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Coyote (*Canis latrans*) Habitat Use
in an Altered Ecosystem

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Cover Photograph: A coyote (*Canis latrans*) crosses a hiking trail in Berkeley, CA. Photograph © Morgan Farmer.

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Persistence in the Face of Change: Effects of Human Recreation on Coyote (*Canis latrans*) Habitat Use in an Altered Ecosystem

Morgan J. Farmer^{1,2,*} and Maximilian L. Allen^{2,3}

Abstract - We investigated the spatiotemporal relationship of *Canis latrans* Say (Coyote) with environmental and human recreation variables in an altered Eucalyptus ecosystem in California, USA using camera traps and vegetation surveys. We documented Coyotes at eight of nine camera trap sites, and our top *a-priori* model to explain Coyote spatial use included tree density and abundance of human recreationists as explanatory variables (wAICc = 0.98). We found low temporal overlap between humans and Coyotes ($\Delta_4 = 0.40$), with Coyote activity peaking around 4 am when humans were not active. This appears to be a shift in Coyote temporal activity to avoid humans, as Coyotes typically exhibit crepuscular activity cycles. Coyotes appeared able to adjust to the altered ecosystem, and instead their spatial use and temporal activity was most affected by human recreation.

Introduction

Preserving ecological functions, including predator-prey interactions, is imperative to overall ecosystem integrity and health (Estes and Palmisano 1974, Miller et al. 2001). *Canis latrans* Say (Coyote) serve several ecological functions, especially in areas where apex carnivores have been extirpated and Coyotes have filled the role of apex carnivores within the system (e.g., Crooks and Soulé 1999, Gommel 2002, Levi and Wilmers 2012, Prugh et al. 2009, Wang et al. 2015). Coyotes and other apex carnivores exert a regulatory effect on both prey species and smaller carnivores. In areas where hunting is prohibited, such as wildland-urban interfaces, Coyotes and other natural predators may be the primary control on herbivore species such as deer and squirrels (Jones et al. 2016, Wambuguh 2008). Furthermore, as a result of trophic cascades, bird diversity is higher when Coyotes are present because they suppress the populations of smaller carnivores, such as *Felis catus* (Domestic Cats), *Procyon lotor* Linnaeus (Raccoons), and *Didelphis virginiana* Kerr (Virginia Oposums), that prey on birds (Crooks and Soulé 1999).

Coyotes are a widespread and adaptable species that is common from Panama to Alaska (Gese et al. 2008); however, Coyotes can exhibit sensitivity to disturbances from human activity and habitat fragmentation from human development through behavioral shifts (Crooks 2002, George and Crooks 2006, Wang et al. 2015). Coyotes are omnivorous, opportunistic feeders, and their diet can include small mammals, birds, reptiles, large invertebrates, carrion, fruits, and plants (Allen et al. 2015, Dumond et al. 2001, Hernández et al. 1994). In some areas, however, Coyotes have been able to use stable, human-provided food subsidies and shelter in urban areas, which could be due to habituation to humans (Larson et al. 2016), or to humans being viewed as a low-effort food source (George and Crooks 2006). Compared to their rural counterparts, urban Coyotes generally have smaller home ranges (Mueller et al. 2018) and a diet composed of more human food (Newsome et al. 2015). Coyotes can also be

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affected by human recreation, with observed spatial shifts due to human recreation and temporal shifts due to *Canis familiaris* Linnaeus (Domestic Dogs) or human recreation (George and Crooks 2006, Reed and Merenlender 2011). In the absence of disturbance, Coyotes are usually crepuscular or diurnal; however, they tend to shift towards nocturnal activity patterns when faced with human disturbance, such as recreation (Kitchen et al. 2000, Wang et al. 2015). Spatiotemporal activity patterns can be driven by prey availability or competition avoidance, so a shift in spatial or temporal activity due to recreation could result in different prey availability or competition with other carnivores (Cozzi et al. 2012, Gosselink et al. 2003, Ramesh et al. 2012).

