Contents lists available at ScienceDirect





Behavioural Processes

journal homepage: www.elsevier.com/locate/behavproc

The influence of periodic increases of human activity on crepuscular and nocturnal mammals: Testing the weekend effect



Joshua H. Nix*, Ryan G. Howell, Lucas K. Hall, Brock R. McMillan

Department of Plant and Wildlife Sciences, Brigham Young University, Provo, UT 84602, United States

ARTICLE INFO

Keywords:

Behavior

Nocturnal

Diurnal

Weekends

Crepuscular

Remote cameras

ABSTRACT

Human recreation can negatively affect wildlife, particularly on weekends when human activity is highest (i.e., the weekend effect). Much of what we understand about the weekend effect is based on research conducted on diurnal species, which have greater temporal overlap with humans. Because nocturnal species generally avoid times when humans are active, they are likely less affected by anthropogenic activity on weekends. Our objective was to test the weekend effect in relation to the degree of nocturnality of mammals in a recreational area. We predicted that as nocturnality increased, the effect of human activity would decrease. To address our objective, we placed 50 remote cameras along the Diamond Fork River in Utah from January to June 2015. We found that three out of the four focal species supported our predictions. Mule deer (crepuscular) reduced activity throughout our entire study area during weekends and avoided campgrounds. Beavers and mountain lions (both nocturnal) did not negatively respond to increased human activity. Raccoons (nocturnal) reduced activity during weekends, but only within campground areas. Our findings indicate that as the temporal overlap increases between wildlife and humans, so does the influence that humans have on wildlife.

1. Introduction

Human recreation has become a threat to many species of wildlife (Benitez-Lopez et al., 2010; Larson et al., 2016). Increasing human populations will likely lead to higher frequencies of recreational activities, resulting in increased interactions with wildlife (Martineau et al., 2016; Marzano and Dandy, 2012). Human-wildlife interactions can alter wildlife behavior, which can lead to increased stress levels, missed foraging opportunities, reduced reproductive success, avoidance of certain habitats, and increased mortality (Longshore et al., 2013; Martin and Réale, 2008). Mitigating and managing the potential negative effects resulting from human-wildlife interactions will be a continual challenge for wildlife conservation and human recreation as populations of humans increase and encroach on wildlife habitat (Krausman et al., 2008).

Outdoor recreational areas near urban settings are ideal locations for testing human-wildlife interactions (Ladle et al., 2016; Ruhlen et al., 2003). Recreational areas near cities are likely to experience the greatest increase in human activity because of proximity and convenience, due to both distance and well developed road networks that enhance ease of access. Yet, increases in human activity are likely periodic in nature, most commonly occurring during weekends (Ladle et al., 2016; Longshore et al., 2013; Ruhlen et al., 2003). Due to the influence that humans have on wildlife (Kays et al., 2016; Martineau et al., 2016; van Doormaal et al., 2015), behavior of wildlife may differ between "busy" weekend periods and relatively "quiet" weekday periods (i.e., the weekend effect; Lafferty, 2001; Longshore et al., 2013; Stalmaster and Kaiser, 1998). However, the weekend effect may differentially affect diurnal and nocturnal wildlife based on contrasting patterns of activity relative to human activity.

Diurnal species may be particularly sensitive to increased activity of humans on weekends due to greater temporal overlap with humans (Longshore et al., 2013; Roy et al., 2014), whereas nocturnal species may avoid periods when humans are most active. The majority of research that has evaluated support for the weekend effect hypothesis has primarily focused on diurnal species (Stalmaster and Kaiser, 1998; Tadesse and Kotler, 2012; Tarjuelo et al., 2015), with much less attention towards crepuscular and nocturnal species. While most of the studies on diurnal species support the weekend effect, the general applicability of this hypothesis to crepuscular and nocturnal species is not as clear. For example, when human activity was high on weekends, some crepuscular and nocturnal species were less active while others became more active (Barrueto et al., 2014; Carrillo and Vaughan, 1993; Jacobson and Lopez, 1994). Given the continual increase of the global human footprint (Venter et al., 2016), developing a better understanding of the periodic influence that humans may have on the

http://dx.doi.org/10.1016/j.beproc.2017.11.002 Received 25 April 2017; Received in revised form 2 November 2017; Accepted 5 November 2017 Available online 06 November 2017

0376-6357/ © 2017 Elsevier B.V. All rights reserved.

^{*} Corresponding author. Department of Forestry and Natural Resources, University of Arkansas at Monticello, Monticello, AR 71656, United States. *E-mail address:* nixjh@uamont.edu (J.H. Nix).

behavior of crepuscular and nocturnal wildlife will allow us to better manage the shared use of recreational areas (Kays et al., 2016; Young et al., 2005).

