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Species differences in temporal response to urbanization alters predator-prey and human overlap in northern Utah

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ABSTRACT

Wildlife are under continuous pressure to adapt to new environments as more land area is converted for human use and human populations continue to concentrate in suburban and exurban areas. This is especially the case for terrestrial mammals, which are forced to navigate these habitat matrices on foot. One way in which mammals may occupy urbanized landscapes is by altering their temporal activity behavior. Typically, studies have found that mammals increase their nocturnal activity within urbanized environments to avoid overlap with humans. However, to date, the majority of studies on this topic have focused on single species, and studying whether this trend holds across an entire community has important ecological implications. Specifically, understanding how differences in species temporal activity response alters predator-prey dynamics and sympatric interspecies competition can provide insight into urban wildlife community assembly and provide a mechanistic understanding of species co-occurrence within these systems. In this study, we used data from a community science camera trapping project in northern Utah to elucidate how human influence alters the temporal activity behavior of five medium- to large-sized mammals and how differences in species response affect predator-prey, human, and sympatric competitor temporal niche overlap. We found community-wide changes in activity across study sites, with increases in late night and midday activity and decreases in crepuscular activity within the more-urbanized site. However, species-specific behavioral changes varied, and these changes resulted in reduced overlap, especially between coyotes (*Canis latrans*) and their potential prey species. These results provide information on how human influence may alter community assembly and species-species interactions within a wildland-urban interface.

1. Introduction

Human activity and changes to landscapes have a direct effect on biodiversity, altering ecosystems around the globe (Cardinale et al., 2006; Estes et al., 2011; Hooper et al., 2012). Continued urbanization (Dearborn and Kark, 2010; Ramalho and Hobbs, 2012) and

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rapid land conversion to suburban and exurban areas (Martinuzzi et al., 2015) is increasing populations of urban wildlife (Magle et al., 2012), making it important to understand the effects these changes have on wildlife behavior and niche partitioning (Ryan and Partan, 2014).

Evidence suggests that human influence and urbanization can alter species' temporal activity patterns (Tigas et al., 2002; George and Crooks, 2006; Gaynor et al., 2018; Patten et al., 2019). However, much of this research focuses on single species, usually predators (Muhly et al., 2011; Monterroso et al., 2014; Patten et al., 2019), and when multiple species are considered they are typically within the same guild (Di Bitetti et al., 2010; Sunarto et al., 2015). Understanding how ecologically dissimilar species, and especially predators and their prey, alter activity within the same urbanized system can answer questions about how these shifts alter trophic interactions (Magle et al., 2014; Patten et al., 2019).

Coyote population growth and subsequent range expansion across much of the North American continent, due to both wolf extirpation and their remarkable adaptability to urbanized systems (Gehrt et al., 2009), makes them a key urban predator (Linnell and Strand, 2000). Given that coyotes are predators of deer (Kilgo et al., 2012; Shuman et al., 2017), especially fawns (Rohm et al., 2007; Grovenburg et al., 2011), they may alter deer behavior in urban landscapes. Furthermore, the coyote diet is extremely plastic (Young et al., 2006; Schrecengost et al., 2008; Larson et al., 2015; Swingen et al., 2015; Cypher et al., 2018), and includes small mammals. Therefore, coyote represent a potential apex predator in urbanized areas, and understanding how their activity overlaps with potential prey can help inform urban trophic dynamics.

In this study, we used data from a community science camera trapping project in northern Utah to investigate the effects of human influence and urbanization on diel activity patterns across the wildlife community shared within the Central Wasatch Mountain-Salt Lake Valley wildland-urban interface (Wasatch WUI), a region where coyote are common. Specifically, we were interested in: 1) How the community in general and the medium- to large-mammal species in particular in the Wasatch WUI alter their temporal activity pattern in response to human influence and urbanization; 2) how the overlap of predator-prey or sympatric carnivore temporal activity in the Wasatch WUI is affected by human influence; and 3) How human influence and environmental factors affect animal activity across the Wasatch WUI. We hypothesized that community temporal dynamics would be altered across study areas, and we predicted increased nocturnal activity in the more-urbanized site and increased crepuscular activity in the less-urbanized site. We also hypothesized that species-specific responses would vary based on whether or not a species is nocturnal or diurnal. Specifically, we predicted more crepuscular and diurnal species like mule deer (*Odocoileus hemionus*) and rock squirrel (*Otospermophilus variegatus*) to alter their activity in the urbanized study site more than the nocturnal species, especially compared to those already well-adapted to

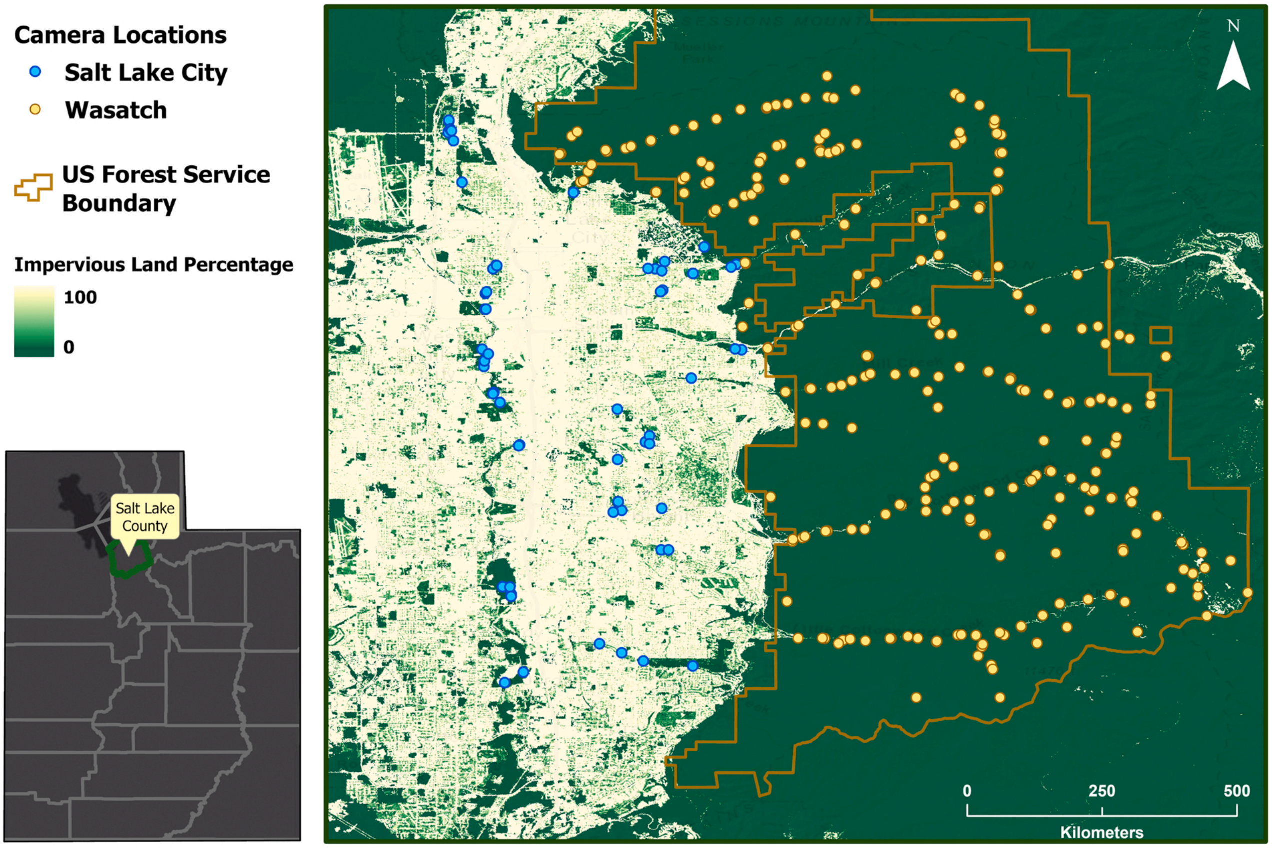

Fig. 1. Map of the study area. Camera locations within each study site are marked across both years. Some sites overlapped in location across years, and thus are represented by only one symbol. The US Forest Service Boundary and Percent Impervious Surface Cover are included to help demarcate the two study sites.

human environments like northern raccoon (*Procyon lotor*) and striped skunk (*Mephitis mephitis*). Finally, we predicted species to alter their temporal activity in ways that decrease overlap with both humans and their natural predators/competitors, especially coyote (*Canis latrans*). We expected this effect would be especially strong for prey species compared to sympatric competitors.