Aside from recreation, urban and suburban wildlife species are also often faced with invasive species. Invasive species are an agent of global ecological change that can affect ecosystem function (Pimentel et al. 2005), lead to decreases in native wildlife species (Steidl et al. 2013) including endangered species (Pimentel et al. 2005), and create altered ecosystems (Hobbs et al. 2006). Despite the negative impacts of invasive species on many native species, it is possible for native wildlife to persist in altered ecosystems (Doody et al. 2009, Wright and Kelsey 1997). For example, *Cervus elaphus nelsoni* Bailey (Elk) and *Odocoileus virginianus* Zimmerman (White-tailed Deer) activity is higher in areas invaded by *Centaurea stoebe* ssp. *micranthos* Gugler (Spotted Knapweed) because Knapweed contains a similar energy and protein content to native forage, and is more easily acquired during the winter months (Wright and Kelsey 1997). Other native wildlife, however, do not benefit from invasive species (Doody et al. 2009, Medina et al. 2011, Steidl et al. 2013, Yamada and Sugimura 2004), as invasions cause losses of essential ecological functions performed by the native vegetation that is replaced. In these cases, the changes in habitat and resource availability can cascade and alter predator-prey interactions. For example, *Bromus tectorum* Klett and Richt (Cheatgrass) is an invasive plant that grows more densely than its native counterpart, which limits foraging and fleeing ability of species such as *Uta* sp. Baird and Girard (Side-blotched Lizards) and *Peromyscus* sp. Gloger (Deer Mice) (Litt and Pearson 2013, Mack 1981).

In Tilden Regional Park, a preserved area with high levels of human recreation located in the San Francisco Bay Area, Coyotes are present in an altered ecosystem composed of Eucalyptus habitat interspersed with the native Oak-Bay habitat. The *Eucalyptus globulus* Labillardière (Eucalyptus) trees were imported and planted as timber plantations between 1905 and 1920. The harvested lumber held little economic value, so the plantations were subsequently abandoned (Sax 2002). Due to a policy of minimal management, the Eucalyptus trees spread unchecked to create the altered ecosystem that is evident today (Robles and Chapin 1995, Sax 2002). After several major fires within the hills bordering the Bay Area cities of Oakland and Berkeley, the East Bay Regional Park Service shifted to active management of the protected areas. The Park Service created a Wildfire Hazard Reduction and Resource Management Plan, with the primary goal to reduce fire hazard through fire breaks along park boundaries and removal of Eucalyptus trees (LSA Associates 2010). Additional goals of the plan include maintaining and increasing plant and wildlife habitat, maintaining the aesthetics of each park for the community, and managing vegetation in a way that is financially and environmentally feasible (LSA Associates 2010).

Coyotes can exhibit sensitivity to habitat fragmentation and human recreation through behavioral shifts, and therefore can be used to indicate whether the altered habitat potentially maintains ecological functions or is unsuitable due to fragmentation (Crooks 2002, George and Crooks 2006, Wang et al. 2015). Our objectives were to use camera traps and vegetation surveys to 1) determine if differences in vegetation composition and structure exist between the native and invasive habitats, 2) determine whether Coyote relative

abundance was based on the vegetation composition and structure or human recreational activity (walking, jogging, biking, and dog walking) within the park by testing a set of *a-priori* hypotheses (Table 1), and 3) determine whether Coyotes were adjusting their temporal patterns to avoid the highest levels of human activity.

Materials and Methods

Study Area

Tilden Regional Park encompasses 2,065 acres (8.36 km²) of land in Contra Costa County and is managed by the East Bay Regional Park District (Wambuguh 2008). The land was originally part of a protected watershed and was purchased by East Bay Parks in 1983 from East Bay Municipal Utilities District. The park borders the cities of Berkeley (2016 population = 121,240 people), Albany (2016 population = 99,688 people), and Kensington (2010 population = 5,077 people) (US Census Bureau 2010, 2016). The area has a Mediterranean climate, with an average annual rainfall of 67.95 cm and average temperatures ranging from 9.11 to 19.89 degrees Celsius (Sax 2002, US climate data).

The landscape is a mosaic of predominantly two habitat types: Oak-Bay woodland and Eucalyptus forest. Oak-Bay woodlands primarily consist of *Quercus agrifolia* Guenée (Coast Live Oak) and *Umbellularia californica* Hook and Arn (California Bay Laurel). The vegetation species composition of the understory varies based on the amount of light that penetrates the canopy. Species such as *Toxicodendron diversilobum* Torr. and Gray (Poison

Table 1. Model table with our a-priori models to determine influences of Coyote (*Canis latrans* Say) habitat use within the study site.