Our objective was to test the weekend effect hypothesis in relation to the degree of nocturnality of mammals in a recreational area near a city. Although humans are primarily diurnal, their activities in recreation areas can also be crepuscular. Therefore, we predicted that temporal overlap with humans would cause crepuscular species to decrease in activity on weekends, particularly in campground areas where human activity is concentrated. Alternatively, nocturnal species have little to no temporal overlap with humans. Thus, we predicted that nocturnal species would not reduce activity in response to increased human activity during weekends (Barrueto et al., 2014; van Doormaal et al., 2015). To test our predictions, we used remote cameras to monitor a recreational area where humans, crepuscular, and nocturnal mammals were common. We then evaluated diel (daily) activity patterns of mammalian wildlife and quantified their activity levels in response to changes in levels of human activity.

2. Methods

2.1. Study area

We conducted this study along the Diamond Fork River located in the Wasatch Mountain Range in central Utah (40° 1'42.04″ N 111° 30'3.70″ W). The Diamond Fork area is a popular location among recreationists because it offers a variety of activities year-round (e.g., fishing, camping, hunting, hiking, etc.) and is relatively close to urban areas (12 km from nearest city). Diamond Fork is located within a small canyon, branching off from the larger Spanish Fork Canyon. Vegetation characteristics of the Diamond Fork area included maple (*Acer* spp.), oak (*Quercus* spp.), juniper (*Juniperus* spp.), serviceberry (*Amelanchier alnifolia*), aspen (*Populus tremuloides*), and cliffrose (*Purshia stansburiana*). Elevation across our study area ranged from 1514 to 1609 m. Temperatures during our study ranged from -13.1 to 32.2° C (mean temperature of 7.9°C). During our study, there was a total of 15.13 cm of precipitation (MesoWest, Bureau of Land Management & Boise Interagency Fire Center).

2.2. Data collection

From January to June 2015, we placed 50 Reconyx PC900 cameras (Reconyx, Inc., Holmen, WI) along 12 km of the Diamond Fork River (spaced approximately every 250 m). We positioned cameras approximately 40 cm off the ground and attached them to metal posts. Each camera was programmed to record two photographs per trigger with a 30 s quiet period. We checked cameras every two weeks to perform camera maintenance (if needed) and to remove any obstructions (e.g., vegetation) from the camera's view.

We used Exifer v.2.1.5 (www.friedemann-schmidt.com/software/ exifer) to extract file paths and date/time stamps from each image. We then created a Microsoft Access database for photo identification with the file paths and date/time information for each image. We classified animals in the photographs to the species level. After photo identification, we compiled species photo sequences into independent visit events separated by 30 min (Hall et al., 2016). All other photographs that occurred within the same visit were consolidated to a single visit. We determined the diel activity patterns of each species by using the time associated with each visit and categorized each species as crepuscular or nocturnal based on their diel activity.

To account for differences in vegetation characteristics between sites, we used Landscape Fire and Resource Management Planning Tools (LANDFIRE) data provided by the U.S. Department of Agriculture Forest Service and the U.S. Department of the Interior. LANDFIRE is a vegetation classification derived from LANDSAT imagery with a spatial resolution of 30 m. Vegetation height was defined as vegetation 0-0.5 m, 0.5-1 m, 1-3 m, shrubs above 3 m, Trees 5-10 m, Trees 10-25 m, and sparse vegetation using LANDFIRE data. With this information, we were able to define the dominant vegetation height within each individual site (defined as within 30 m of the camera location).

2.3. Statistical analysis

We used a Kruskal-Wallis and a Dunn's post hoc test to determine if there were differences in anthropogenic activity between weekdays and weekends. We defined "weekdays" as Monday through Thursday and "weekends" as Friday through Sunday (Barrueto et al., 2014; Moore and Seigel, 2006; Ruhlen et al., 2003) with the exception of three Mondays due to national holidays resulting in uncharacteristic long weekends (Ladle et al., 2016). To account for the overnight presence of humans in designated camping areas, we included a binary "campground" covariate. "Campground" sites were considered a categorical covariate (0 = non-campground, 1 = campground) and consisted of sites S00–S20 (approximately 40% of our study area) as these camera locations were found within the designated camping areas of a national forest campground.

We used a two-stage modelling approach to determine if increased human activity on weekends influenced mammalian wildlife (Morrison et al., 2014). Given our zero-heavy data (characteristic of camera trapping studies), we used generalized linear mixed models with a zeroinflated distribution. In stage one, we determined the best environmental variables to use for each species at each camera location. We evaluated environmental variables such as vegetation height, daily temperature (maximum, minimum, and average), and the percentage of moonlight emitted during nighttime hours (to account for potential differences on activity of nocturnal species during moonlit nights). We also added camera location and Julian day as random effects to help account for re-sampling occurring at the same sites across days (Ladle et al., 2016). Using AIC model selection, we evaluated model performance and ranked competing models using AICc values and model weights (Burnham and Anderson, 2002). We considered models to be competing if they were within 2.0 Δ AICc of each other.

