreation sites (Fig 13).

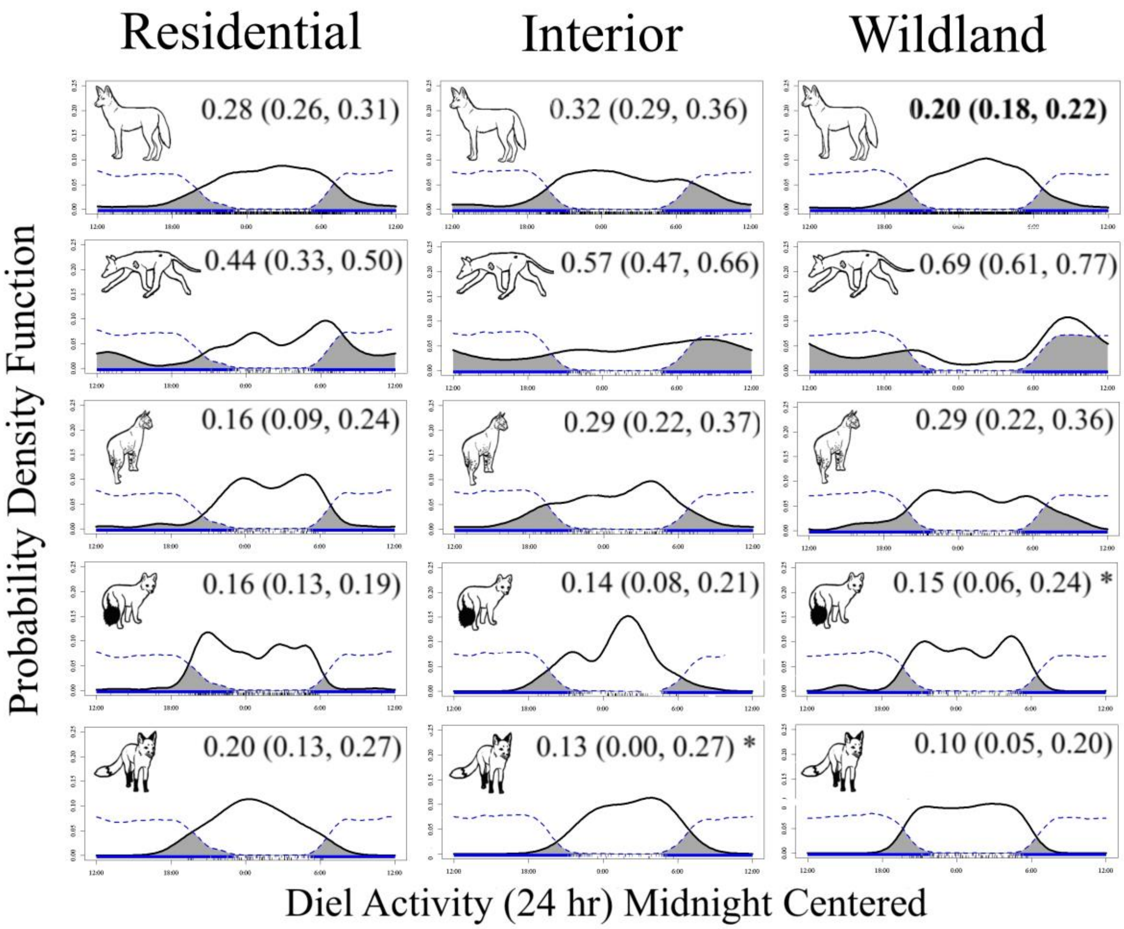

Figure 12. Overlapping 24 hr diel activity patterns (dark gray) between carnivore species (black solid line) and recreationists (blue dashed line) observed in control and treatment habitats in Tilden-Sibley from 1 June to 1 November 2019. The activity of healthy coyotes, diseased coyotes, bobcats, gray foxes, and red foxes are shown in descending order. Overlap coefficients are reported with 95% confidence intervals. Bold text denotes when a species is significantly more nocturnal in residential edge, park interior, or wildland edge habitat. Asterisks denote low sample size.