| Model name | Variables | Hypothesis |
|--------------|-----------|--|
| Dogs | DOGS | The relative abundance of Dogs will be inversely related to the relative abundance of Coyote (Lenth et al. 2008). |
| Walkers | WALK | The relative abundance of human walkers will be inversely related to the relative abundance of Coyote (George and Crooks 2006, Wang et al. 2015). |
| Joggers | JOGG | The relative abundance of human joggers will be inversely related to the relative abundance of Coyote, due to the increased movement speed (George and Crooks 2006, Reed and Merenlender 2008). |
| Bikers | BIKE | The relative abundance of bikers will be inversely related to the relative abundance of Coyote, due to the increased movement speed and the lack of noise (George and Crooks 2006, Reed and Merenlender 2008). |
| Humans | HUMA | The relative abundance of humans will be inversely related to the relative abundance of Coyotes (George and Crooks 2008, Reed and Merenlender 2008, Wang et al. 2015). |
| Tree species | TRSP | Coyotes will preferentially select habitat with native trees (Ewers et al. 2002, Lin et al. 1996). |
| Tree density | TDEN | Coyotes will select areas with lower tree density (Barrett et al. 2012, Kamler et al. 2005, Koehler and Hornocker 1991). |

Oak) and *Dryopteris argute* Kaulf (Woodfern) are common in areas with closed canopies, whereas *Rubus ursinus* Cham. and Schldl (California Blackberry), *Gaultheria shallon* Pursh (Salal), and *Trientalis latifolia* Hook (Starflower) are common in areas where more light penetrates to the ground (LSA Associates 2008). The understory of the Eucalyptus habitat is primarily composed of non-native species, although *Heteromeles arbutifolia* Lindl. (Toyon) and *Baccharis pilularis* D.C. (Coyote Brush) do occur.

Data Collection

We used nine camera traps (m880i Gen2, Moultrie, Birmingham, AL USA) to measure human and wildlife activity at three sampling sites per each of three habitat types. For the duration of the study, fuel reduction treatments were being conducted throughout the park, in accordance with the Wildfire Hazard Reduction, Resource Management Plan. Since there were stands of selectively thinned Eucalyptus, in addition to the un-thinned Eucalyptus, we divided the study site into three habitat types: 1) Oak-Bay woodland, 2) thinned Eucalyptus, and 3) un-thinned Eucalyptus for comparison. Since the park encompasses only 8.36 km², we attempted to avoid pseudoreplication by ensuring that our camera trap density was approximately 1 camera trap per 1 km², which is often the recommended maximum density for camera placement (Maffel and Noss 2008, Moruzzi et al. 2002, O’Brien et al. 2003). Studies of larger carnivores suggest an even smaller maximum camera trap density of 2 or 4 km² to avoid pseudoreplication (Datta et al. 2008, Johnson et al. 2006, Kawanishi and Sunquist 2004). However, camera trap density

Table 1. Continued.

| Model Name | Variables | Hypothesis |
|--------------------|--|--|
| Canopy density | CDEN | Canopy density is related to understory composition, and Coyotes will select areas with higher canopy density because the understory will be thinner (Ehrenfeld 1980, Kamler et al. 2005). |
| Humans and cover | TDEN * HUMA | High human relative abundance will have negative effects on Coyotes, but can be mitigated or increased by the cover available based on tree density (Krausman et al. 2008). |
| Recreation | DOGS + HUMA | The combined effect of human recreation with Dogs will negatively affect Coyote relative abundance (Reed and Merenlender 2011). |
| Habitat | TDEN+TRSP | Tree species grow at different densities and less dense areas are more similar to historical Coyote home range (Ewers et al. 2002, Kamler et al. 2005, Lin et al. 1996). |
| Humans and habitat | TDEN+TRSP+HUMA | Tree species grow at different densities and will provide different levels of cover from humans (Ewers et al. 2002, Krausman et al. 2008, Lin et al. 1996). |
| Null model | - | |
| Global model | DOGS+CDEN+TRSP + TDEN + WALK + JOGG + BIKE | |

should be based on the minimum home range of the target species, which for urban Coyotes is 1 km² (Gese et al. 2012, González-Esteban et al. 2004). We therefore placed 9 camera traps to have a camera trap density of approximately 1 km².

To select possible camera trap sites, we used GIS shapefiles and management records from East Bay Regional Parks District and randomly generated points in ArcGIS version 10.4.1 (Environmental Systems Research Institute, Redlands, CA). We based selection of possible sites on two criteria: 1) the site must be in one of the three habitat types of interest, and 2) must be within 15 m of a recreational trail (to increase accessibility for data retrieval). We placed the camera traps at each site, within 1 m of the ground on trees that were located next to the trail. We directed the field of view of the camera trap down the trail to maximize the amount of time that an animal was within view of the camera trap and therefore maximize detections.