In stage two, we created baseline and main effect models. Based on the varying quantities of human photos, depending on the day of the week, we categorized the days as either weekday or weekend and used this as our main effect variable. These categories corresponded to "low" (weekday) and "high" (weekend) human activity (George and Crooks, 2006; Ladle et al., 2016; Longshore et al., 2013). Our baseline habitat/ environmental model consisted of precipitation and the most competitive vegetation and temperature variables from stage one (see Tables 1 and 2) (Morrison et al., 2014). We then created main effect models that were identical to the baseline model, except that they included weekend, campground, and weekend*campground (to account for the potential interaction of high human activity in campgrounds on weekends) variables. For mammals that are generally considered prey (e.g., mule deer [Odocoileus hemionus]), we included the occurrence (number of photos/day) of carnivores (covotes [Canis latrans], bobcats [Lynx rufus], and mountain lions [Puma concolor]) as covariates to account for potential behavioral changes due to presence of predators (Berger, 2007; Krishna et al., 2016). We then performed model selection to determine top models for mammalian wildlife following the same evaluation criteria from stage one. We averaged competing top models within 2.0 AAICc to acquire beta coefficients. This approach allowed us to compare the relative importance of the weekend effect on the activity of mammals after controlling for environmental factors. We used R package "glmmADMB" to run linear mixed effects models (http://glmmadmb.r-forge.r-project.org/). To test for the occurrence of spatial autocorrelation (i.e., lack of independence) between cameras we used Moran's I spatial autocorrelation analyses in ArcGIS Pro (version 1.4, Environmental Systems Research Institute, Redlands, CA).

Table 1

Model Selection results assessing the effects of vegetation variables on the daily activity of mule deer (*Odocoileus hemionus*), beavers (*Castor canadensis*), northern raccoons (*Procyon lotor*), and mountain lions (*Puma concolor*). Data were collected from the Diamond Fork Area in central Utah, USA from January to June 2015.

Model	K	LL	ΔAICc	w _i
Mule Deer				
Null (intercept with random effects)	4	-3101.52	0.00	0.44
Trees 5–10 m	5	-3101.38	1.72	0.19
Shrubs 3 m	5	-3101.40	1.76	0.18
Vegetation 0.5-1 m	5	-3101.45	1.86	0.18
Trees 10–25 m	5	-3101.47	1.90	0.17
Vegetation 1–3 m	5	-3101.51	1.98	0.16
Vegetation 0-0.5 m	5	-3101.52	2.00	0.16
Sparse vegetation	5	-3101.52	2.00	0.16
Beaver				
Sparse vegetation	5	-1594.50	0.00	0.44
Trees 5–10 m	5	-1595.67	2.34	0.14
Vegetation 0-0.5 m	5	-1595.70	2.40	0.13
Null (intercept with random effects)	4	-1597.08	3.16	0.09
Vegetation 0.5-1 m	5	-1596.49	3.98	0.06
Shrubs 3 m	5	-1596.53	4.06	0.06
Vegetation 1–3 m	5	-1596.94	4.88	0.04
Tree 10–25 m	5	-1597.07	5.14	0.03
Raccoon				
Tree 5–10 m	5	-1580.21	0.00	0.44
Sparse vegetation	5	-1581.00	1.58	0.20
Null (intercept with random effects)	4	-1582.63	2.84	0.11
Vegetation 0.5-1 m	5	-1581.92	3.42	0.08
Trees 10–25 m	5	-1582.54	4.66	0.04
Vegetation 0-0.5 m	5	-1582.60	4.78	0.04
Vegetation 1–3 m	5	-1582.61	4.80	0.04
Shrubs 3 m	5	-1582.61	4.80	0.04
Mountain Lion				
Vegetation 1–3 m	5	-331.54	0.00	0.64
Vegetation 0.5-1 m	5	-333.43	3.77	0.10
Null (intercept with random effects)	4	-334.82	4.57	0.06
Trees 5–10 m	5	-333.94	4.81	0.06
Trees 10–25 m	5	-334.11	5.15	0.05
Sparse vegetation	5	-334.20	5.33	0.04
Shrubs 3 m	5	-334.72	6.37	0.03
Vegetation 0–0.5 m	5	-334.74	6.41	0.03

Table 2

Model Selection results assessing the effects of temperature variables on the daily activity of mule deer (*Odocoileus hemionus*), beavers (*Castor canadensis*), northern raccoons (*Procyon lotor*), and mountain lions (*Puma concolor*). Data were collected from the Diamond Fork Area in central Utah, USA from January to June 2015.