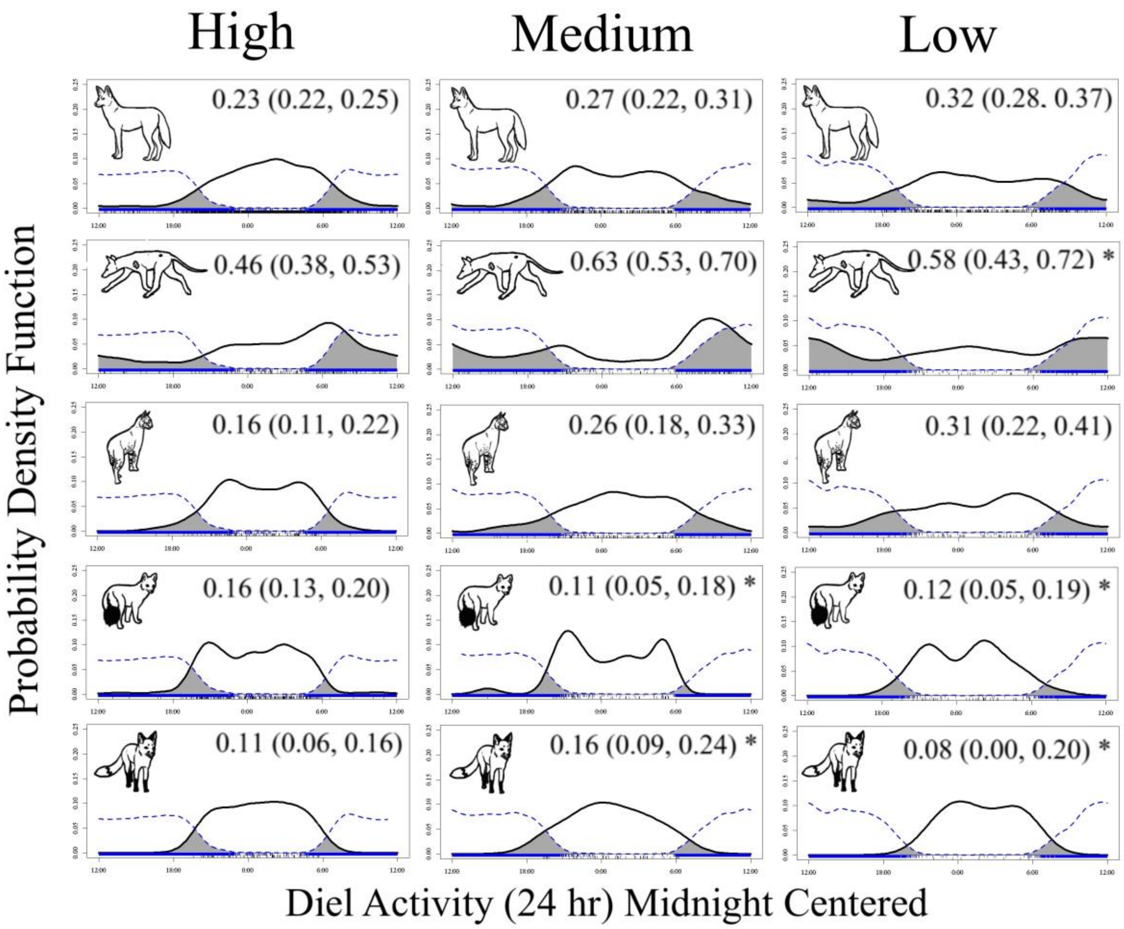

Figure 13. Overlapping 24 hr diel activity patterns (dark gray) between carnivore species (black solid line) and recreationists (blue dashed line) observed in control and treatment habitats in Tilden-Sibley from 1 June to 1 November 2019. The activity of healthy coyotes, diseased coyotes, bobcats, gray foxes, and red foxes are shown in descending order. Overlap coefficients are reported with 95% confidence intervals. Asterisks denote low sample size.

