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Original Article

Detecting Short-Term Responses to Weekend Recreation Activity: Desert Bighorn Sheep Avoidance of Hiking Trails

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ABSTRACT To study potential effects of recreation activity on habitat use of desert bighorn sheep (*Ovis canadensis nelsoni*), we placed Global Positioning System collars on 10 female bighorn sheep within the Wonderland of Rocks–Queen Mountain region of Joshua Tree National Park (JOTR), California, USA, from 2002 to 2004. Recreation use was highest from March to April and during weekends throughout the year. Daily use of recreation trails was highest during midday. By comparing habitat use (slope, ruggedness, distance to water, and distance to recreation trails) of female bighorn sheep on weekdays versus weekends, we were able to detect short-term shifts in behavior in response to recreation. In a logistic regression of bighorn sheep locations versus random locations for March and April, female locations at midday (1200 hours) were significantly more distant from recreation trails on weekends compared with weekdays. Our results indicate that within this region of JOTR, moderate to high levels of human recreation activity may temporarily exclude bighorn females from their preferred habitat. However, the relative proximity of females to recreation trails during the weekdays before and after such habitat shifts indicates that these anthropogenic impacts were short-lived. Our results have implications for management of wildlife on public lands where the co-existence of wildlife and recreational use is a major goal. Published 2013. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS desert bighorn sheep, logistic regression, national parks, *Ovis canadensis nelsoni*, recreation.

Animals select habitat through a series of innate and learned behavioral decisions that determine their location in a hierarchy of different spatial and temporal scales of the environment (Hutto 1985, Mayor et al. 2009). Selection at varying spatial scales ranges from fine (e.g., sites for foraging; Johnson et al. 2002) to landscape scale (e.g., home range movements; Boyce 2006). On a temporal scale, habitat selection ranges from short-term daily responses to environmental conditions to medium-term seasonal variations in physiological status and environmental conditions (Bangs et al. 2005, Ratikainen et al. 2007) and to long-term annual or decadal-variations in community structure and demographic and environmental parameters (Ratikainen et al. 2007). These decisions are influenced by a number of factors that can affect an animal's fitness, such as predation (Mech 1977, Creel et al. 2005, Kittle et al. 2008), forage distribution (Fryxell et al. 2005), climatic conditions (Dussalt et al. 2004), terrain features (Boyce et al. 2003), and competition (Fretwell and Lucas 1970). There is also increasing evidence that anthropogenic activities such as recreation can affect habitat selection and subsequently, fitness (Gill et al. 2001, Seip et al. 2007).

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Desert bighorn sheep (*Ovis canadensis nelsoni*) are distributed as several metapopulations throughout the North American Southwest that are particularly vulnerable to detrimental changes in habitat availability due to their low dispersal rates and long distances between populations (Bleich et al. 1996, Epps et al. 2004). They are medium-sized ungulates that rely on rocky, precipitous terrain to detect and escape from predators (Geist 1971, Shackleton 1985). Bighorn sheep can be affected by many anthropogenic activities, including human recreation (McCutchen, 1981, 1995; Papouchis et al. 2001). Disturbance from human recreation has been implicated in the abandonment of bighorn sheep habitat (and extirpation of the population) in the Pusch Ridge Wilderness, Arizona, USA (Etchberger et al. 1989, Schoenecker and Krausman 2002), the San Gabriel Mountains, California, USA (Graham 1971), and in some areas of southeastern Utah, USA (King and Workman 1986). Recreation use is one of the primary factors that prompted the listing of the California peninsular population of desert bighorn sheep (*O. c. nelsoni*) as endangered (U.S. Fish and Wildlife Service 1999). There is also evidence that through learning in response to predictable, localized, and avoidable disturbance, bighorn sheep may habituate to anthropogenic disturbances, such as hiking (Hicks and Elder 1979, Hamilton et al. 1982, Holl and Bleich 1987, Papouchis et al. 2001), aircraft (Krausman et al. 1998) and highway traffic (Horesji 1976). However, these animals may still incur fitness costs associated with risk avoidance behaviors (e.g., vigilance, fleeing, and habitat selection; Gill et al. 2001, Frid and Dill 2002, McGowan and Simons 2006).