Model	K	LL	ΔAIC_{c}	w _i
Mule Deer				
Average daily temp	5	-3098.22	0.00	0.69
Maximum daily temp	5	- 3099.36	2.28	0.22
Null (intercept with random effects)	4	-3101.52	4.60	0.07
Minimum daily temp	5	-3101.45	6.46	0.03
Beaver				
Maximum daily temp	5	-1584.30	0.00	0.95
Average daily temp	5	-1587.34	6.08	0.05
Null (intercept with random effects)	4	-1597.08	23.56	0.00
Minimum daily temp	5	-1597.05	25.50	0.00
Raccoon				
Null (intercept with random effects)	4	-1582.63	0.00	0.46
Minimum daily temp	5	-1582.56	1.86	0.18
Average daily temp	5	-1582.59	1.92	0.18
Maximum daily temp	5	-1582.60	1.94	0.18
Mountain Lion				
Maximum daily temp	5	-333.41	0.00	0.38
Average daily temp	5	-333.74	0.67	0.27
Null (intercept with random effects)	4	-334.82	0.82	0.25
Minimum daily temp	5	-334.82	2.82	0.09

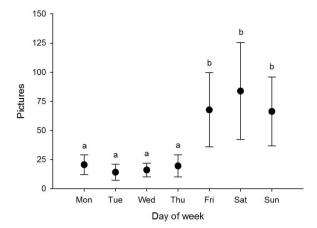


Fig. 1. Human (*Homo sapiens*) and domestic dog (*Canis familiaris*) activity (95% CI) by day of week. Significance differences between plots are denoted by different lowercase letters. Data were collected from the Diamond Fork Area in central Utah, USA from January to June 2015.

3. Results

In 6850 camera days, we recorded a total of 46,529 pictures, of which, 21,508 pictures contained human and non-human mammals. We documented 11,665 pictures of humans (representing the most pictures for a single species in our study) and 1565 pictures of domestic dogs (C. familiaris). We found a difference in human activity between individual days of the week (H = 106.07, df = 6, p < 0.001) and post hoc analyses revealed a significant increase in human activity on weekends (Friday to Sunday) compared to weekdays (Monday to Thursday; Fig. 1). We also captured 8119 images of mammalian wildlife representing 17 species. In decreasing order of species captured, nonhuman mammals included: mule deer, American beaver (Castor canadensis), northern raccoon (Procyon lotor), mountain lion, mountain cottontail (Sylvilagus nuttallii), American mink (Neovison vison), red fox (Vulpes vulpes), striped skunk (Mephitis mephitis), red squirrel (Tamiasciurus hudsonicus), coyote, moose (Alces alces), chipmunk (Tamias spp.), elk (Cervus elaphus), muskrat (Ondatra zibethicus), yellow-bellied marmot (Marmota flaviventris), bobcat, and North American porcupine (Erethizon dorsatum) (Fig. 2).

Despite the number of species documented, we only had sufficient data to conduct statistical analysis for four species. Mule deer was the most common species in our study (56% of all non-human mammals),

Fig. 2. Number of pictures of species of mammalian wildlife captured with remote cameras. Data were collected from the Diamond Fork Area in central Utah, USA from January to June 2015.

J.H. Nix et al.

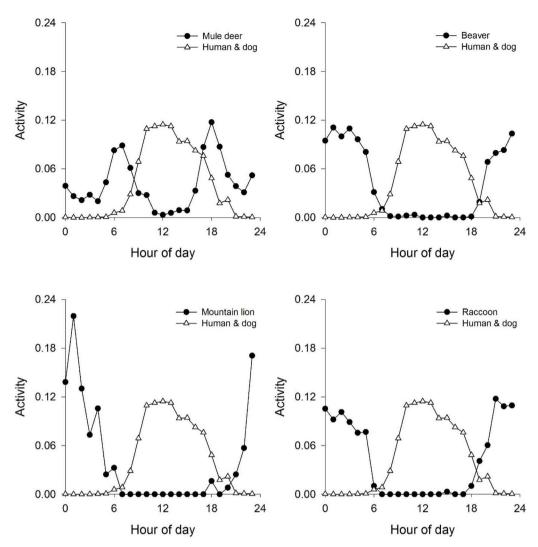


Fig. 3. Diel activity patterns of the four most prominent species of mammalian wildlife in our study area (mule deer [Odocoileus hemionus], beavers [Castor canadensis], raccoons [Procyon lotor], and mountain lions [Puma concolor]) compared to diel activity of humans (Homo sapiens) and dogs (Canis familiaris). Data were collected from the Diamond Fork Area in central Utah, USA from January to June 2015.