Sympatric Overlap with Coyotes

Bobcats overlapped temporally with coyotes significantly more ($\hat{\Delta}_4$ = 0.94, 95% CI 0.90, 0.97) than both red foxes ($\hat{\Delta}_4$ = 0.83, 95% CI 0.78, 0.88) and gray foxes ($\hat{\Delta}_4$= 0.83, 95% CI 0.79, 0.86) but overlap between the sympatric carnivores and coyotes was high overall (Fig 14).

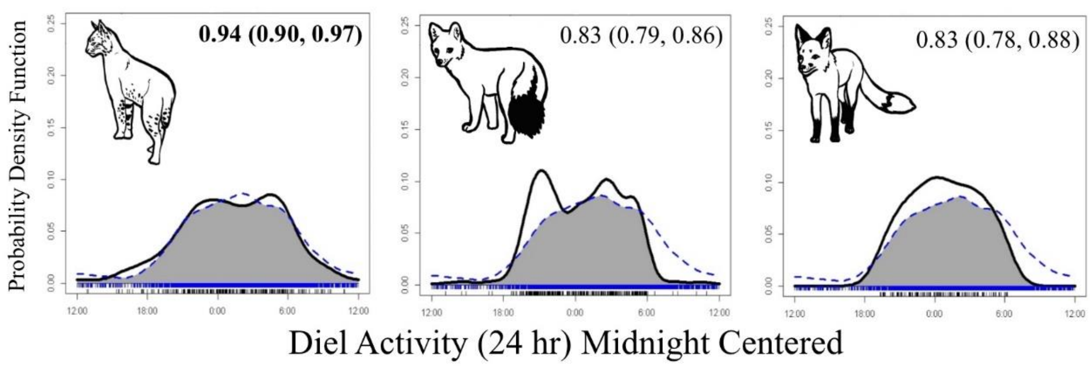

Figure 14. Overlapping probability density functions (gray) displayed with coefficients of overlap and 95% confidence intervals between bobcats (left), gray foxes (middle), and red foxes (right) and coyotes detected in Tilden-Sibley from 1 June to 1 November 2019. Coyote temporal activity is denoted by the dashed blue line while bobcats, red foxes, and gray foxes are represented by unbroken black lines.

DISCUSSION

All forms of anthropogenic disturbance - recreation, vegetation management, and development - played different roles in shaping the spatiotemporal distribution of focal mesocarnivore species along the WUI and within the Tilden-Sibley park system. A two-pronged detection approach enabling simultaneous surveying of recreation trails and wildlife trails proved successful in revealing significant yet variable alterations to the spatiotemporal detectability of focal species, which serve as indices for underlying activity patterns (Mackenzie et al. 2002, Ridout and Linkie 2009). Nocturnality is an increasingly ubiquitous behavioral adaptation that allows mammals to persist on the urban interface. When carnivore species that would normally be active throughout the day have their activity bottlenecked to low light hours, wildlife community dynamics are altered by the increased likelihood of intraguild antagonism (Gaynor et al. 2018, Moll et al. 2018, Patten et al. 2019, Nickel et al. 2020).

Habitat disturbance can confer competitive advantages to the life history strategies of some species over others, creating a homogenizing effect for biodiversity in human-dominated landscapes (McKinney et al. 2006). This trend has greatly benefited coyotes that have almost doubled their historic range in the continental United States in only a few decades and their genome change in response to an urban lifestyle (Prugh et al. 2009, Bateman and Fleming 2012, Santini et al. 2019, Adducci et al. 2020). This study confirmed the results of previous research conducted in the East Bay Hills finding that coyotes were the most detectable carnivore species (Farmer and Allen 2019); I found coyotes were detected over 10 times more frequently than any other carnivore in Tilden-Sibley.

I predicted that coyotes would be more active in habitat disturbed by recreation, vegetation treatment, and development than bobcats and foxes and found instead that coyotes showed varied responses to different forms of anthropogenic disturbance, bobcats only responded to recreation spatially and vegetation treatment temporally, and both fox species were primarily nocturnal and not influenced spatially by disturbance. Coyote and bobcat detectability increased and decreased with recreation intensity, respectively. These results were somewhat surprising for coyotes but not for bobcats, considering several studies in Southern California have demonstrated adverse effects of recreation on both species (George and Crooks 2006, Baker and Leberg 2018). Studies conducted in California's central coastal region, however, suggest that diel activity shifts were a more common response to recreationist presence than altered space use patterns (Wang et al. 2015, Nickel et al. 2020).