The Wonderland of Rocks–Queen Mountain region of Joshua Tree National Park (JOTR), California is inhabited by a small population of desert bighorn sheep (54 ad [95% CI = 39–68] in 2003; 59 ad [95% CI = 28–89] in 2004 [Thompson et al. 2007]). This population is one of an estimated 5 populations that occur within the park. Over 1 million people/year visit JOTR. Visitor use in the Wonderland of Rocks–Queen Mountain region began increasing in 1994, when JOTR was elevated from National Monument to National Park status. This region is especially popular with hikers and campers and has the highest concentration of rock climbing routes in the world (Murdock 2004). Visitation is greatest during spring and autumn months when temperatures are moderate. As a result of the increase in recreational use, resource managers at the park became concerned that this population was at risk from disturbance caused by human recreation.

In situations where disturbance is predictable and repeated, such as that caused by weekend recreation activity in parks or public land located in close proximity to large urban populations, the effects of disturbance on wildlife can be studied by assessing how changes in behavioral state (Morales and Ellner 2002, Patterson et al. 2008) or shifts in habitat selection coincide with the initiation of periods of high recreation activity and whether disturbance effects persist in subsequent periods of relatively low recreation activity. By choosing the appropriate measurement interval, it is possible to use short-term behavioral responses and changes in habitat selection to assess the sensitivity of wildlife to disturbance and to predict the long-term consequences of more chronic disturbance on habitat selection before the disturbance is severe enough to cause abandonment of habitat. Previous studies of the impact of human activity on resource selection by wildlife have compared use of geographic areas with high and low levels of disturbance (Seip et al. 2007) or have compared use of different areas with respect to the temporal period of disturbance (Fernández-Juricic and Tellería 2000, Bruggeman et al. 2006). Here, we compare habitat selection at 3 different times of day on weekends and weekdays to determine whether repeated periods of high and low outdoor recreation activity alter the probability of desert bighorn sheep occurrence at observed verses random points. The method we propose is designed to detect short-term effects of disturbance by focusing on geographic areas where anthropogenic disturbance occurs repeatedly on weekends and to quantify changes in habitat selection that coincide with different intervals or time scales of disturbance. By focusing on the desert habitats of JOTR, where most recreational activity coincides with a spring season of intensive use and high-intensity recreational use on weekends, we are able to test the impact of anthropogenic disturbance on habitat use over relatively short time scales.

STUDY AREA

Our study took place in the Queen Mountain–Wonderland of Rocks Region of JOTR, California, USA. This region was located in the northwestern portion of the park and contained 2 general types of habitat. The Queen Mountain region was primarily mountainous, with elevations between 675 m and 1,710 m. Dominant vegetation consisted of *Larrea tridentata–Ambrosia dumosa* associations at lower (<1,000 m) elevations; *Yucca schidigera*, *Y. brevifolia*, and *Coleogyne ramosissima* associations at mid-elevations (900–1,400 m); and *Juniperus californica* associations at higher (>1,100 m) elevations (Leary 1977). Two permanent water sources, 49 Palms Oasis and Pine City guzzler, were available during the study period. The Wonderland of Rocks region, east and adjacent to Queen Mountain, was composed of large granitic boulder outcrops and cliffs (many >100 m in ht) separated by sandy washes. Elevation was between 920 m and 1,310 m. The area had a relatively low density of vegetation dominated by *Y. schidigera* and *Y. brevifolia* associations and scattered *J. californica* trees (Leary 1977). Water was available during spring months at 3 man-made dams: Barker Dam, Cow Camp Dam, and Keys Ranch Dam. The climate in JOTR is seasonal—summer temperatures could be >44°C and winter low temperatures could be <−2°C. Average rainfall was <10.0 cm/year, with most occurring during winter and summer months.