We deployed the camera traps on 15 June 2016, and they remained in the field until 4 October 2016. During this time, we checked and serviced the camera traps every two to four weeks. We reviewed the photographs from the memory cards and recorded the date, timestamp, temperature, species, and number of animals in each photograph. We accounted for pseudoreplication by considering multiple photographs of a species that occurred within two minutes of a previous photograph to be the same event.

To gather vegetation data, we conducted vegetation surveys on all nine study sites on 8–9 October 2016. Each study site consisted of a 15 m² quadrat with the camera trap as the center point. We used a spherical densiometer to take four canopy density measurements per site while standing one meter in front of the camera trap and facing each cardinal direction, and then we averaged the four canopy density readings for a single canopy density measurement per site. We used a diameter tape to measure the diameter at breast height (dbh) of every tree over 7.62 cm in diameter contained within the 15 m² study site. Each tree within the square was identified to species, and tree density was calculated based on the number of trees in each site.

Statistical Analyses

We performed all statistical analyses using R version 3.3.1 (R Core Team 2016). We first tested for differences in vegetation composition and structure among the three habitat types. Vegetation variables tested included average dbh, canopy density, percent native tree species as a proxy for habitat type, and tree density (Table 2). We used Levene's test to test for normality of our data. We then used an Analysis of Variance (ANOVA) when the data was normally distributed, and in cases where the data was not normally distributed, we used a Welch's test (Whitlock and Schluter 2015).

We calculated a relative abundance index (*RAI*) at each camera trap site for each species as:

$$RAI = (D / TN) \times 100$$

where *D* is the number of detections and *TN* is the total number of trap nights that a camera trap was active (Allen et al. 2018, Jenks et al. 2011). We calculated relative abundance as opposed to using raw counts of events because relative abundance can be an accurate proxy for abundance (Parsons et al. 2017).

To determine the influences on Coyote relative abundance, we tested our *a-priori* hypotheses (Table 1) using generalized linear models (GLMs) with a Poisson distribution (log link) in the *lme4* package (Bates et al. 2015). We performed a GLM for each *a-priori* hypothesis, in addition to a null and a global model. We used Coyote events as our dependent variable and varied our fixed independent variables in each *a-priori* model. We calculated and used *RAI* as the indepen-

dent variable in the models for the four recreational variables: walkers, joggers, bikers, and dogs. We compared the models based on AICc weight (wAICc), and we considered our top models to be all the models within 0.90 cumulative wAICc (Burnham and Anderson 2002).

We used the *activity* (Meredith and Ridout 2017) and *overlap* (Rowcliffe 2016) packages to compare the temporal activity distributions of Coyotes and humans to determine whether Coyotes were temporally avoiding humans. First, we converted the time for each event into radians and then kernel densities. We then calculated overlap as a $\hat{\Delta}_4$ value with a 95% confidence interval for the temporal overlap between Coyotes and humans.

Results

Camera Traps

Our nine camera traps were operational for a total of 171 camera days ($\bar{x} = 19.0$, SE = 4.4). The camera traps at sites Ob_1 and Ob_3 malfunctioned during the study period and were replaced. A total of 11,305 pictures were taken, with a mean of 1,255 (± 299 SE) pictures at individual camera traps.

We documented wildlife species at all 9 camera sites. We detected Coyotes at eight of the nine sampling sites (all except for E_2), with an average \overline{RAI} of 86.4 Coyote events per one hundred camera trap days (Fig. 1). In total, there were 120 captures of Coyotes with a total of 130 Coyotes, with 92% of pictures containing a lone Coyote and 8% of pictures containing a pair of Coyotes. Pictures containing more than one Coyote were counted as one detection. Wildlife other than Coyotes accounted for 2.1% of the total pictures taken during the study period (Table 3). Aside from Coyotes, *Odocoileus hemionus californicus* Caton (Mule Deer) were the most common species, with a total of 122 pictures ($\overline{RAI} = 53.40$). Other species included *Lynx rufus californicus* Mearns (Bobcat) ($\overline{RAI} = 17.40$),

Table 2. Vegetation survey data for each camera location.