beaver was the second most common (21%), raccoon was the third most common (12%), and mountain lion was the fourth most common (2%; Fig. 2). Of these four species, only mule deer were crepuscular, whereas beavers, raccoons, and mountain lions were nocturnal (Fig. 3). We did not detect any evidence for spatial autocorrelation among sites for beavers (Moran's I = 0.09, z = 0.83, p = 0.41), mule deer (Moran's I = 0.14, z = 1.33, p = 0.18), raccoons (Moran's I = 0.01, z = 0.87, p = 0.38), or mountain lions (Moran's I = 0.01, z = 0.98).

Three out of the four focal species in our study supported our predictions. As we predicted for crepuscular species (i.e., mule deer), increased human activity during weekends was an important factor (Table 3). Mule deer reduced activity during weekends and within campgrounds during weekends (Table 4). Alternatively, we expected increased human activity on weekends to be less important for nocturnal species; activity by beavers and mountain lions (both nocturnal species) were consistent with this prediction as their top models included only environmental factors (Table 3). Neither beavers nor mountain lions reduced activity due to increased human activity on weekends (Table 4). However, anthropogenic activity was important for raccoons, which were also nocturnal (Table 3). Raccoons were less active in campground areas during weekends (with high activity of humans), but more active in campgrounds during weekdays (Table 4).

4. Discussion

Our results provided support for the prediction that species with

temporal overlap with humans (i.e., crepuscular species; Fig. 3) would decrease activity in response to increased human recreation on weekends. Our findings corroborate previous research indicating that wildlife avoid increased human activity on weekends (Cardoni et al., 2008; Marzano and Dandy, 2012; Trulio and Sokale, 2008). We also found that nocturnal species, which have minimal temporal overlap with humans, primarily did not reduce activity because of increased human activity during weekends. However, we observed differences between individual species of mammals in our study area and their responses to periodic increases in human activity depending on the level of temporal overlap with humans.

We provide additional evidence demonstrating that diurnal and crepuscular ungulates decrease activity in response to increased anthropogenic activity (Barrueto et al., 2014; Rogala et al., 2011; van Doormaal et al., 2015). Larger-bodied mammals, such as ungulates, likely have a heightened level of sensitivity to human activity (Brown et al., 2012), which is particularly evident on weekends (Longshore et al., 2013; Sibbald et al., 2011). Similar to other ungulates, we observed decreased activity of mule deer in response to increased human activity during weekend periods. Evidence was not as strong for the model with the weekend*campground interaction for mule deer compared to just the weekend model. Overall, the activity of mule deer decreased along our entire study area, providing further support of their heightened sensitivity and suggests that they may be avoiding human activity altogether on the weekends.

Results for beavers and mountain lions supported our hypothesis, as

Table 3

Model Selection results assessing the effects of weekend variables, campgrounds, and environmental factors on the daily activity of mule deer (*Odocoileus hemionus*), beavers (*Castor canadensis*), northern raccoons (*Procyon lotor*), and mountain lions (*Puma concolor*). Data were collected from the Diamond Fork Area in central Utah, USA from January to June 2015.

Model	K	LL	$\Delta \text{AIC}_{\text{c}}$	w _i
Mule deer				
Veg, temp, precip, moonlight, weekend	9	- 3074.85	0.00	0.58
Veg, temp, precip, moonlight, campground,	11	-3073.20	0.71	0.41
weekend, campground*weekend				
Veg, temp, precip, moonlight, campground	9	-3084.06	10.40	0.00
Veg, temp, precip, moonlight	8	-3080.68	11.66	0.00
Carnivores	9	-3083.70	11.69	0.00
Null	5	-3083.85	11.99	0.00
Beaver				
Veg, temp, precip, moonlight	9	-1575.88	0.00	0.47
Veg, temp, precip, moonlight, campground	10	-1575.30	0.85	0.31
Veg, temp, precip, moonlight, weekend	10	-1575.85	1.95	0.18
Veg, temp, precip, moonlight, campground,	12	-1575.27	4.80	0.04
weekend, campground*weekend				
Null	5	-1587.74	15.70	0.00
Carnivores	6	-1587.30	16.83	0.00
Raccoon				
Veg, temp, precip, moonlight, campground, weekend, campground*weekend	11	-1557.83	0.00	0.64
Veg, temp, precip, moonlight, campground	9	-1560.48	1.29	0.34
Veg, temp, precip, moonlight	8	-1564.34	7.00	0.02
Veg, temp, precip, moonlight, weekend	9	-1564.16	8.65	0.00
Null	5	-1571.54	15.39	0.00
Competitors	7	-1570.04	16.40	0.00
Mountain lion				
Veg, temp, precip, moonlight	9	- 309.823	0.00	0.45
Veg, temp, precip, moonlight, weekend	10	-309.487	1.33	0.23
Veg, temp, precip, moonlight, campground	10	- 309.606	1.57	0.21
Null	5	-315.662	3.66	0.07
Veg, temp, precip, moonlight, campground,	12	-309.224	4.82	0.04
weekend, campground*weekend				