METHODS

Bighorn Sheep Captures

We captured 10 adult female desert bighorn sheep within the study area during October 2002. We fitted captured sheep with satellite uplink Global Positioning System (GPS) collars that included an automatic breakaway release and mortality sensor (TGW-3580; Telonics, Inc., Mesa, AZ). Nine of the 10 sheep fitted with radio-collars survived for the entire 2-year study. We recovered seven of the 10 collars and successfully downloaded 3 locations/day. We derived locations from 3 unrecovered collars from the ARGOS satellite over-flights taken during the study period. Satellite-dependent data from the 3 unrecovered collars were generally less reliable in terms of temporal consistency than data derived directly from collars. We collected no fewer than 480 locations for any one animal.

Within the study area, we estimated population size at 54 bighorn sheep (95% CI = 39–68) in 2003 and 59 bighorn sheep (95% CI = 28–89) in 2004 (Thompson et al. 2007). Under the assumption that females comprised 50% of the population, these 10 collared animals represented approximately one-third of the females in the population.

We programmed the GPS collars to record locations from January through April of 2003 and 2004 3 times/day (0500 hours, 1200 hours, and 2000 hours Pacific Standard Time [PST]). These times were chosen to evaluate sheep response during the time of day when recreation activity on trails (0500 PST) was very low (or none), when recreation activity on trails was high (1200 PST), and then at 2000 PST, when activity was low again (see Methods section, below). Daily activity patterns for bighorn sheep generally consist of short bedding periods that alternate with feeding periods (Chilelli and Krausman 1981, Krausman et al. 1985). Feeding activity is generally highest during early morning (0500–0700 PST) and early evening hours (1600–2000) and is lowest during midday (Chilelli and Krausman 1981, Krausman et al. 1985).

We collected over 5,500 locations and removed those resulting from satellite error (<0.5% of total) before analyses. We confirmed the validity of outliers (possible errors) by documenting that previous and subsequent locations were within reasonable (approx. 1.0 km) proximity to the outlier; we removed locations outside this criterion. Collars retrieved from the field were found within 10 m of the reported satellite coordinates.

Categorization of Recreation Areas, Recreation Activity, and Time Periods

Given our focus on the effects of recreation activity, we restricted our analysis of changes in habitat selection to sheep locations within JOTR where recreational trail use could affect bighorn sheep. We used past investigations of bighorn sheep habitat to delineate potential habitat and then located 3 recreation areas within the potential habitat that had comparable amounts of habitat, access to water, and distance to trails (Fig. 1). We first used Geographic Information System (GIS; ArcMap 9.1) to find areas of available bighorn sheep habitat using the criteria of slope >40% and ruggedness >0.025, derived from habitat models constructed previously for this population (Thompson et al. 2007). We delineated within this habitat 3 areas with comparable distance to water sources and to recreation trails by calculating average distances from water and recreation trails for 100 random points within each potential recreation area. Recreation trails in bighorn habitat were located in steep, rugged, terrain and in relatively flat terrain (Fig. 1). To further delineate recreation areas, we chose a 600-m distance from recreation trails as the maximum limit at which bighorn sheep may be affected by the presence of humans (Papouchis et al. 2001). Categorization of recreation areas was further supported by confirmation of consistent recreation use by JOTR park staff and trail counter data. The 3 recreation areas had similar size, proportional habitat availability, and distance to a water source (i.e., 1) 49 Palms Oasis in the Queens Mountain, 2) Barker Dam in the Wonderland of Rocks area, and 3) the Pine City guzzler; Fig. 1). In our analyses, we used a combined data set of all locations of collared sheep and random points within these 3 areas (Table 1).

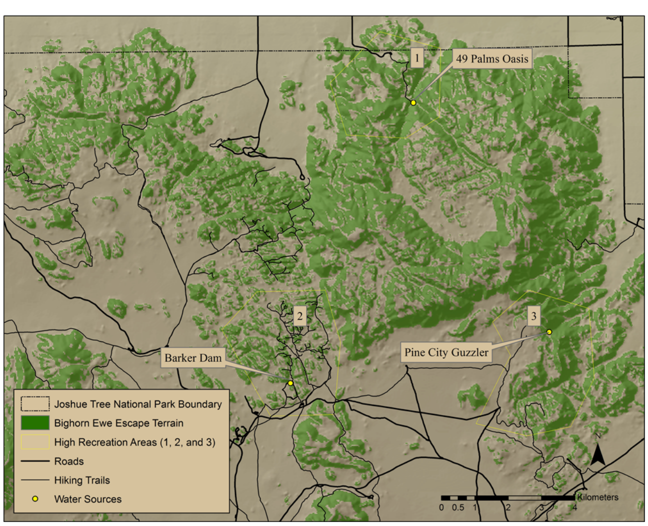

Figure 1. Map of the study area showing areas with recreation trails in the Wonderland of Rocks–Queen Mountain region of Joshua Tree National Park, California, USA, 2002–2004. Escape terrain is defined as terrain with slope >40% and ruggedness (Vector Ruggedness Measure) >0.025.