2. Methods and analysis

2.1. Study area

This study used data from the Wasatch Wildlife Watch project (https://wildutahproject.org/wasatch-wildlife-watch). The project is based along the wildland-urban interface of the Central Wasatch Mountain Range and surrounding urban Salt Lake Valley in northern Utah (41.90815 N 111.54250 W; Fig. 1). The Central Wasatch Mountain Range composes the most highly recreated portion of the Uinta-Wasatch-Cache National Forest (e.g., skiing, fishing, camping, hunting, hiking, climbing, and other outdoor activities), which receives approximately 9,000,000 visitors every year, nearly equal to the visitation rate of all five of Utah's National Parks combined (U.S Forest Service, personal communication; National Park Service: https://www.nps.gov/aboutus/visitation-numbers.htm). Furthermore, the national forest is immediately bordered by the densely populated Salt Lake Valley, which houses a population of over 1.1 million people and includes the Salt Lake City Metropolitan Area (U.S Census Bureau: https://www.census.gov/data.html; Fig. 1). The total study area covers approximately 1000 km^2 and is characterized by a gradient of urbanization and undeveloped land (Fig. 1). For this study, we separated the project area into two sites: Wasatch and SLC.

2.1.1. Wasatch site

The Wasatch site is defined by the Uinta-Wasatch-Cache National Forest boundary within Salt Lake County, Utah, comprising approximately 695 km^2 of the Central Wasatch Mountain Range (Fig. 1). Vegetation is characterized by a number of tree species, including oak (*Quercus* spp.), aspen (*Populus tremuloides*), maple (*Acer* spp.), spruce (*Picea* spp.), fir (*Abies* spp.), and juniper (*Juniperus* spp.). Temperatures vary greatly along elevation, and annual precipitation ranges from 400 mm at lower elevations to well over 1000 mm at the highest elevations (NOAA 2018: https://www.ncdc.noaa.gov/data-access). Camera locations in this study site are characterized by relatively high elevation (mean = 2075 m, min = 1421 m, max = 3194 m), high slope (mean = 17.55°, min = 0.53°, max = 45.92°), low percent impervious surface cover (mean = 0.41%, min = 0%, max = 24%), low housing density (mean = 24.87 units/km^2, min = 0 units/km^2, max = 2500.83 units/km^2), low population density (mean = 35.84 persons/km^2, min = 0 persons/km^2, max = 3241.46 persons/km^2), low road density (mean = 1.90 km/km^2, min = 0 km/km^2, max = 21.40 km/km^2), and high wildland vegetation percentage (mean = 93.36%, min = 6.56%, max = 100%).

2.1.2. SLC site

The SLC site is defined by the portion of Salt Lake County not within the Uinta-Wasatch-Cache National Forest and comprises approximately 305 km^2 (Fig. 1). Vegetation in the valley is characterized by swaths of native and non-native tree species and varies significantly across the age and socioeconomic status of individual neighborhoods (Avolio et al., 2018). Summer temperatures in the valley consistently reach or exceed 37 °C, and average precipitation is approximately 500 mm (NOAA 2018: https://www.ncdc.noaa.gov/data-access). Camera locations in this study site are characterized by relatively low elevation (mean = 1383 m, min = 1283 m, max = 2153 m), low slope (mean = 6.71°, min = 0.12°, max = 30.89°), high percent impervious surface cover (mean = 16.22%, min = 0%, max = 89%), high housing density (mean = 390 units/km^2, min = 0 units/km^2, max = 2500.83 units/km^2), high population density (mean = 1033 persons/km^2, min = 0 persons/km^2, max = 8099.2 persons/km^2), high road density (mean = 15.30 km/km^2, min = 0.49 km/km^2, max = 23.06 km/km^2), and low wildland vegetation percentage (mean = 13.72%, min = 0%, max = 100%).

2.2. Camera trapping

Camera trapping for this study took place across two summer seasons of Wasatch Wildlife Watch. The first was from 28 April 2018 to 29 August 2018, and the second from 13 April 2019 to 25 August 2019. Each season, camera locations were established across both study sites by teams of trained community scientists and researchers. Each participant underwent a four-hour training on proper camera installation and maintenance before deployment. Camera locations were selected by overlaying a 1-km^2 grid across the study area, thus ensuring that cameras were, on average, 1-km apart. Grid cells with an average slope $< 30°$ were selected for sampling, as pilot studies had shown camera locations above this threshold to result in significantly fewer detections across species (Green, unpublished data). A random GPS location was generated within each sampling cell. Participants were then given a 100-m radius around each location to find the best spot for camera placement (e.g., along trails, streams, and other funneling landscape features). Cells located on private property were excluded from sampling. We used one of a combination of Bushnell Trophy Cams and Bushnell Aggressor HDs at each camera location, each equipped with a motion-sensitive, passive infrared trigger (Bushnell Corporation, Overland Park, Kansas, US). All cameras were placed horizontally on trees at a height of approximately 0.4 m, oriented to avoid direct contact with the sun, assigned GPS coordinates, and set to record date and time when triggered. Cameras were programmed to take three photographs per trigger, and the sensitivity was set to HIGH with a 15-second time interval between subsequent triggers. All cameras were active 24 h a day. When focused on a particular landscape feature (e.g., trail, stream, or crossing), cameras were positioned at a 45° angle relative to it to maximize detection along its travel path. Surrounding or impeding vegetation was cleared by hand to maximize camera detection windows. No bait was used at any camera location. Photographs were considered independent detections at a given site when at least 30 min had surpassed between the preceding photo of the same species. Each season was broken into three five-week rotations, where cameras were checked every two weeks to either ensure they were still functioning and had adequate battery life and storage space or to move them to a new location and switch out SD cards. 172 camera locations were established during the 2018 season, and 171 camera locations were established during the 2019 season.

2.3. Data analysis

A species had to have at least 30 detections within each of the SLC and Wasatch study sites, as well as a naïve occupancy rate of at least 10%, to be included in analysis. This criterion was based off of recommendations from previous research (Ridout and Linkie, 2009; Frey et al., 2017) and to minimize zero-inflation in resultant species-specific datasets (Martin et al., 2005). However, although multiple studies have been able to accurately estimate activity patterns from smaller sample sizes (Houngbegnon et al., 2020; Viviano et al., 2020, 2021; Frey et al., 2020), a recent review recommended that a sample size of > 100 detections be used for camera trap research interested in investigating diel activity patterns (Lashley et al., 2018). Two of our species, coyote (*Canis latrans*) and rock squirrel (*Otospermophilus variegatus*), did not reach this threshold in the SLC site, with 47 and 64 detections, respectively. These lower sample sizes may hinder our ability to detect significant differences in activity overlap across species-species pairs by producing wide 95% Confidence Intervals, but we elected to include these two species in our analysis. When comparing across study sites to estimate if there was a difference between the shared medium- to large- mammal community's temporal activity patterns across study sites, we only used species detected in both study sites. All analysis was conducted within R (R Core Team, 2020).