In this study, coyotes were significantly more nocturnal at highly recreated sites where they were detected more frequently. Behavioral plasticity allows coyotes to make use of human dominated landscapes via temporal partitioning, thus coyotes' positive association with recreation in this study should not be interpreted as preference for disturbed habitat. Indeed, the probability of detecting coyotes increased with slope, elevation, canopy cover, and was highest on Tilden-Sibley's wildland edge, suggesting that coyotes were more active in habitats limiting human access and visibility (Gehrt et al. 2009, Nagy et al. 2011, Gese et al. 2012). Bobcats did not show a strong negative association with development despite previous findings, but the spatial extent of this study may have been too small to detect this effect as even the least developed habitat was only several kilometers away from the study area's residential edge (Riley et al. 2002, Ordeñana et al. 2010, Larson et al. 2015, except see Lewis et al. 2015).

Both gray foxes and red foxes have a demonstrable record of positive association with recreation intensity and development, albeit commensurate with available adjacent green space (Riley 2006, Erb et al. 2012, Kapfer and Kirk 2012, Larson et al. 2015, Moll et al. 2018), but no human disturbance covariates were identified as influential to their detectability in this study. Spatial modeling did not suggest evidence of anthropogenic impacts most likely because both fox species were detected in only 3% of occupancy surveys. Low detectability overall may suggest competitive exclusion of gray foxes and red foxes from most of Tilden-Sibley by coyotes, which in contrast were detected in a quarter of surveys. Unfortunately, the low detectability of fox species combined with a limited amount of spatial sampling replicates obscured spatial covariate effects.

Coyotes were less detectable in habitat designated for fuel reduction treatment than in control habitat while both coyotes and bobcats were significantly more nocturnal in treatment areas. These results suggest that eucalypt habitat could provide less diurnal refugia for mesocarnivores than native habitat. It is also possible that treatment habitat could act as local heat islands, as eucalyptus trees dry their immediate surroundings as a competitive strategy, potentially explaining increased nocturnality as a thermoregulatory behavior (Ferreira et al. 2000). If this were the case, the impetus to restore these habitats to reduce fire risk would also benefit mammalian wildlife. Alternatively, features such as canopy cover that are known to alter coexistence dynamics between people and wildlife by providing refugia may be partially responsible for the treatment impacts observed as treatment areas were in varying stages of planned thinning (Riley 2006, Kapfer and Kirk 2012, Breck et al. 2019, Nickel et al. 2020). This study found that increasing canopy cover increased the detectability of coyotes, bobcats, and gray foxes, indicating that the achievement of WHRRMP's target reduction of tree cover to 50% could disturb the activity of these species.

I predicted that all carnivores would be more nocturnal on recreation trails than wildlife trails in order to avoid primarily diurnal recreationists and that trail type would disproportionately affect coyotes exhibiting greater range in diel activity than bobcats or foxes, and the results of this study supported these predictions. Coyotes and bobcats were more detectable and more nocturnal on recreation trails than wildlife trails while the detectability of fox species was not influenced by trail type. In Canada, coyotes overlapped with recreationists significantly less on recreation trails than wildlife trails in and around Banff National Park (Hojnowski 2017), but coyotes in Tilden-Sibley were two times more likely to be detected nocturnally on recreation trails and were more nocturnal overall, highlighting that the impact of recreation is intensified by urbanization, as the Bay Area is much more populous and built up than Banff National Park. This significant skew of coyote activity toward nocturnality in anthropogenically disturbed habitat, which recreation trails represent, increases the probability of intraguild antagonism, especially with primarily nocturnal fox species that are both competitors and prey to coyotes (Moll et al. 2018, Patten et al. 2019).