these nocturnal species did not reduce activity in response to increased anthropogenic activity. The top model for beavers and mountain lions did not contain the weekend and campground variables and the modelaveraged estimates for these variables were not significant. The lack of a strong response towards increased human activity is likely due to these species being nocturnal when human activity is generally at its lowest (Swinnen et al., 2015). In addition, beavers constantly remain close (< 20 m) to the perceived safety of water (Rosell and Czech, 2000) and mountain lions are extremely adept at avoiding interactions with humans (Morrison et al., 2014; Sweanor et al., 2008).

Raccoons did not follow the same patterns as the other nocturnal species, as they had contrasting activity patterns during weekdays and weekends. During weekdays when human activity was minimal, raccoon activity was concentrated in campgrounds, likely to capitalize on anthropogenic refuse (Carrillo and Vaughan, 1993; Prange et al., 2004). Alternatively, during weekends, raccoon activity decreased in campground areas when human activity was high, contrasting what has been previously observed for Procyon species (Carrillo and Vaughan, 1993). An explanation for this pattern may relate to the presence of domestic dogs on weekends in our study area, particularly in campground areas. Domestic dogs can reduce activity of raccoons during nocturnal periods (Suraci et al., 2016) and this may have occurred in our study. This suggests that being nocturnal does not necessarily preclude a species from being influenced by anthropogenic activity (in our case, dogs) occurs at night. For example, green sea turtles (Chelonia mydas) nest on beaches at night, but have decreased activity during weekends as human activity increased to observe the nesting process (Jacobson and Lopez, 1994).

We found a strong correlation between periodic increases in anthropogenic activity and subsequent decreases in the activity of species

Table 4

Model-averaged coefficients, associated *p*-values, and 95% confidence intervals from the top models assessing the effects of weekends, campgrounds, and environmental factors on the daily activity of mule deer (*Odocoileus hemionus*), beavers (*Castor canadensis*), northern raccoons (*Procyon lotor*), and mountain lions (*Puma concolor*). Data were collected from the Diamond Fork Area in central Utah, USA from January to June 2015.

Coefficient	Estimate	SE	z	р	Lower	Upper
					95% CI	95% CI
Mule deer						
Intercept	-2.12	0.17	12.30	< 0.01	-2.55	-1.90
Ave temp.	0.02	0.01	2.13	0.03	< 0.01	0.03
Precip.	0.20	0.20	0.99	0.32	-0.20	0.59
Moonlight	-0.02	0.11	0.21	0.84	-0.25	0.20
Weekend	-0.30	0.09	3.24	< 0.01	-0.49	-0.08
Campground	0.17	0.25	0.68	0.50	-0.03	0.87
Campground*weekend	-0.03	0.09	0.34	0.73	-0.32	0.17
Beaver						
Intercept	- 3.94	0.37	10.55	< 0.01	-4.67	-3.20
Sparse vegetation	-6.80	3.08	2.21	0.03	-12.84	-0.76
Max temp.	0.05	0.01	4.20	< 0.01	0.02	0.07
Precip.	-0.14	0.33	0.41	0.68	-0.78	0.51
Moonlight	-0.17	0.18	0.96	0.34	-0.53	0.18
Campground	-0.58	0.53	1.08	0.28	-1.62	0.47
Weekend	-0.03	0.13	0.24	0.81	-0.28	0.22
Raccoon						
Intercept	-3.51	0.28	12.77	< 0.01	-4.05	-2.97
Trees 5–10 m	-4.15	1.55	2.67	2.67	-7.20	-1.10
Precip.	-1.04	0.36	2.89	2.91	-1.75	-0.34
Moonlight	-0.05	0.36	2.91	< 0.01	-0.44	0.23
Campground	1.15	0.37	3.10	< 0.01	0.42	1.87
Weekend	0.17	0.16	1.07	0.28	-0.15	0.50
Campground*weekend	-0.42	0.19	2.22	0.03	-0.79	-0.05
Mountain lion						
Intercept	-5.42	0.80	6.81	< 0.01	-6.98	-3.86
Vegetation 1-3 m	-2.46	0.97	2.55	0.01	-4.36	-0.57
Max temp.	-0.04	0.04	1.09	0.28	-0.12	0.03
Precip.	1.71	1.02	1.67	0.10	-0.30	3.71
Moonlight	-0.14	0.66	0.21	0.83	-1.44	1.16
Campground	-0.32	0.50	0.65	0.52	-1.31	0.66
Weekend	0.39	0.48	0.81	0.42	-0.55	1.32