2.3.1. Covariate extraction and principal component analysis

We extracted the following variables for each camera location using ArcGIS Pro Software (ESRI, 2020): wildland vegetation percentage, housing density, population density, percent impervious surface cover, road density, net primary productivity, elevation, and slope. A spatial dataset from Radeloff et al. (2017), which included analysis of US Census data, TIGER block geography data, and the Multi-Resolution Land Characteristics Consortium (MRLC) National Land Cover Dataset (NLCD) across the United States, provided values for wildland vegetation percentage, housing density, and human population density (Radeloff et al., 2017). Wildland vegetation percentages and percent impervious surface cover values, defined as the proportion of area covered by hard surfaces within a watershed (rooftops, streets, sidewalks, and other like surfaces) impermeable to infiltration of rainfall into underlying soils, were obtained through NLCD imagery provided by the US Geological Survey (Radeloff et al., 2017; U.S. Geological Survey, 2019) at a 30-m resolution. Housing and population densities were calculated using the US Census and TIGER block dataset by dividing housing units and persons by square kilometer of area, respectively (Radeloff et al., 2017). These variables were also calculated for each camera location at a resolution of 30 m. Road density values were derived using an authoritative ESRI landscape layer which utilized the US Census TIGER dataset to produce values within a 1-km buffer around each site (ESRI, 2020). Gross primary productivity values were obtained from the NASA Earth Observation Moderate-Resolution Imaging Spectroradiometer (MODIS) at a resolution of 11 km (NASA Earth Observations, 2016). Therefore, multiple sites within the same 11-km patch were assigned the same productivity value. Finally, elevation and slope were obtained from the US Geological Survey at a digital elevation model resolution of 10 m (US Geological Survey 2019). However, there existed strong collinearity across many of the variable pairs (Pearson's $r > 0.5$), so we conducted a Principal Component Analysis (PCA) on these variables and used the first three principal components (PC1, PC2, and PC3), which collectively accounted for 69% of the total variation across all values (Supplementary Table 1), in subsequent analysis. The variables included in the PCA were: elevation, slope, gross primary productivity, wildland vegetation percentage, percent impervious surface cover, housing density, population density, road density, and human encounter rate (measured as the total number of detections of humans divided by the number of surveys days at a camera location).

2.3.2. Community diel activity analysis

When comparing un-weighted community temporal activity, species with more detections would dominate the resultant activity patterns, leading to a potentially invalid representation of actual activity patterns across all species. Therefore, we first crafted species-specific activity distributions using circular kernel density analysis within the 'overlap' package in R (Meredith and Ridout, 2014). We then sampled from each species' resultant activity distribution using empirical bootstrapping, which resulted in 10,000 simulated detections for each species. To ensure the temporal integrity of the resultant simulations, we compared the temporal overlap between each species' actual data to the simulated data by calculating the overlap coefficient between the two datasets (Schmid and Schmidt, 2006; Ridout and Linkie, 2009; Miller et al., 2018). The mean overlap coefficient across species was 0.99, and all species' bootstrapped confidence intervals included 1.00 (data not shown). This meant that the simulated datasets represented nearly identical activity patterns to the actual data from each species. We then combined the simulated datasets from each species within each study site, where now all species contributed equally to the community temporal activity pattern. Finally, we tested whether the resultant community activity distributions were different across study sites using a Watson's Two-Sample Test of Homogeneity (Rao and SenGupta, 2001), within the package 'circular' (Agnostinelli and Lund, 2017), where alpha was set to 0.05.

Using the simulated datasets described above from each study site, we calculated total activity using the 'activity' package (Rowcliffe, 2014) and estimated associated 95% Confidence Intervals (CI) using empirical bootstrapping. We assessed whether activity levels were different across study sites by comparing the overlap of CIs from both sites, where a significant difference was assessed by whether or not the CIs overlapped. We also conducted a Wald Test (Rowcliffe, 2014) to assess the difference in activity between study sites, where alpha was set to 0.05. Therefore, we considered strong changes in activity to be comparisons whose CIs did not overlap and whose Wald Test p-value < 0.05. Moderate changes were considered to be when one of the two significance criteria above was met.

Finally, we used the methodology described by (Oliveira-Santos et al., 2013) to calculate and describe the 50% isopleth for each study site's activity distribution, which we hereafter refer to as 'core activity.'.

2.3.3. Species diel activity analysis

To assess whether species-specific temporal activity differed across study sites, we first grouped each species' detections into either day (representing detections captured between 0800 and 1859 h), night (representing detections captured between 2200 and 0459 h), or crepuscular (representing detections captured between both 0500–0759 h and 1900–2159 h) detections. Since all data was gathered during the summer season, where sunset and sunrise times did not differ more than approximately one hour from the start of the season to the end of the season, we elected to follow other studies that did not alter crepuscular times to account for seasonal variation (Houngbegnon et al., 2020; Havmoller et al., 2020; NOAA Sunrise/Sunset Calculator: https://www.esrl.noaa.gov/gmd/grad/solcalc/sunrise.html). However, we do recognize that this choice may lead to potential differences in what may be perceived as 'crepuscular' activity, and we present the results of any changes in crepuscular analyses with caution, instead focusing on more general conclusions in activity change across environmental predictors. After grouping data into specific timeframes, we then compared the detections across sites to the expected number based on total detection proportions across sites using chi-squared analysis, with alpha set to 0.05. Some groupings resulted in expected numbers of detections being less than five, in which case we discarded these groupings from analysis. Specifically, we did not include daytime detections in northern raccoon (*Procyon lotor*) analysis, and we did not include nighttime detections in rock squirrel (*Otospermophilus variegatus*) analysis (Table 1).

We calculated total activity and core activity for each species within each study site using the same methodology described above, and we assessed significant differences between study sites using the same criterion as in the community analysis (see Section 2.3.2).

We tested whether species-specific activity distributions, species-human overlap, and species-coyote overlap differed across the two study sites by crafting species-specific activity distributions in both study sites using circular kernel density analysis within the 'overlap' package (Meredith and Ridout, 2014). We first compared the resultant distributions for each species across study sites by calculating the coefficient of overlap (Δ_1), and used empirical bootstrapping to calculate 95% confidence intervals for each overlap coefficient. We then tested whether each species' temporal overlap with both humans and coyotes differed across study sites. As above, we used activity distributions for each species from each study site and calculated their coefficient of overlap with both humans and coyotes. We compared the activity overlap across sites for each species and assessed for significant differences in the overlap coefficients by whether or not their CIs overlapped.

Finally, we tested how the principal components from the human influence and environmental factors PCA explained in Section 2.3.1, as well as coyote traffic (calculated as the total number of coyote detections divided by survey days at each camera location), latitude and longitude (to account for potential spatial autocorrelation), the log-transformed number of survey days per camera location (held as an offset), and study site, affected animal activity through a generalized linear modeling approach. To do this, we first grouped all species detections into four temporal categories: day (representing detections captured between 0800 and 1859), night (representing detections captured between 2200 and 0459), dawn (representing detections captured between 0500 and 0759), and dusk (representing detections captured between 1900 and 2159; Table 1). We then assessed which species-time groups could be included in analysis by checking whether they met the > 30 detections with a naïve occupancy rate of at least 10% across the entire study area criterion outlined above. Species-time groupings that did not reach these thresholds were excluded from analysis, and a full list of species-time groupings included in analysis can be found in Table 1. Before analysis, all continuous covariates were scaled to have a mean $= 0$ and standard deviation $= 1$. Furthermore, if the above-mentioned criteria for data inclusion was met across study sites for a particular species-time group, then a categorical predictor for study site was also included in that model (Table 1).