| Site | Site abbreviation | Tree density (Trees per m ²) | Percent native | Mean diameter at breast height (in) | Canopy density |
|-------------------|-------------------|--|----------------|-------------------------------------|----------------|
| Thin Eucalyptus 1 | Te_1 | 0.004 | 0.00 | 11.00 | 0.667 |
| Thin Eucalyptus 2 | Te_2 | 0.031 | 1.00 | 13.29 | 0.839 |
| Thin Eucalyptus 3 | Te_3 | 0.100 | 0.67 | 15.47 | 0.784 |
| Thin Eucalyptus 4 | Te_4 | 0.053 | 0.00 | 19.31 | 0.704 |
| Eucalyptus 1 | E_1 | 0.020 | 0.00 | 26.36 | 0.623 |
| Eucalyptus 2 | E_2 | 0.089 | 0.75 | 07.98 | 0.693 |
| Oak-bay 1 | Ob_1 | 0.020 | 1.00 | 07.08 | 0.888 |
| Oak-bay 2 | Ob_2 | 0.058 | 1.00 | 08.67 | 0.808 |
| Oak-bay 3 | Ob_3 | 0.031 | 1.00 | 09.83 | 0.693 |

Vulpes vulpes Linnaeus (Fox) ($\overline{RAI} = 5.57$), *Puma concolor* Linnaeus (Mountain Lion) ($\overline{RAI} = 0.25$), *Procyon lotor* Linnaeus (Raccoon) ($\overline{RAI} = 7.73$), *Mephitis mephitis* Schreber (Skunk) ($\overline{RAI} = 10.11$) and *Felis catus* Linnaeus (Domestic Cat) ($\overline{RAI} = 11.41$).

Humans either walking, jogging, or biking were detected at all nine cameras (Fig. 2). A total of 13,045 pictures of humans were taken with 85.7% walkers ($\overline{RAI} = 8989.66$), 9.1% joggers ($\overline{RAI} = 1108.07$), and 5.2% bikers ($\overline{RAI} = 649.40$). Dogs also were detected at all nine cameras, with a total of 2,532 pictures of dogs ($\overline{RAI} = 2346.30$). *Equus caballus* Linnaeus (Horses) were also observed at four of the cameras, with a total of 27 pictures ($\overline{RAI} = 13.90$).

Study Sites

None of the vegetation variables we tested varied significantly between habitat types. These included average dbh (Welch’s test, $p = 0.1794$), percent native (Welch’s test, $p = 0.324$), canopy density (ANOVA, $p = 0.253$), and tree density (ANOVA, $p = 0.859$).

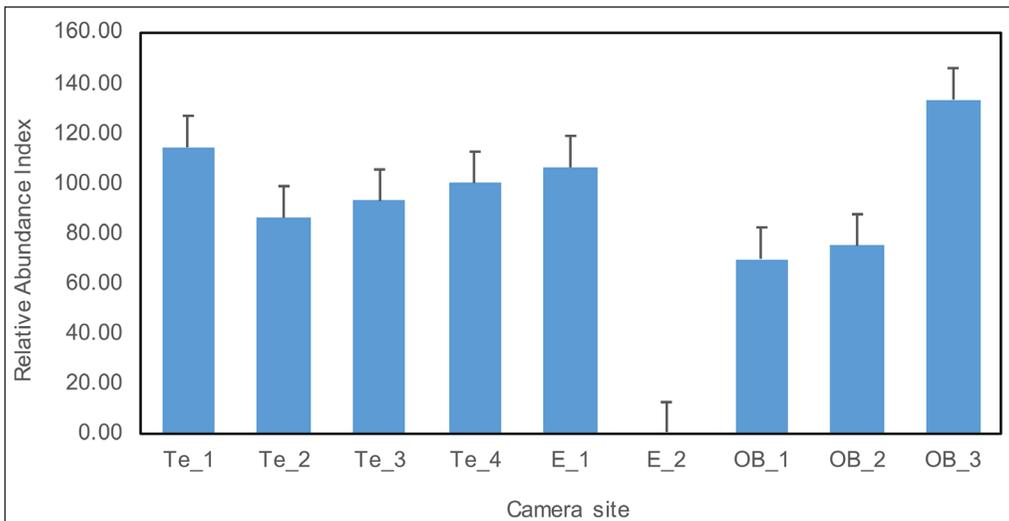


Figure 1. Relative Abundance Index (events per 100 camera trap days) for Coyotes (*Canis latrans* Say) (mean and SE) for each camera site within the study site.