The persistence of dense coyote populations in WUI natural areas frequented by people and their pets is considered a leading source of human-wildlife conflict across the continental United States; therefore, this study's discovery that coyotes were significantly more detectable using recreation trails than more natural habitat could cause alarm to some stakeholders (Poessel et al. 2016). This alarm is especially salient in light of recent incidents of coyotes biting people in East Bay Parks (NBC Bay Area 2020, CDFW 2021). Increased use of recreation trails by carnivore species should not necessarily be interpreted as a display of preference for anthropogenically disturbed habitat, however, as the linear travel routes established trails provide may facilitate passing through a disturbed area more quickly than a species could using wildlife-made trails.

I also predicted that bobcats, red foxes, and gray foxes would be least detectable when and where coyotes are most active but found only bobcat detectability to be influenced by coyotes. Notably, bobcats exhibited directly opposing natural habitat preferences to coyotes in addition to being less detectable with daily coyote detections. Together, these trends suggest coyotes are competitively excluding bobcats (Fedriani et al. 2000, Crooks 2002, Larson et al. 2015, Smith et al. 2018). Gray foxes and red foxes overlapped temporally significantly less with coyotes than bobcats because they were significantly more nocturnal, which was also observed in the neighboring Santa Cruz Mountains (Wang et al. 2015, Nickel et al. 2020). Although it is unclear whether fear of the human ‘super predator’ or intraguild predation takes precedence for foxes, it is clear from the lack of detectable activity that Tilden-Sibley represents sub-optimal habitat for foxes (Fedriani et al. 2000, Gaynor et al. 2019, Patten et al. 2019, Suraci et al. 2019).

Disease also emerged as highly influential to the behavior of coyotes. In light of the recent global health crisis caused by a novel coronavirus with zoonotic origins, disease in wildlife populations has taken a devastating new spotlight, although it has long been a major source contributing to human-wildlife conflict especially in urban or urbanizing environments (Bradley and Altizer 2006, Brearley et al. 2012, Bar-Massada et al. 2014). Mange, in particular, has been well studied due to its conspicuousness and capacity for interspecific transmission that has been known to impact humans (Niedringhaus et al. 2019, Pisano et al. 2019). This study found that temporal activity overlap between recreationists and mangy coyotes on park trails was double that of healthy coyotes, confirming the prediction that positive disease state would influence coyote activity in ways that would increase the likelihood of their co-occurrence with people (Murray et al. 2015). Activity patterns of healthy coyotes on wildlife trails and mangy coyotes on recreation trails were almost identical, suggesting that coyotes with mange are less likely to avoid recreationists spatially or temporally and thus are significantly bolder than apparently healthy coyotes, which is likely due to their compromised state altering risk assessment (Breck et al. 2019).

Human disturbance can adversely impact the fitness of wildlife species, especially by way of stress and environmental toxicants. When carnivores consume anticoagulant rodenticides used by people to control unwanted rodent populations, for example, by preying on poisoned rodents, the resulting immune system suppression exacerbates the hypersensitive response to mite infestation (Fraser et al. 2018, Serieys et al. 2018). California legislators placed a consumer ban on second generation ARs in 2014 due to concerns over the prevalence of poisoned predator species, but the law allowed commercial use of hyper potent second generation ARs to continue and no limitations were placed on household first generation AR use (CDPR 2018). Thus, a growing problem faced by public agencies managing WUI land is their lack of control over private actions that may jeopardize public health and ecological resiliency (NPS 2019).