We chose two classes of models to fit the detection datasets. Specifically, we fit both standard negative binomial regression models, as well as zero hurdle negative binomial regression models. We chose to include models that account for overdispersion and zero-inflation because the naturally low naïve occupancy rates of some of the species would intuitively introduce these sources of bias into our model set. Zero hurdle models are two-component models, which in this case included a truncated negative binomial count model and a binomial hurdle model for the zero vs. non-zero component (Franchini et al., 2020; Qiu et al., 2020). Although this type of model does not explicitly adjust estimates based on the premise that nearly all species detection probabilities at a camera location are < 1.0 like a standard occupancy model (MacKenzie et al., 2017), it does have the advantage of separating the detection of activity at a site (zero hurdle component) vs. the intensity of activity at a site (truncated count component), each of which being a parameter of

Table 1
Detections across study sites. Total detections grouped across study sites and time periods for each species included in analysis. Activity models included for each species are based on a whether each species-time grouping met a criteria of > 30 detections and a naïve occupancy rate of at least 10%.

	Wasatch					SLC					
Species	Day	Night	Dawn	Dusk	Total	Day	Night	Dawn	Dusk	Total	Activity models included
Coyote	102	124	36	25	287	11	30	4	2	47	Total[a], Night
Deer	2375	925	1279	1154	5733	332	106	118	107	663	Total[a], Day[a], Night[a], Dawn[a], Dusk[a]
Raccoon	1	317	50	44	412	3	666	52	68	789	Total[a], Night[a],Dawn, Dusk
Squirrel	423	11	31	18	483	63	0	1	0	64	Total[a], Day[a]
Skunk	38	242	57	53	390	3	71	15	13	102	Total[a], Night[a], Dawn

[a] Represents species activity models run with 'Area' (Wasatch v. SLC) included as a covarite.

interest in this study. All models were run using the ‘MASS’ and ‘*hurdlr*’ packages in R (Ripley et al., 2021; Balderama and Trippe, 2017). We compared the fit of the two models for each species-time grouping using AIC (Burnham and Anderson, 2004), and we report the results from the most supported model, where the significance of predictors was assessed at the α = 0.01 level. The full results of both model comparisons and the most supported models are available in Supplementary Table 3.

3. Results

We obtained a total of 19,034 detections of 33 mammal species (69,346 including humans) and eight bird species at 343 camera locations across 9949 camera days (Supplementary Table 2). Restricting the dataset to species with > 30 detections and a naïve occupancy rate of 10% in both study sites resulted in a dataset of 8970 detections (59,282 including humans) of five mammal species, including coyote (*Canis latrans*), mule deer (*Odocoileus hemionus*; hereafter referred to as ‘deer’), northern raccoon (*Procyon lotor*; hereafter referred to as ‘raccoon’), rock squirrel (*Otospermophilus variegatus*; hereafter referred to as ‘squirrel’), and striped skunk (*Mephitis mephitis*; hereafter referred to as ‘skunk’) (Table 1), and this dataset was used in all subsequent analyses. Total detections ranged from 334 of coyote to 6396 of deer (Table 1). Detections varied by time of day. Daytime detections ranged from 4 of raccoon to 2707 of deer. Dawn and dusk activity ranged from 50 detections of squirrel to 2658 detections of deer. Nighttime detections varied from 11 detections of squirrel to 1031 detections of deer (Table 1). Finally, detections varied across study sites, with detections in the SLC site ranging from 47 of coyote to 789 of raccoon, and detections in the Wasatch site ranging from 287 of coyote to 5733 of deer

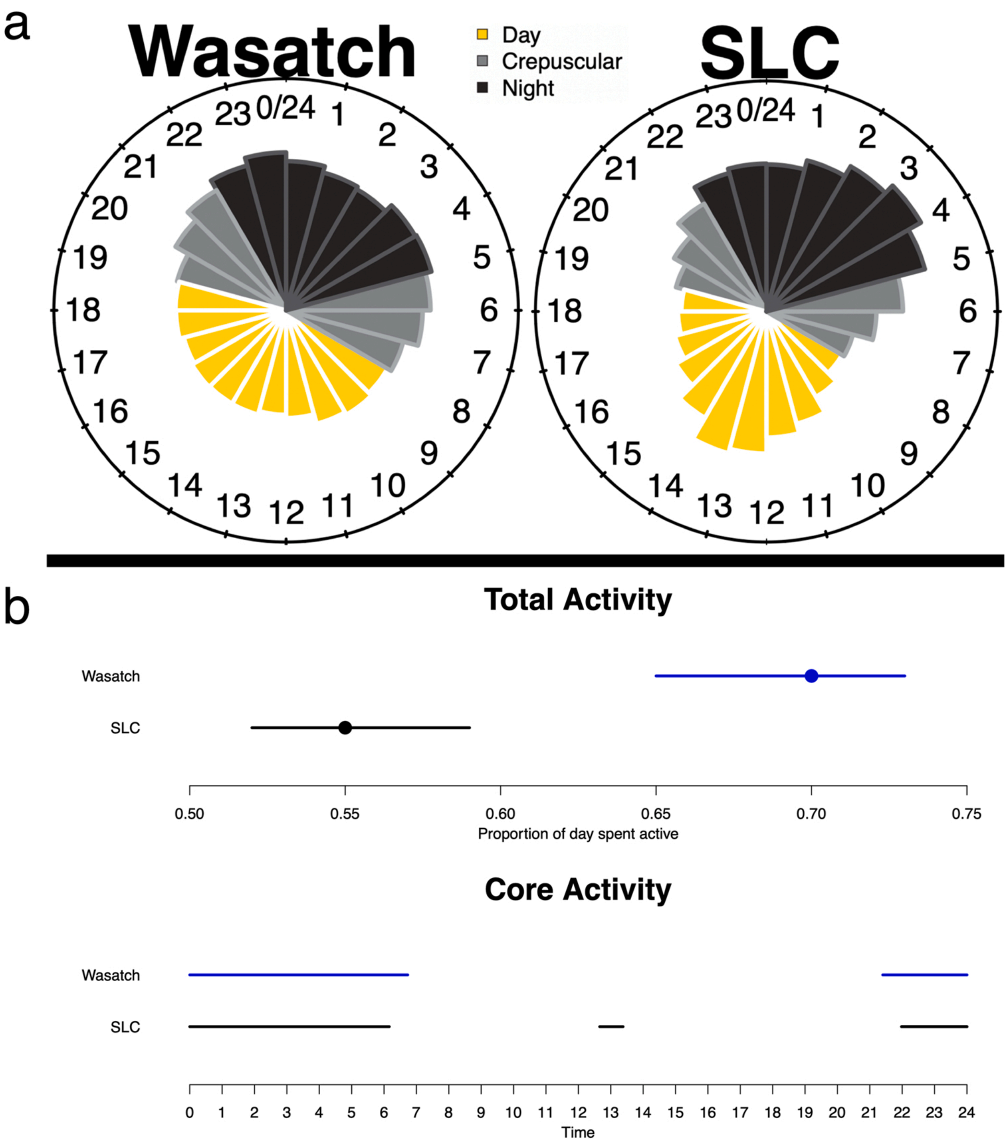

Fig. 2. Community activity across study sites. Wedges in (a) correspond to relative activity across hours of the day. Points in (b) represent mean estimates of the proportion of day spent active, with error bars representing bootstrapped 95% Confidence Intervals. Segments in (b) represent times of the day comprising core activity (i.e., the smallest range of time where 50% of all activity is concentrated).