Table 3. Relative abundance index (events per 100 camera trap days) for mule deer and other carnivores at each camera site within the study site.

| Site | Mule deer | Bobcat | Mountain lion | Fox | Raccoon | Skunk | Feral cat |
|------|-----------|--------|---------------|-------|---------|-------|-----------|
| Te_1 | 42.86 | 14.29 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Te_2 | 55.17 | 6.90 | 0.00 | 10.34 | 6.90 | 0.00 | 0.00 |
| Te_3 | 114.29 | 0.00 | 0.00 | 25.00 | 21.43 | 46.43 | 96.43 |
| Te_4 | 23.08 | 0.00 | 0.00 | 0.00 | 7.69 | 15.38 | 0.00 |
| E_1 | 25.00 | 18.75 | 0.00 | 12.50 | 31.25 | 12.50 | 6.25 |
| E_2 | 8.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Ob_1 | 137.21 | 0.00 | 2.00 | 2.33 | 2.33 | 0.00 | 0.00 |
| Ob_2 | 75.00 | 100.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Ob_3 | 0.00 | 16.67 | 0.00 | 0.00 | 0.00 | 16.67 | 0.00 |

The site with the highest rate of Coyote observations (RAI = 133) was Ob_3 (Fig. 1). The site with the highest rate of human observations (RAI = 21,125) was Ob_2, and the site with the least number of human captures (RAI = 1,168) was Te_3 (Fig. 2). The site with the highest rate of dog observations (RAI = 7800) was Ob_2 while the site with the lowest rate of dog observations (RAI = 16) was Ob_1.

Models

Our top model was “Humans and Cover” (wAICc = 0.98). “Recreation” (wAICc = 0.01) and “Bikers” (wAICc = 0.01) were the next best models; however, “Humans and Cover” contained almost all of the AICc weight, indicating strong evidence that it is the best model (Table 4). In our best model, humans had a slight positive effect ($\beta = 0.0006$, SE = 0.0002), and the interaction of tree density and humans had a negative effect on relative Coyote abundance ($\beta = -0.0179$, SE = 0.0053); tree density by itself had a positive effect ($\beta = 8.4670$, SE = 3.9647). Before testing our *a-priori* hypotheses, we tested all of our dependent variables for correlation. Tree species and canopy density were the only correlated variables, and so they are only together in the global model.

Temporal overlap

Coyote and human activity had low overlap ($\hat{\Delta}_4 = 0.396$, 95% CI = 0.32–0.47) (Fig. 3). Coyote activity peaked between 1 am and 6 am, coinciding with a period of very little human activity. Coyote activity was lowest between 11 am and 1 pm. Human activity peaked at 11am, and then declined until 11 pm.

Discussion

Our study site was an altered ecosystem of invasive Eucalyptus and native Oak-Bay forest, with a high level of human recreation. Unexpectedly, Coyotes did not seem affected by the altered ecosystem, but instead, their spatial distribution and temporal activity pattern appeared primarily affected by human recreation. Our top model (cumulative wAICc = 0.98) included all forms of human recreation (walkers, joggers, and bikers) and

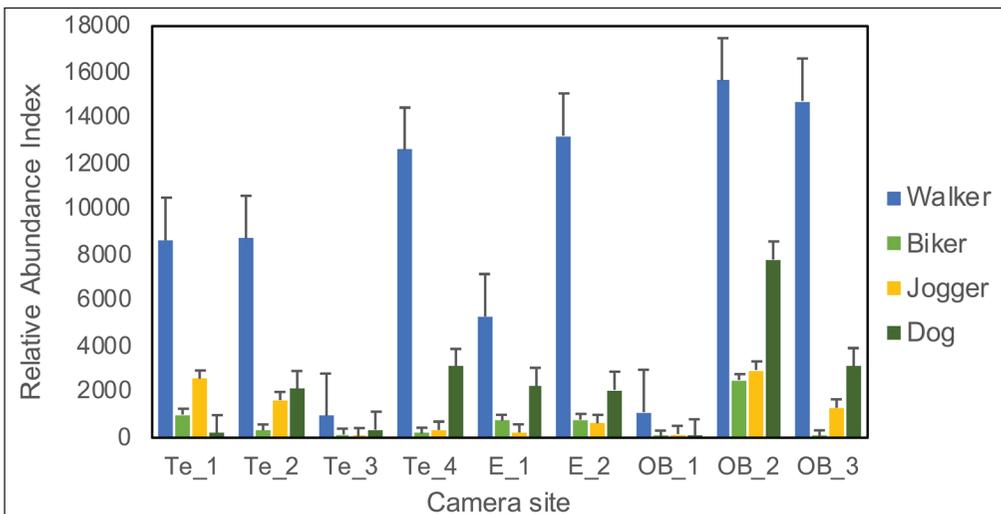


Figure 2. Relative Abundance Index (events per 100 camera trap days) for human recreation (mean and SE) for each camera site within the study site.