with greater levels of temporal overlap with humans. The only crepuscular species in our study, mule deer, and one of the three nocturnal species, raccoons, both reduced activity during weekends. However, this pattern was not evident for the remaining two nocturnal species, beavers and mountain lions. Questions regarding wildlife responses to anthropogenic activities are becoming increasingly important to understand as use of recreation areas by humans is increasing. Our work adds to the growing understanding that increased human activity on weekends can influence the behavior of crepuscular species, but less so for species with limited temporal overlap with humans (Cardoni et al., 2008; Marzano and Dandy, 2012; Trulio and Sokale, 2008). We provide evidence that as temporal overlap between humans and wildlife increases, so does the negative influence that humans have on wildlife.

Acknowledgments

We would like to thank J. Fullmer for assistance in the field. We are also grateful for the assistance with statistical analyses by R. Larsen. In addition, we would like to express our gratitude to the recreationists that allowed us to work around their activities. Funding and equipment were provided by Brigham Young University.

References

Barrueto, M., Ford, A.T., Clevenger, A.P., 2014. Anthropogenic effects on activity patterns of wildlife at crossing structures. Ecosphere 5, 19.

Benitez-Lopez, A., Alkemade, R., Verweij, P.A., 2010. The impacts of roads and other infrastructure on mammal and bird populations: a meta-analysis. Biol. Conserv. 143, 1307–1316.

- Berger, J., 2007. Fear: human shields and the redistribution of prey and predators in protected areas. Biol. Lett. 3, 620–623.
- Brown, C.L., Hardy, A.R., Barber, J.R., Fristrup, K.M., Crooks, K.R., Angeloni, L.M., 2012. The effect of human activities and their associated noise on ungulate behavior. PLoS One 7, e40505.
- Burnham, K.P., Anderson, D.A., 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach, second ed.). Springer, New York.
- Cardoni, D.A., Favero, M., Isacch, J.P., 2008. Recreational activities affecting the habitat use by birds in Pampa's wetlands: argentina: implications for waterbird conservation. Biol. Conserv. 141, 797–806.
- Carrillo, E., Vaughan, C., 1993. Behavioral change in Procyon spp. (Carnivora: procyonidae) caused by tourist visitation in a Costa Rican wildlife area. Rev. Biol. Trop. 41, 843–848.
- George, S.L., Crooks, K.R., 2006. Recreation and large mammal activity in an urban nature reserve. Biol. Conserv. 133, 107–117.
- Hall, L.K., Larsen, R.T., Westover, M.D., Day, C.C., Knight, R.N., McMillan, B.R., 2016. Influence of exotic horses on the use of water by communities of native wildlife in a semi-arid environment. J. Arid Environ. 127, 100–105.
- Jacobson, S.K., Lopez, A.F., 1994. Biological impacts of ecotourism tourists and nesting turtles in Tortuguero National Park. Costa Rica.Wildl. Soc. Bull. 22, 414–419.
- Kays, R., Parsons, A.W., Baker, M.C., Kalies, E.L., Forrester, T., Costello, R., Rota, C.T., Millspaugh, J.J., McShea, W.J., 2016. Does hunting or hiking affect wildlife communities in protected areas? J. Appl. Ecol. 54, 242–252.
- Krausman, P.R., Smith, S.M., Derbridge, J., Merkle, J.A., 2008. Suburban and Exurban Influences on Wildlife and Fish. FWP Project 2801. Wildlife Division, Montana Fish, Wildlife & Parks, Helena, MT, USA.
- Krishna, Y.C., Kumar, A., Isvaran, K., 2016. Wild ungulate decision-making and the role of tiny refuges in human-dominated landscapes. PLoS One 11, e0151748.
- Ladle, A., Avgar, T., Wheatley, M., Boyce, M.S., 2016. Predictive modeling of ecological patterns along linear-feature networks. Methods Ecol. Evol. 1–10.
- Lafferty, K.D., 2001. Birds at a southern California beach: seasonality: habitat use and disturbance by human activity. Biodivers. Conser. 10, 1949–1962.
- Larson, C.L., Reed, S.E., Merenlender, A.M., Crooks, K.R., 2016. Effects of recreation on animals revealed as widespread through a global systematic review. PLoS One 11, e0167259.
- Longshore, K., Lowrey, C., Thompson, D.B., 2013. Detecting short-term responses to weekend recreation activity: desert bighorn sheep avoidance of hiking trails. Wildl. Soc. Bull. 37, 698–706.
- Martin, J.G.A., Réale, D., 2008. Animal temperament and human disturbance: implications for the response of wildlife to tourism. Behav. Process. 77, 66–72.
- Martineau, J., Pothier, D., Fortin, D., 2016. Processes driving short-term temporal dynamics of small mammal distribution in human-disturbed environments. Oecologia 181, 831–840.
- Marzano, M., Dandy, N., 2012. Recreationist behaviour in forests and the disturbance of wildlife. Biodivers. Conserv. 21, 2967–2986.
- Moore, M.J.C., Seigel, R.A., 2006. No place to nest or bask: effects of human disturbance on the nesting and basking habits of yellow-blotched map turtles (Graptemys flauimaculata). Biol. Conserv. 130, 386–393.