(Table 1).

3.1. *Community diel activity*

We found significant changes in community diel activity patterns across our two study sites (Fig. 2b; Watson's $U^2 > 1.20$, $p < 0.001$). Total community activity decreased in the SLC site compared to the Wasatch site (Wald Test $W = 39.39$, $p = 3.46e^{-10}$; Fig. 2a), with a mean decrease in core activity of 0.43 h (Fig. 2a). Core activity in the SLC site was during the intervals from 21.98 h to 06.16 h, as well as from 12.66 h to 13.38 h, whereas core activity in the Wasatch site was from 21.40 h to 06.73 h (Fig. 2a).

3.2. *Species diel activity*

3.2.1. *Diel activity across study sites*

Activity pattern differences across study sites varied by species (Fig. 3). Chi-squared analysis showed that coyote increased nocturnal activity and decreased both crepuscular and diurnal activity in the SLC site ($X^2_{\text{SLC-Total}} = 5.96$, df = 2, p = 0.05), but did not alter time period activity in the Wasatch site ($X^2_{\text{Wasatch-Total}} = 0.98$, df = 2, p = 0.61); deer increased diurnal activity and decreased crepuscular activity in the SLC site ($X^2_{\text{SLC-Total}} = 18.69$, df = 2, $p = 9.00e^{-5}$), but did not alter time period activity in the Wasatch site ($X^2_{\text{Wasatch-Total}} = 2.16$, df = 2, p = 0.34); raccoon increased crepuscular activity in the Wasatch site ($X^2_{\text{Wasatch-Total}} = 6.98$, df = 1, $p = 8.00e^{-3}$), but did not alter time period activity in the SLC site ($X^2_{\text{SLC-Total}} = 3.65$, df = 1, p = 0.06); squirrel increased diurnal activity and decreased crepuscular activity in the SLC site ($X^2_{\text{SLC-Total}} = 4.56$, df = 1, p = 0.03), but did not alter time period activity in the Wasatch site ($X^2_{\text{Wasatch-Total}} = 0.62$, df = 1, p = 0.43); and skunk did not alter time period activity across study sites ($X^2_{\text{SLC-Total}} = 4.15$, df = 2, p = 0.13; $X^2_{\text{Wasatch-Total}} = 1.08$, df = 2, p = 0.58).

Total activity differences across study sites varied by species (Fig. 4). Coyote activity strongly decreased in the SLC study site compared to the Wasatch study site (Wald Test $W = 18.23$, $p = 1.95e^{-5}$), with a mean decrease in core activity of 3.09 h. Coyote core activity in the SLC site was between 23.80 and 05.58 h, and between 20.97 and 05.84 h in the Wasatch site (Fig. 4). Deer activity moderately increased in the SLC study site compared to the Wasatch study site (Wald Test W = 4.47, p = 0.03), but we also measured a mean decrease of core activity of 0.12 h. Deer core activity in the SLC site was between 05.39 and 14.17 h, and between 05.12–9.89 h and 17.53– 21.66 h in the Wasatch site (Fig. 4). Raccoon activity did not change across study sites (Wald Test W = 0.17, p = 0.68), with raccoon core activity decreasing in the SLC site by a mean of 0.42 h. Raccoon core activity in the SLC site was between 23.41 and 04.01 h and between 23.41 and 04.43 h in the Wasatch site (Fig. 4). Squirrel activity strongly decreased in the SLC site compared to the Wasatch site (Wald Test $W = 24.96$, $p = 5.85e^{-7}$), with squirrel core activity decreasing in the SLC site by a mean of 1.75 h. Squirrel core activity in the SLC site was between 11.38 and 15.05 h and between 09.47 and 15.89 h in the Wasatch site (Fig. 4). Skunk activity did not change across study sites (Wald Test W = 0.01, p = 0.94), with skunk core activity increasing in the SLC site by a mean of 0.81 h. Skunk core activity was between 21.77 and 03.63 in the SLC site and between 23.15 and 04.20 h in the Wasatch site (Fig. 4). Finally, temporal overlap across study sites, measured through the coefficient of overlap, differed across species (Fig. 5). Mean overlap coefficients ranged from 0.66 for squirrel (CI = 0.56–0.76) to 0.92 for raccoon (CI = 0.87–0.95).

3.2.2. *Human diel activity overlap across study sites*

Differences in human activity overlap, measured by comparing overlap coefficients and associated bootstrapped confidence intervals across study sites, varied by species (Table 2). Deer-human overlap increased significantly in the SLC site, compared to the Wasatch site (Table 2). Squirrel-human overlap decreased significantly in the SLC site compared to the Wasatch site (Table 2). Coyote-human overlap decreased in the SLC site compared to the Wasatch site, but these results were not statistically significant (i.e., CI's overlapped across study sites; Table 2). And raccoon-human and skunk-human overlap did not change across study sites (Table 2).

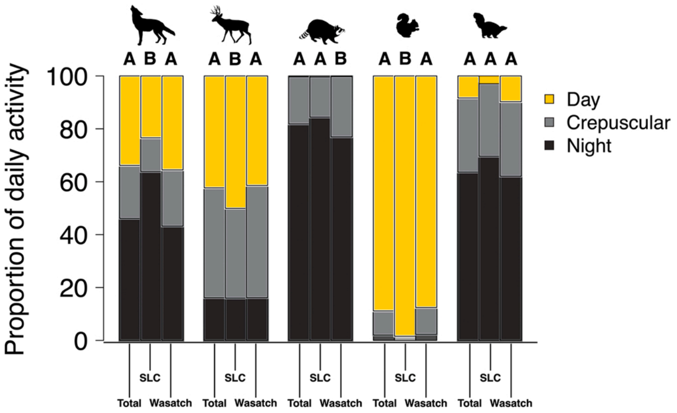

Fig. 3. Species comparisons of time-period activity across study sites. Length of colored bars corresponds to the proportion of total activity within each time period across comparisons. Different letter groupings, for each species, represent significant differences at α = 0.05.