only one habitat variable (tree density as a proxy for cover). The effects of humans on wildlife are well-studied (e.g., Larson et al. 2016, Wang et al. 2015), and these appear to outweigh the effects of the invasive altered ecosystem. Our study appears to be another case of native wildlife persisting in altered ecosystems (e.g., Wright and Kelsey 1997). It is possible that we could have detected an effect if we had sampled more sites; however, sampling more sites would have introduced pseudoreplication. It is also possible that because the Eucalyptus stands were planted approximately a century ago, Coyotes and other wildlife have had time to adjust and learn to exploit them. Since there were no differences between the novel and native habitats with respect to the vegetation variables that we measured, the novel Eucalyptus may be functionally similar to the Oak-Bay, therefore still providing the same services to Coyotes. This also suggests that the park management plan of managing for diversity is effective, as selectively thinning the Eucalyptus does not appear to affect Coyote habitat use.

Coyote spatial use was primarily influenced by human recreation, but not as expected. We predicted that all types of human recreation and dog use would negatively affect Coyote use, but both walkers and joggers had a positive correlation to Coyote RAI, while dogs had a negative relation to Coyotes. This is contrary to the current trends in the literature (George and Crooks 2006; Reed and Merenlender 2008, 2011; Larson et al. 2016), where the effects of recreation on canids have significant negative results. Reed and Merenlender (2008, 2011) found that Coyote densities in areas that allow recreation are only 20–25% of Coyote densities in similar areas without recreation, indicating a spatial displacement. Also contrary to our results, Reed and Merenlender (2011) found no relation between dogs and the species richness and abundance of native carnivores, and instead, attributed differences in species abundance between protected areas and public areas to the number of

Table 4. Results of our a-priori model testing for influences of Coyote (*Canis latrans* Say) relative abundance within the study site.

| Model name | AICc | ΔAICc | wAICc | Cumulative wAICc |
|--------------------|-------|-------|-------|------------------|
| Humans and cover | 62.48 | 0.00 | 0.98 | 0.98 |
| Recreation | 71.81 | 9.33 | 0.01 | 0.99 |
| Bikers | 72.31 | 9.83 | 0.01 | 1.00 |
| Walkers | 75.30 | 12.82 | 0.00 | 1.00 |
| Humans | 76.62 | 14.14 | 0.00 | 1.00 |
| Tree density | 82.13 | 19.65 | 0.00 | 1.00 |
| Null | 83.42 | 20.94 | 0.00 | 1.00 |
| Humans and habitat | 83.87 | 21.39 | 0.00 | 1.00 |
| Tree species | 84.08 | 21.60 | 0.00 | 1.00 |
| Habitat | 84.37 | 21.89 | 0.00 | 1.00 |
| Joggers | 84.65 | 22.17 | 0.00 | 1.00 |
| Canopy density | 86.71 | 24.23 | 0.00 | 1.00 |
| Global | 86.85 | 24.37 | 0.00 | 1.00 |

human visitors. While this could be an artifact of low sample size, it appears that Coyotes within the study site are spatially attracted to areas of high human activity, but are making corresponding temporal changes in activity to avoid human activity.

Many wildlife species that exploit urban environments adjust their temporal patterns to be active when humans are least active (e.g., George and Crooks 2006, Wang et al. 2015), and this appears to be the strategy used by Coyotes within our study area. The regional park in which our study was conducted is heavily used for recreation and is located adjacent to a densely populated area, so human activity continued into the night, only abating from midnight until 5 am. In the absence of human disturbance, Coyotes display crepuscular or diurnal activity patterns (Kitchen et al. 2000); however, Coyotes in our study site displayed cathemeral activity patterns, and had a strong peak when human activity was lowest. This indicates a shift in activity patterns, as an apparent temporal shift to avoid human recreation (e.g., George and Crooks 2006, Wang et al. 2015). It may be that Coyotes temporally avoid areas that are heavily used by humans, but are spatially attracted to larger preserved areas that are used for recreation (e.g., Mueller et al. 2018) or to the manicured trails within the preserved areas (Gese et al. 2013, Switalski et al. 2007), which would explain the positive relation with walkers and joggers, despite the temporal avoidance.