Recreation activity in JOTR occurred year round; however, there were periods of greater and lesser use. We used monthly totals of numbers of persons entering the park as an index of monthly recreation activity (source: National Park Service). Daily activity was derived from vehicle entry data at the west entrance station (UTM 588885E, 3771225N), the entrance that was closest to the study area and had the most complete records of activity. Daily car entry to the park confirmed our division of seasonal periods into January–February (a period of low recreation activity) and March–April (a period of increased recreation activity; Fig. 2). The daily car-entry data also illustrated the change in recreational activity through the week typical of a park located near a large urban area (Fig. 3). The average cars per day peaked sharply on Saturday and Sunday, days that represent high recreation activity in our study.

We also utilized trail counter data from 3 locations to confirm that recreation trail use differed between days of the

Table 1. Summary of habitat variables for female bighorn sheep locations (3 times of day) in 2-month intervals, January to February and March to April (years 2003 and 2004 combined) and for random locations in the Wonderland of Rocks–Queen Mountain region of Joshua Tree National Park, California, USA.

Variable	Distance to water (km)	Distance to trail (km)	Slope	Ruggedness
Female locations Jan to Feb ($n = 142$)				
Mean (median)	1.35 (1.40)	0.73 (0.68)	0.49 (0.47)	0.016 (0.010)
Variance	0.47	0.27	0.04	0.0003
Minimum, maximum	0.09, 2.66	0, 1.93	0.06, 1.0	0.001, 0.085
Skew	0.021	0.619	0.37	2.07
Kurtosis	−1.07	−0.378	0.086	4.72
Female locations Mar to Apr ($n = 341$)				
Mean (median)	1.22 (1.09)	0.78 (0.78)	0.47 (0.49)	0.019 (0.012)
Variance	0.39	0.16	0.04	0.0003
Minimum, maximum	0.12, 2.91	0, 1.71	0.05, 1.0	0.0, 0.12
Skew	0.77	−0.18	0.11	1.73
Kurtosis	−0.24	−0.72	−0.16	3.88
Random locations ($n = 471$)				
Mean (median)	1.39 (1.18)	0.63 (0.59)	0.33 (0.32)	0.012 (0.008)
Variance	0.64	0.19	0.04	0.0001
Minimum, maximum	0.04, 3.36	0, 2.03	0.0, 0.91	0.0, 0.10
Skew	0.51	0.57	0.46	2.69
Kurtosis	−0.81	−0.29	−0.41	11.31

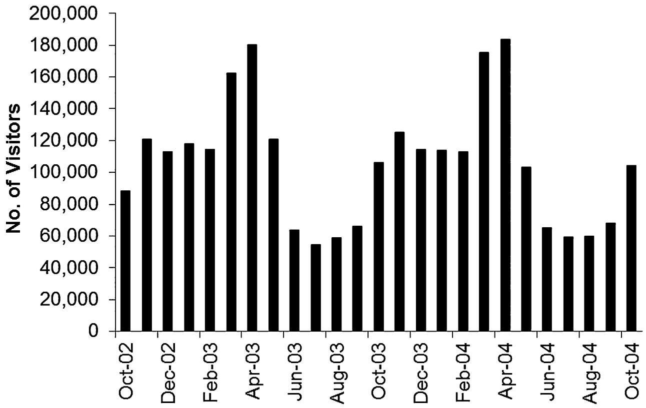

Figure 2. Monthly visitation to Joshua Tree National Park, California, USA, 2002–2004, showing peak seasonal activity during March and April and low activity from June to September. No variance estimates were reported. Source: Joshua Tree National Park, California.