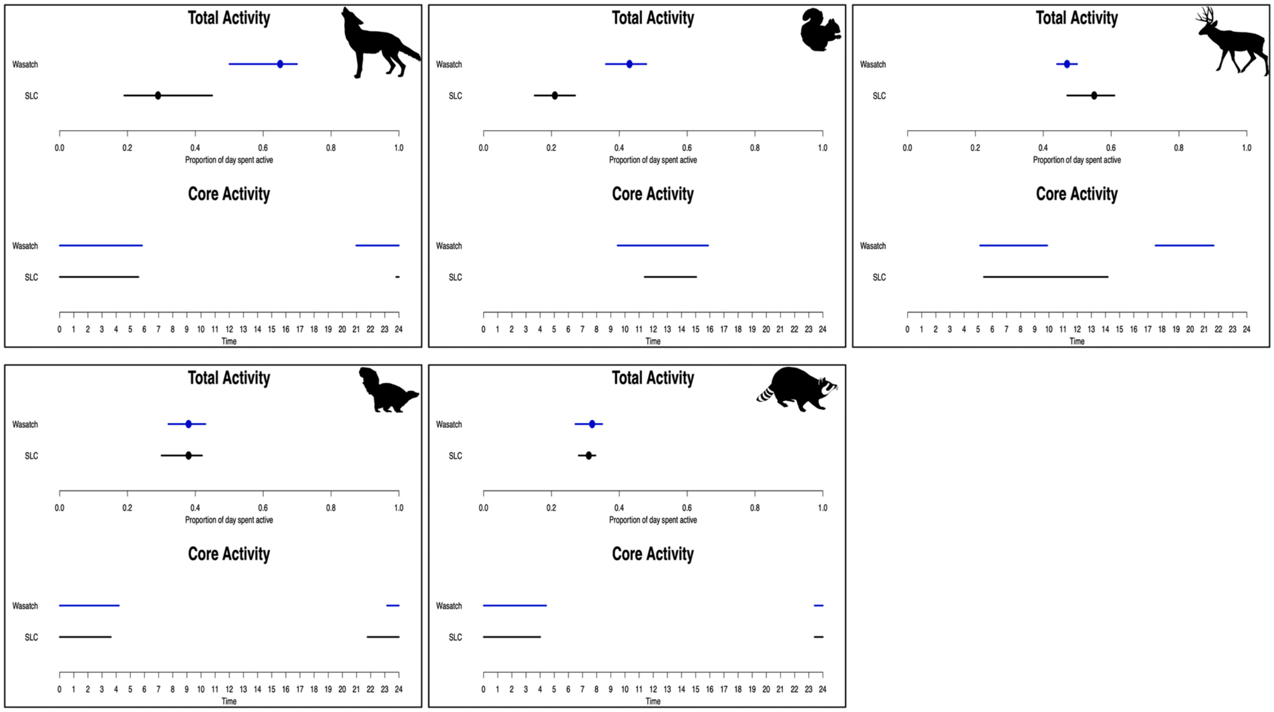

Fig. 4. Species-specific total and core activity across study sites. Points represent mean estimates of the proportion of day spent active, with error bars representing bootstrapped 95% Confidence Intervals. Segments represent times of the day comprising core activity (i.e., the smallest range of time where 50% of all activity is concentrated). Each graph belongs to the species represented by the symbol within it.

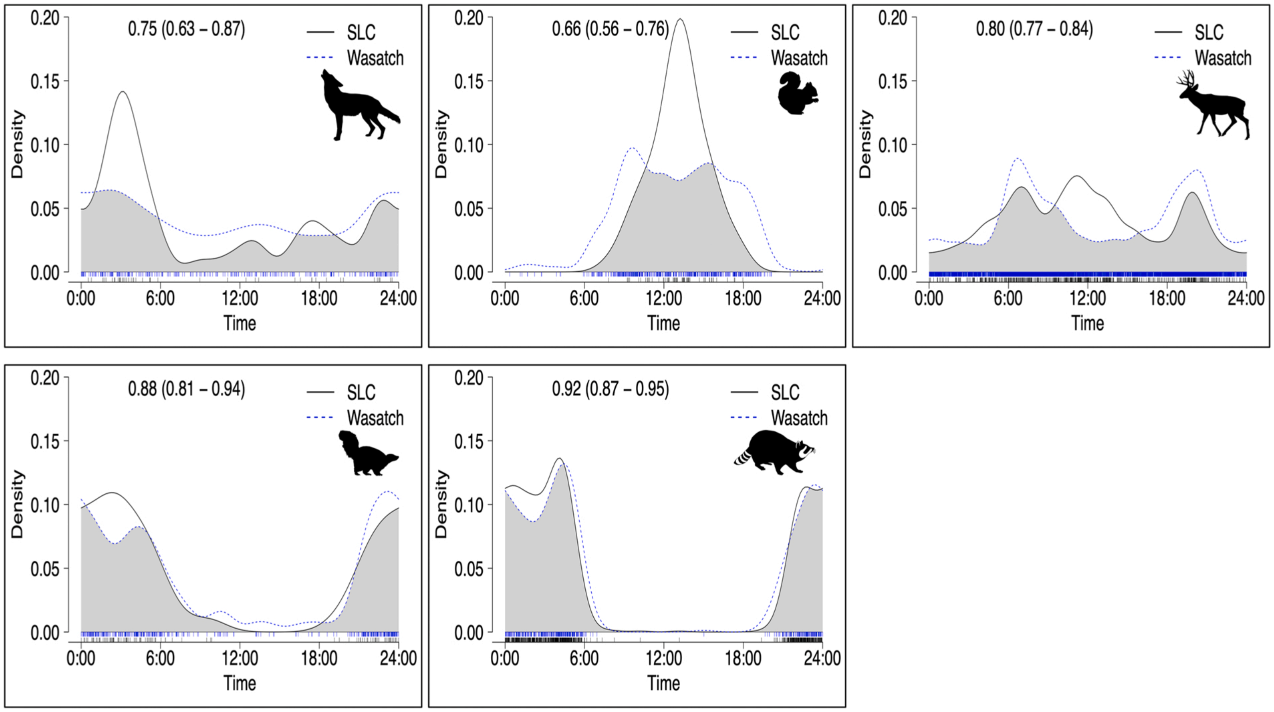

Fig. 5. Species-specific temporal activity distributions across sites. Curves represent results from circular kernel density analysis from each study site. Grey shaded region represents the overlap between the two curves. Colored dashes just above the x-axis represent detection data from each study site. Value represents the mean estimated coefficient of temporal activity overlap (Δ_1), with values in the parentheses corresponding to the bootstrapped 95% Confidence Intervals. Each graph belongs to the species represented by the symbol within it.

Table 2

Human temporal overlap estimates across study sites. Values represent mean estimates of coefficient of temporal activity overlap (Δ_1) with humans at each study site, with values in parentheses representing bootstrapped 95% Confidence Intervals. Bold values represent significant differences across study sites. (+/-) represents the direction of change in overlap from the Wasatch study site to the SLC study site.

Species	Wasatch Human overlap coefficient		SLC Human overlap coefficient
Coyote	0.50 (0.45–0.55)		0.35 (0.23–0.48)
Deer	**0.62 (0.61–0.63)**	(+)	**0.77 (0.74–0.80)**
Raccoon	0.10 (0.08–0.11)		0.10 (0.08–0.11)
Squirrel	**0.89 (0.86–0.92)**	(-)	**0.56 (0.48–0.65)**
Skunk	0.23 (0.20–0.26)		0.22 (0.15–0.28)

3.2.3. *Coyote diel activity overlap across study sites*

Differences in coyote activity overlap across study sites varied by species (Table 3). Deer-coyote and squirrel-coyote overlap decreased significantly in the SLC site compared to the Wasatch site (Table 3). Raccoon-coyote and skunk-coyote activity overlap did not change across sites (Table 3).