Despite the dominant presence of Eucalyptus in the forest composition, Coyotes did not exhibit any preference between altered and native habitat. There were no differences between the vegetation factors that we tested, and this could indicate an even mixing of species diversity and richness between habitat types that possibly mitigated any effect that the altered habitat might have had on Coyotes. Currently, species richness and diversity of understory plants, amphibians, and birds is similar between the Oak-Bay and Eucalyptus woodlands; however, species composition differs, with few species found in both woodland types (Sax 2002). As opportunistic hunters, the Coyotes are possibly able to use the altered ecosystem because the prey species richness and diversity is similar to that of other habitats.

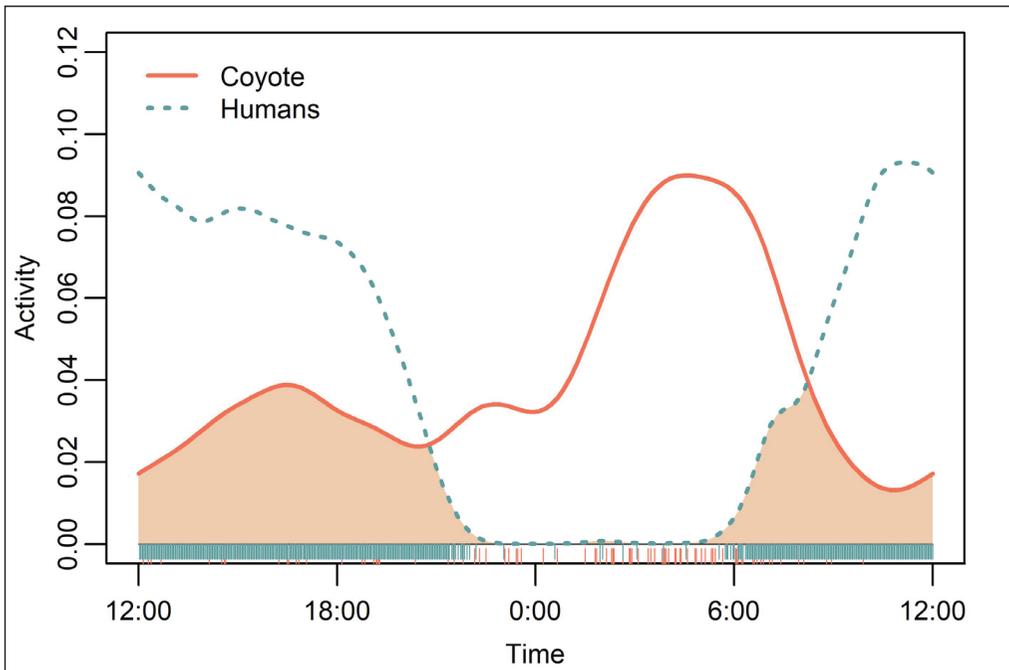


Figure 3. Temporal overlap between Coyote (*Canis latrans* Say) and human activity.

Within an urban regional park in northern California, we found that Coyote spatiotemporal patterns were affected by human recreation and tree density. Since Coyotes prefer lower tree density, thinning the Eucalyptus in relation to fire management should be beneficial to Coyotes, as they appear to be using the Eucalyptus habitat despite different vegetation species composition. As altered ecosystems become more widespread, studies should determine whether species diversity and richness are maintained when faced with a non-native species, as this may allow native wildlife to continue thriving. Within this study, Coyotes appeared to be attracted to areas that were heavily used for human recreation, but temporally adjusted their activity to peak when humans were not present. This could indicate that Coyotes, as an adaptable species, have learned to use the novel habitat and have habituated to humans within this study site, may consider humans to be a food source (George and Crooks 2006), or are dependent on large tracts of natural land that are used for recreation in urban areas (e.g., Mueller et al. 2018). Future studies should determine the effects of habituation in areas with high levels of human activity, which could potentially account for the opposing results of many studies looking at the wide-spread effects of non-consumptive recreation (e.g., Larson et al. 2016).

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