week as well as time of day (Fig. 4). Trail counters (TrailMaster TM-550; TrailMaster Co., Lenexa, KS) were placed on the trail 150 m west of the Pine City water source, on the trail approximately 80 m from the water source of the 49 Palms Oasis, and at the trailhead of the Wonderland of Rocks region near Barker Dam. Trail counter data were available from February 2003 through May 2003 for Barker Dam, February 2004 through May 2004 for the 49 Palms Oasis, and April 2004 through May 2004 for Pine City. Counters were placed 1 m above ground and approximately 2 m from the trail. The total daily accumulated trail-counter detections pooled for all 3 sites for weekdays (Monday–Friday) were: 1,014 (19.1%), 760 (14.3%), 868 (16.3%), 1,375 (25.9%), and 1,292 (24.3%) hiker detections, respectively. Total numbers of hiker detections recorded on weekends were 2,520 (55.0%) on Saturdays, and 2,064 (45.0%) on Sundays. The total numbers of hiker detections recorded on Saturday and Sunday were 2.53 times greater than the combined total numbers of hiker detections on Tuesday, Wednesday, and Thursday, the days we categorized as weekend and weekday, respectively. Trail use was greatest during daylight hours, with 95.2% of all hiker activity occurring between 0700 hours and 1900 hours (Fig. 4). The greatest numbers of hikers per hour were recorded between 1000 hours and 1600 hours, with 71.7% of all activity occurring from 2 hours before to 2 hours after the 1200 hour GPS location of sheep in all 3 recreational areas (Fig. 4). In contrast, <4.8% of trail use occurred during early morning and evening hours (0500 and 2000, respectively).

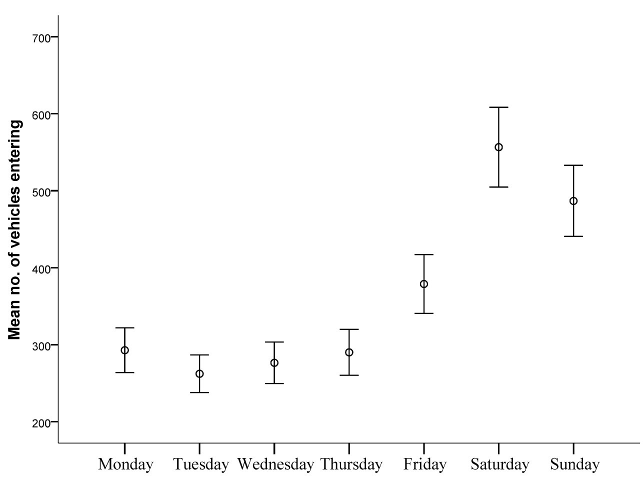

Figure 3. Daily means for number of vehicles entering Joshua Tree National Park, California, USA, at the west entrance station between 15 October 2002 and 15 October 2004. Bars represent ± 2 standard errors. Visitor use on Saturday and Sunday was considered high recreation use; visitor levels were considered low from Monday through Thursday ($F_{1,98} = 107.0$, $P < 0.001$). Source: National Park Service, Denver, Colorado.

Analysis of Effects of Recreation Activity on Habitat Use and Movement Patterns

We analyzed changes in female sheep habitat use between weekday and weekend at 3 times of day and in 2 seasonal periods with binary logistic regression analyses using environmental variables calculated for sheep locations and random points (Manly et al. 2002, Johnson et al. 2006). We used the Hawth's tools© extension within ArcMap to generate random points within the study area and spatially enforced a minimum distance of 10 m between points. Habitat use of adult female bighorn sheep was determined by measuring slope (percent converted to a proportional scale from 0 to 1), distance to permanent water (km), ruggedness (Vector Ruggedness Measure with range 0–1; Sappington et al. 2007), and distance to major recreation trails (km) for all satellite-recorded locations. The first 3 variables have been used to accurately predict habitat use and model desert bighorn occurrence (Holl 1982, Bleich et al. 1997, Zeigenfuss et al. 2000, Sappington et al. 2007, Longshore et al. 2010). All habitat variable measurements were determined using GIS (ArcView 3.2 and ArcMap 9.1). The Vector Ruggedness Measure was calculated using an ArcView script that first calculated the angles of a 3-dimensional vector orthogonal to each 30 × 30-m cell in a grid covering the study area and then, for each cell, quantified the dispersion of vectors or variation in terrain angles and aspect across a 3 × 3 moving window (grid of 9 cells centered on the focal cell; Sappington et al. 2007). Data from 2 years of sheep locations within the 3 recreation areas were pooled (Table 1).