3.2.4. *Diel activity across environmental factors*

Activity response to environmental conditions varied by species (Table 4; Supplemental Table 3). PC1, describing axes of increasing wildland vegetation percentage and decreasing road density (Supplemental Table 1), had a significantly positive effect on deer activity in general ($\beta = 10.92$, SE = 3.18) and during dawn ($\beta = 10.05$, SE = 3.70), a significantly positive effect on coyote activity during the day ($\beta = 28.05$, SE = 8.49), a significantly negative effect on raccoon activity in general ($\beta = -18.96$, SE = 5.07) and during the night ($\beta = -13.32$, SE = 4.60), and a significantly positive effect on skunk activity at dawn ($\beta = 15.02$, SE = 4.49). PC1 did not affect squirrel activity (Table 4). PC2, describing axes of decreasing slope and housing and population density (Supplemental Table 1), had a significantly positive effect on raccoon activity in general ($\beta = 14.78$, SE = 4.33) and during both night ($\beta = 8.42$, SE = 2.46) and dusk ($\beta = 14.03$, SE = 4.28). PC2 did not affect coyote, deer, squirrel, or skunk activity (Table 4). PC3, describing axes of increasing gross primary productivity and decreasing human encounter rate measured at the camera site, had a significantly positive effect on mule deer activity at dusk ($\beta = 0.36$, SE = 0.13) and a significantly negative effect on raccoon activity in general ($\beta = -0.33$, SE = 0.11) and at night ($\beta = -0.35$, SE = 0.12). PC3 did not affect coyote squirrel, or skunk activity (Table 4). Coyote traffic rate measured at each camera site had a significantly positive effect on deer activity rate in general ($\beta = 0.28$, SE = 0.08), during the night ($\beta = 0.40$, SE = 0.09), dawn ($\beta = 0.27$, SE = 0.09), and dusk ($\beta = 0.36$, SE = 0.09), but not during the day (Table 4). Coyote traffic rate did not affect raccoon, squirrel, or skunk activity (Table 4). Area did not have an effect on any species except skunk, which preferred the Wasatch site in general and at night (Table 4).

4. Discussion

4.1. *Community diel activity*

In this study, we investigated whether or not human influence altered community activity patterns. We found that, consistent with our hypothesis, as a whole, the community shared between the Wasatch and SLC study sites altered their temporal activity in response to urbanization, with species, on average, being less active in the SLC site. Specifically, the community became less crepuscular but had subsequent activity increases in late night and midday hours. This increase in late night activity seems to correspond well with what other researchers have found (Gaynor et al., 2018), where species increase nocturnality in response to urbanization. Furthermore, the decreases in crepuscular activity correspond well with the highest levels of activity for humans (Supplementary Fig. 1), which supports evidence presented by past studies that animals avoid times of relatively high human activity (van Doormaal et al., 2015; Agetsuma et al., 2016; Naidoo and Burton, 2020). The increase in midday activity is intriguing, however, and it was even represented as a portion of core activity across the community (Fig. 2). It is interesting given that this represents some of the hottest parts of the day, where temperatures can exceed 37 °C. One possible explanation for this is that it corresponds well with marked drops in human activity during this same period (Supplementary Fig. 1), corroborating previous evidence that animals in urban communities may adopt unique

Table 3

Coyote temporal overlap estimates across study sites. Values represent mean estimates of coefficient of temporal activity overlap (Δ_1) with coyotes at each study site, with values in parentheses representing bootstrapped 95% Confidence Intervals. Bold values represent significant differences across study sites. (+/-) represents the direction of change in overlap from the Wasatch study site to the SLC study site.

Species	Wasatch Coyote overlap coefficient		SLC Coyote overlap coefficient
Coyote	NA		NA
Deer	**0.69 (0.64–0.73)**	(-)	**0.50 (0.40–0.61)**
Raccoon	0.60 (0.54–0.65)		0.70 (0.59–0.79)
Squirrel	**0.47 (0.42–0.53)**	(-)	**0.21 (0.11–0.33)**
Skunk	0.73 (0.67–0.79)		0.74 (0.62–0.85)

Table 4

Effects of environmental and human influence factors on temporal activity. Symbols represent the direction of response of species activity to factors included in generalized linear models. PC1 represents axes of increasing wildland vegetation percentage and decreasing road density, PC2 represents axes of decreasing slope and housing and population density, and PC3 represents axes of increasing gross primary productivity and decreasing human encounter rate measured at each camera location. Results separated by total, daytime, nighttime, dawn, and dusk activity. Blank values represent non-significant effects. NA's represent models that were not run due to a lack of data. 'SLC' or 'Wasatch' represents the study site where activity was significantly greater. (+/-) represents the direction of significant effects at α = 0.01. Full model results are available in Supplementary Table 3.

Total					
Species	PC1	PC2	PC3	Coyote traffic	Study site
Coyote					
Total	-	-	-	NA	-
Day	(+)*	-	-	NA	NA
Night	-	-	-	NA	NA
Deer					
Total	(+)*	-	-	(+)[a]	-
Day	-	-	-	-	-
Night	-	-	-	(+)[a]	-
Dawn	(+)[a]	-	-	(+)[a]	-
Dusk	-	-	(+)[a]	(+)[a]	-
Raccoon					
Total	(-)[a]	(+)[a]	(-)[a]	-	-
Night	(-)[a]	(+)[a]	(-)[a]	-	-
Dawn	-	-	-	-	NA
Dusk	(-)[a]	(+)[a]	-	-	NA
Squirrel					
Total	-	-	-	-	-
Day	-	-	-	-	-
Skunk					
Total	-	-	-	-	(Wasatch)[a]
Night	-	-	-	-	(Wasatch)[a]
Dawn	(+)[a]	-	-	-	NA

[a] Measured difference on the rate of activity.

activity patterns that represent a tradeoff between human avoidance, predation avoidance, and energy conservation (Ditchkoff et al., 2006; Lowry et al., 2013; Ryan and Partan, 2014). This idea warrants further investigation, and identifying the effects of this type of behavioral change on individual fitness and reproductive success would provide additional evidence to whether or not it represents an adaptive trait.

To the best of our knowledge, evidence for this type of activity change, where midday activity increases in response to human influence, is scarce. This may be due to the fact that urban ecology research on this topic is particularly lacking (Blount et al., 2021). However, similar, drastic activity pattern and behavioral changes have been found for multiple species inhabiting areas along a wildland-urban interface gradient (Gaynor et al., 2018). Furthermore, the lack of evidence for this type of activity change may also be due to limited analysis on community diel activity patterns. Our novel approach to community activity analysis has the utility of addressing how entire communities, not just individual species, alter their temporal activity behavior, providing an avenue for investigating novel questions in community composition and behavior. This is especially important as more studies on wildlife ecology focus on multiple species (Blount et al., 2021; Magle et al., 2021; Suraci et al., 2021; Naderi et al., 2021).

4.2. *Diel activity across study sites*

Focusing on species-specific responses, this study investigated the effects of human influence and urbanization on species-specific time-period activity (i.e., daytime, nighttime, and crepuscular activity). Overall, we found relatively consistent patterns across species' activity decreases, where coyote, deer, and squirrel all decreased their crepuscular activity in the SLC site (Fig. 3). However, this pattern was not consistent across species, as skunk did not alter their time-period activity across sites and raccoon actually slightly increased crepuscular activity in the SLC site (Fig. 3). Time-period analysis also illustrated strong species-specific increases in activity in response to human influence and urbanization which, at times, conflicted with our initial hypotheses. In particular, both deer and squirrel increased diurnal activity in the SLC site, whereas coyote increased nocturnal activity. The increase in coyote nocturnality follows what many previous studies have found for species in urban habitats, especially carnivores (Oriol-Cotterill et al., 2015; Wang et al., 2015; Shamoon et al., 2018). However, we do not see this response in both deer and squirrel. The increase in diurnal activity in squirrels corresponds with the species' natural activity patterns, where, in SLC, we see more activity in the middle of the day, which corresponds well with the measured decrease in human activity we found during our study (Supplementary Fig. 1). Furthermore, given this species' is naturally diurnal (Young, 1997), such a shift is not a drastic alteration from its norm. However, with deer, which are typically crepuscular (Eberhardt et al., 1984), the increase in diurnal activity was unexpected. As with squirrel, the increase in midday activity corresponds well with the dip in activity for humans; however, it represents a drastic shift from the species' natural pattern. One potential explanation for this is the presence of fawns, where previous research from white-tailed deer (*Odocoileus virginianus*), a very closely-related species to mule deer, showed that nursery groups exhibited strong diurnal activity periods in the presences of predators, whereas single adult bucks and does exhibited more crepuscular activity (Higdon et al., 2019).