- Morrison, C.D., Boyce, M.S., Nielsen, S.E., Bacon, M.M., 2014. Habitat selection of a recolonized cougar population in response to seasonal fluctuations of human activity. J. Wildl. Manag. 78, 1394–1403.
- Prange, S., Gehrt, S.D., Wiggers, E.P., 2004. Influences of anthropogenic resources on raccoon (Procyon lotor) movements and spatial distribution. J. Mammal. 85, 483–490.
- Rogala, J.K., Hebblewhite, M., Whittington, J., White, C.A., Coleshill, J., Musiani, M., 2011. Human activity differentially redistributes large mammals in the Canadian Rockies national parks. Ecol. Soc. 16, 1–24.
- Rosell, F., Czech, A., 2000. Responses of foraging Eurasian beavers castor fiber to predator odours. Wildl. Biol. 6, 13–21.
- Roy, C.L., Herwig, C.M., Zicus, M.C., Rave, D.P., Brininger, W.L., McDowell, M.K.D., 2014. Refuge use by hatching-year ring-necked ducks: an individual-based telemetry approach. J. Wildl. Manag. 78, 1310–1317.
- Ruhlen, T.D., Sue, A., Stenzel, L.E., Page, G.W., 2003. Evidence that human disturbance reduces snowy plover chick survival. J. Field Ornithol. 74, 300–304.
- Sibbald, A.M., Hooper, R.J., McLeod, J.E., Gordon, I.J., 2011. Responses of red deer (Cervus elaphus) to regular disturbance by hill walkers. Eur. J. Wildl. Res. 57, 817–825.
- Stalmaster, M.V., Kaiser, J.L., 1998. Effects of recreational activity on wintering bald eagles. Wildl. Monogr. 137, 3–46.
- Suraci, J.P., Clinchy, M., Dill, L.M., Roberts, D., Zanette, L.Y., 2016. Fear of large carnivores causes a trophic cascade. Nat. Commun. 7, 1–7.
- Sweanor, L.L., Logan, K.A., Bauer, J.W., Millsap, B., Boyce, W.M., 2008. Puma and human spatial and temporal use of a popular California State Park. J. Wildl. Manag. 72, 1076–1084.
- Swinnen, K.R.R., Hughes, N.K., Leirs, H., 2015. Beaver (*Castor fiber*) activity patterns in a predator-free landscape. What is keeping them in the dark? Mamm. Biol. 80, 477–483.
- Tadesse, S.A., Kotler, B.P., 2012. Impact of tourism on Nubian Ibex (Capra nubiana) revealed through assessment of behavioral indicators. Behav. Ecol. 23, 1257–1262.
- Tarjuelo, R., Barja, I., Morales, M.B., Traba, J., Benitez-Lopez, A., Casas, F., Arroyo, B., Paula Delgado, M., Mougeot, F., 2015. Effects of human activity on physiological and behavioral responses of an endangered steppe bird. Behavioral Ecology 26, 828–838.
- Trulio, L.A., Sokale, J., 2008. Foraging shorebird response to trail use around San Francisco Bay. J. Wildl. Manag. 72, 1775–1780.
- Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A., Watson, J.E.M., 2016. Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. Nat. Commun. 7, 12558.
- Young, J., Watt, A., Nowicki, P., Alard, D., Clitherow, J., Henle, K., Johnson, R., Laczko, E., McCracken, D., Matouch, S., Niemela, J., Richards, C., 2005. Towards sustainable land use: identifying and managing the conflicts between human activities and biodiversity conservation in Europe. Biodivers. Conserv. 14, 1641–1661.
- van Doormaal, N., Ohashi, H., Koike, S., Kaji, K., 2015. Influence of human activities on the activity patterns of Japanese sika deer (Cervus nippon) and wild boar (Sus scrofa) in Central Japan. Eur. J. Wildl. Res. 61, 517–527.