We modeled use of habitat relative to the 4 environmental variables (slope, ruggedness, distance to water, distance to major recreation trails), at the 3 times of day using logistic regression. We assessed statistical significance with chi-square tests of likelihood ratios and model fit with Akaike's second-order information criteria (AIC) and the area under a Receiver Operator Curve (ROC) using SAS (SAS Institute, Inc., Cary, NC; version 9.3). To determine whether increased recreation activity affected bighorn sheep habitat use and movement patterns we tested the interaction between a categorical independent variable, day of week (0 for Tuesday, Wednesday, Thursday; 1 for weekend days Saturday, Sunday), and each of the 4 continuous environmental variables. The interaction effects represent the change in the relationship between habitat use and environmental

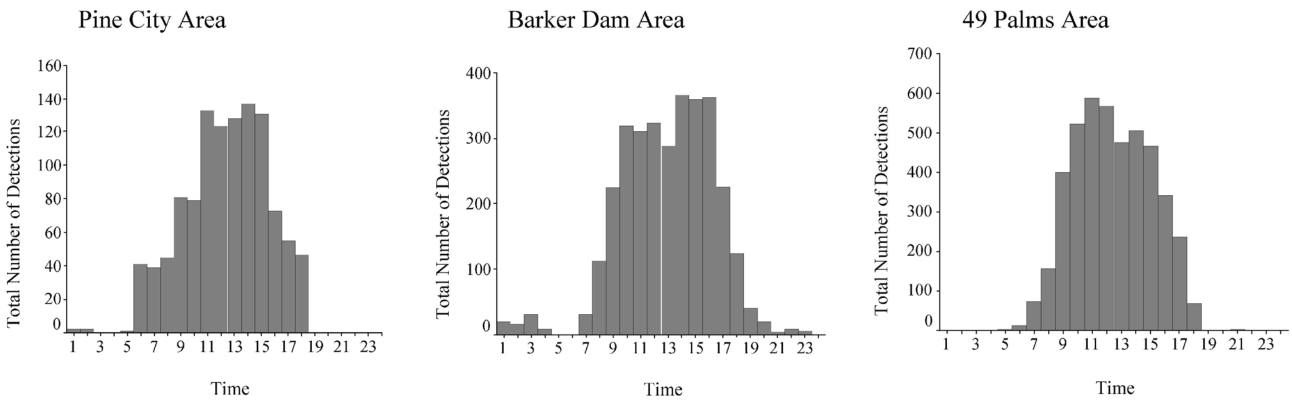

Figure 4. Total number of hikers detected by trail counters in the Wonderland of Rocks–Queens Mountain region of Joshua Tree National Park, California, USA. Trail counters were placed at 3 locations: 1) the trailhead of the Wonderland of Rocks region near Barker Dam (Feb 2003 through May 2003); 2) the trail approximately 80 m from the water source of the 49 Palms Oasis (Feb 2004 through May 2004); and 3) on the trailhead leading to the Pine City water source (Apr 2004 through May 2004).

variables in transitioning from weekday to weekend. The logistic regression coefficient for an environmental variable in a model with interaction, estimates the relationship for the base level of the class variable, weekday in our analyses; whereas, the interaction term estimates the additive amount by which the coefficient changes in shifting to the other level of the class variable, weekend (Jaccard 2001).