We also compared how total activity, as well as core activity, changed in response to human influence and urbanization. As with time-period activity, species-specific responses varied considerably. Both raccoon and skunk, species that did not show major differences in time-period activity, also did not show major differences in total and core activity across study sites (Fig. 3). This was an expected finding, as both species' activity patterns seem well-adapted to both urban and rural environments (Fidino et al., 2020; Suraci et al., 2021), and we see very little change in temporal activity behavior across the wildland-urban interface of our study area. Also, as expected, coyote strongly decreased their total activity in the SLC site, where core activity decreased by nearly 33%. Coyote are typically a cathemeral or crepuscular species throughout much of its range (Young et al., 2006), but became nearly strictly nocturnal in the SLC study site, drastically increasing activity during the relatively few hours where human activity was at its lowest. On the other hand, deer moderately increased their total activity in the SLC site, with marked changes to core activity (Fig. 3). Specifically, deer in the Wasatch site followed a crepuscular activity pattern typical of the species throughout much of its range, with core activity focused around the dawn and dusk hours. However, in the SLC site, deer diel activity exhibited a tri-modal pattern, with a peak in midday activity and subsequent smaller peaks during dawn and dusk (Fig. 3). Furthermore, core activity in this study site ranged from the dawn hours to early afternoon, with no subsequent core activity during the dusk hours. This is a marked change for an animal whose activity has long been thought to be controlled, at least in part, by physiological constraints like digestion (Beier and McCullough, 1990). This pattern, to the best of our knowledge, has only been documented once before (Higdon et al., 2019), for white-tailed deer, where the authors found that only nursery groups altered their temporal activity in the summer to become mainly diurnal, whereas single adults remained crepuscular. Finally, squirrel total activity also strongly decreased within the SLC site, with core activity shrinking by just over 25% (Fig. 3). These changes seem to correspond well with the idea that squirrel alter their activity in the SLC site to decrease overlap with both humans and coyotes. An interesting area of future research in this area would be to investigate whether the presence of dogs accounts for any variation in this observed trend.

4.3. Human and coyote diel activity overlap across study sites

We investigated the effects of human influence and urbanization on species-human and species-coyote temporal overlap. We found that species altered their overlap with both humans and coyote in varying ways (Table 2; Table 3). Consistent with our original hypotheses, raccoon and skunk did not alter human or coyote overlap across areas. Both raccoon and skunk exhibit nocturnal activity patterns, and therefore already segregate themselves temporally from humans. Furthermore, evidence suggests that interference competition between coyotes and both species is rare (Gehrt and Prange, 2007; Prange and Gehrt, 2007; Lesmeister et al., 2015) and that the presence of coyotes does not typically elicit a behavioral response from either species (Prange and Gehrt, 2007; Chitwood et al., 2020). We did, however, find significant changes in deer-human, deer-coyote, squirrel-human, and squirrel-coyote overlap (Table 2; Table 3). Both deer and squirrel decreased their temporal overlap with coyote in the SLC site, and in much the same way. Specifically, both deer and squirrel increased their activity during midday hours and decreased activity during crepuscular time periods. This resulted in decreased squirrel-human overlap as well, as squirrel were able to decrease overlap with coyote while also decreasing overlap with humans by simply shrinking their total activity period (Fig. 3). However, for deer, this decrease in deer-coyote overlap resulted in a significant increase in deer-human temporal overlap. Deer are a common prey item for coyote (Rohm et al., 2007; Grovenburg et al., 2011; Kilgo et al., 2012; Shuman et al., 2017), and evidence suggests that coyote may be a main factor in deer habitat usage in urban areas (Magle et al., 2014). Furthermore, evidence also suggests that deer become habituated to humans relatively quickly, and they may even select urban habitats as ways to decrease overlap with predators or increase nutrient intake (Berger, 2007; Ditmer et al., 2020). Therefore, our study seems to corroborate recent evidence that deer may occupy urban habitats and adopt more diurnal activity periods, in part, as a way to avoid predation by carnivores, especially when raising fawns (Higdon et al., 2019). Repeating this study during different seasons would help further elucidate whether this behavioral response is related to fawn predation, as would conducting a similar analysis on nursery groups vs. single, adult individuals.

4.4. Diel activity across environmental factors

Finally, we assessed the effects of environmental factors on the presence of species activity, as well as on species activity rate. We found that increasing wildland vegetation, increasing gross primary productivity, decreasing human encounter rate, and decreasing road density (PC1 & PC3) had a positive effect on mule deer activity. Coyote activity was positively affected by wildland vegetation and decreasing road density (PC1). Raccoon activity was negatively affected by increasing wildland vegetation, increasing gross primary productivity, decreasing human encounter rate, and decreasing road density (PC1 & PC3), but positively affected by slope, housing density, and population density (PC2). Finally, skunks were more active in the Wasatch site than the SLC site and were positively affected by increasing wildland vegetation and decreasing road density (PC1). This supports previous work on habitat selection for these species (Fidino et al., 2020; Suraci et al., 2021). However, raccoon activity significantly decreased with increasing slope, housing density, and population density (PC2), which suggests that, although raccoons are human commensals and are well-adapted to urban environments, they prefer suburban and exurban areas more so than metropolitan areas. Finally, coyote traffic rate had a positive effect on mule deer activity rate, but only during the non-daytime hours, further supporting the idea that mule deer diurnal activity is in direct response to avoiding coyote activity (Higdon et al., 2019). We also found that coyote traffic rate was positively associated with the presence of deer activity during the nighttime, dawn, and dusk hours, which supports the idea that coyote use habitats frequented by deer and increase their activity when deer are present.

5. Conclusion

In this study, we measured the effects of human influence and urbanization on animal diel activity patterns across the Wasatch Mountain-Salt Lake Valley wildland-urban interface. As a whole, the community shared between the Wasatch and SLC sites altered their temporal activity in response to urbanization, with the SLC site community becoming more active during nocturnal and midday hours and less active during crepuscular periods. These changes, in general, seem to correspond well with human activity. We also found that species-specific changes varied considerably across our study species. Raccoon and skunk, common urban commensals, did not alter activity across study sites, whereas coyote, deer, and squirrel significantly changed their activity behavior. Coyote became more nocturnal, whereas both deer and squirrel became more diurnal. These changes resulted in changes in temporal overlap amongst species-humans and species-coyote pairs, where both deer and squirrel decreased overlap with coyote in the SLC site, and squirrels decreased overlap with humans but deer increased overlap with humans. With previous research suggesting that deer may alter their activity periods and occupy urban habitats to avoid predation, our study both corroborates these findings and provides avenues for potentially new and insightful research into this topic.

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CRediT authorship contribution statement

AG Green: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Visualization, Writing – original draft. **KA Barnick:** Data curation, Investigation, Methodology, Visualization, Writing – review & editing. **ME Pendergast:** Funding acquisition, Project administration, Resources, Supervision, Validation, Writing – review & editing. **ÇH Şekercioğlu:** Project administration, Supervision, Validation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Availability of data and material

Once published, all data will be made publicly available within the Global Biodiversity Information Facility's online data repository.

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Conflicts of interests/Competing interests

We have no conflicts of interest or competing interests to declare.

Code availability

All code for analysis is available upon request.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2022.e02127.

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