Whether other causes of immune system dysfunction can illicit similarly extreme mange pathologies in mammals remains unknown. Ingesting food from aggregated sources such as residential compost piles exposed coyotes to both rodent hosts of *Sarcoptes scabiei* and immunosuppressive levels of mycotoxins in Canada and so was hypothesized to have advanced mange pathogenesis, making a poor diet of anthropogenic food subsidies another potential cause of epizootic disease (Murray et al. 2016). Exposure to herbicides such as Garlon 4 Ultra and Roundup have not been linked to disease in wild mammals and deforestation has been linked to leishmaniasis but not mange in wild canids (Aguirre et al. 2009). Mange has only been correlated with vegetation removal in semiarboreal species such as gorillas (*Gorilla beringei beringei*; Kalema-Zikusoka et al. 2002). However, immunosuppression is a well-substantiated symptom of physiological stress in mammals, which can occur as a reaction to numerous forms of landscape disturbance including vegetation management (Bradley and Altizer 2006, Brearley et al. 2012, Rowe et al. 2019). Ultimately, this study serves to showcase the importance of accounting for multi-faceted, potentially additive, and disparate effects of different types of anthropogenic disturbance on wildlife activity when evaluating land management practices intended to promote biodiversity and restore native habitat.

Caveats

This study's paired camera trap design delivered robust temporal inferences but notably failed to detect any covariate effects on focal species habitat use or occupancy. Occupancy model performance is enhanced with high replication of spatial sampling units so discerning the impacts of different covariates becomes constrained with fewer sites. The spatial extent of the study area coupled with high landscape heterogeneity likely obscured occupancy covariate effects. Vegetation treatment also occurred on a rolling basis so longitudinal monitoring will be necessary for determining the long-term impacts of management actions on the activity and apparent health of focal mammal species. As more treatment areas within camera trap surveyed parks are mechanically and chemically treated, a higher percentage of the local landscape will be disturbed through time, thus enabling the observation of associated changes in apparent disease status and habitat use of mammals whose home ranges include both treatment and control habitat. In addition to extending monitoring efforts through time, expanding the spatial extent of monitoring by deploying additional cameras may be equally necessary to disentangle the effects of treatment habitat, treatment schedule, and other influential factors on mesocarnivore space use.

CONCLUSION

Managing multi-use WUI landscapes in ways that support native biodiversity while meeting peoples' needs for safety and satisfaction where they live and recreate poses a major challenge to human populations worldwide as urbanization expands. This study attempted to explicate how various forms of anthropogenic disturbance, namely, recreation, development, and vegetation treatment converge to shape wildlife activity and thereby influence fitness outcomes for competitively advantaged and disadvantaged species (Gaynor et al. 2018, Moll et al. 2018, Patten et al 2019, Santini et al. 2019). Coyotes were identified as the superior competitor to bobcats, gray foxes, and red foxes in Tilden-Sibley, and spatiotemporal analyses illuminated the behavioral plasticity that enabled coyotes to dominate the area, possibly outcompeting smaller mesocarnivores, but also succumbing to a contagious disease - a devastating consequence of high population density and an urbanized diet (Bateman and Fleming 2012).

The structure of Tilden-Sibley's carnivore guild with coyotes as the top competitor is becoming increasingly ubiquitous across the continental United States, with resounding calls from the American public to either enhance coexistence practices or engage in futile attempts at eradication (Poessel et al. 2016, CDFW 2021). Mobile phone apps such as iNaturalist have seen a steady rise in interactions between coyotes and people, ranging from benign sightings to antagonism resulting in injury or property damage (CDFW 2021). Currently, there is little established knowledge regarding the efficacy of many well-known coexistence strategies such as hazing, administering birth control, or even which domestic animal enclosures are capable of deterring depredation. Instead, management actions concerning coyotes often take the form of lethal removal of problem individuals that threaten human safety and property (CDFW 2021).

Ultimately, stakeholders from land management specialists to casual recreationists must be willing to take steps towards limiting anthropogenic impacts by removing pollutants, developing methods for sustainable, equitable, and secure waste disposal, protecting remnant natural habitat from development, improving transportation infrastructure, and attempting to restore degraded habitat. The WHRRMP is one such attempt to slowly phase out exotic and highly flammable habitat to promote the reestablishment of native floral assemblages. Indeed, this study revealed that habitat dominated by eucalyptus does disturb the activity patterns of mammalian carnivores in ways that increase the probability intraguild antagonism, which could result in the guild changing irreversibly over time. Therefore, native habitat restoration even without limiting recreation access, could help deter both interspecific and human-wildlife conflict and promote coexistence and biodiversity.

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