Our primary goal was to determine whether daily recreation activity caused sheep to move away from trails or to change location with respect to water or escape terrain rather than to find the habitat models that had the best fit to our location data. Thus, we included all 4 environmental variables (slope, ruggedness, distance to water, and distance to major recreation trails) in every model and focused on tests of the interactions of day of the week with the environmental variables using the conservative ROC comparison test (DeLong et al. 1988) implemented in SAS (version 9.3). For a given season and time of day, we compared the Area Under the Curve (AUC) of a model with all 4 environmental variables with a model with all 4 variables and their interaction with day of week. For the models with a significant interaction (e.g., distance to trail × week in Mar–Apr), we used AICs from the subset of all models that contained the environmental variable and interaction term to calculate delta AICs and Akaike weights for the interaction term. The model-averaged estimate of the interaction term and its standard error was calculated using the set of all models that contained the interaction term.

RESULTS

There are 2 comparisons of time intervals that can indicate an influence of recreational activity on bighorn habitat selection. First, the change in habitat selection could occur in March and April in response to increased usage of recreation trails and park locations compared with preceding months and, second, the change in habitat selection could be restricted to weekend days, which have increased recreational activity in comparison to mid-week days. Comparing January–February to March–April for each of the 3 sampling times in the day, the variables that significantly predict bighorn sheep locations in January and February were distance to water, slope, and ruggedness (Table 2); whereas, in addition to these 3 variables, distance to recreation trails, and the interaction of week with distance to recreation trails and slope were significant in March and April (Table 3).

Table 2. Maximum likelihood estimates of logistic regression coefficients (MLE) and standard error (SE) and model Akaike Information Criterion (AIC) in the low-recreation-activity season for 4 habitat variables and their interaction with day of week (Tuesday, Wednesday, Thursday vs. Saturday, Sunday) derived from analyses of female bighorn sheep locations at 3 times of day (Pacific Standard Time) in January and February (years 2003 and 2004 combined) versus random available locations in the Wonderland of Rocks–Queen Mountain region of Joshua Tree National Park, California, USA.

Time of day (24-hr scale)	0500		1200		2000	
AIC	188.6		201.2		184.8	
Variable	MLE	SE	MLE	SE	MLE	SE
Distance to water	0.001[a]	0.001	−0.00012	0.0003	0.00006	0.00032
Distance to trail	0.0001	0.0004	0.000276	0.0005	−0.00004	0.00048
Slope	0.066[b]	0.014	0.00351	0.011	0.090[b]	0.0172
Ruggedness	1.233[b]	0.356	0.5917	0.324	0.5204	0.2273
Distance to trail × week	0.0003	0.0004	0.00022	0.0005	0.0004	0.00048
Distance to water × week	0.0002	0.0003	0.00032	0.0003	0.0003	0.00032
Ruggedness × week	0.410	0.356	0.0748	0.324	0.1703	0.2273
Slope × week	0.004	0.014	0.0132	0.011	−0.00154	0.0172

[a] $P < 0.01$ for estimate based on Wald chi-square (χ^2).
[b] $P < 0.001$ for estimate based on Wald chi-square (χ^2).

Table 3. Maximum likelihood estimates of logistic regression coefficients (MLE) and standard error (SE) and model Akaike Information Criterion (AIC) in the high-recreation-activity season for 4 habitat variables and their interaction with day of week (Tuesday, Wednesday, Thursday vs. Saturday, Sunday) derived from analyses of female bighorn sheep locations at 3 times of day (Pacific Standard Time) in March and April (years 2003 and 2004 combined) versus random available locations in the Wonderland of Rocks–Queen Mountain region of Joshua Tree National Park, California, USA.

Time of day (24-hr scale)	0500		1200		2000	
AIC	207.9		219.2		204.7	
Variable	MLE	SE	MLE	SE	MLE	SE
Distance to water	0.0003	0.0002	−0.056[a]	0.0002	−0.00009	0.0002
Distance to trail	0.076[a]	0.0004	0.110[b]	0.0003	0.0002	0.0004
Slope	0.055[b]	0.009	−0.009	0.007	0.073[b]	0.011
Ruggedness	0.905[b]	0.164	−0.083	0.142	0.512[b]	0.128
Distance to trail × week	0.0002	0.0004	0.776[a,c]	0.0003	0.0002	0.0004
Distance to water × week	0.00014	0.0002	0.00001	0.0002	0.00008	0.0002
Ruggedness × week	−0.0930	0.164	0.026	0.142	0.147	0.128
Slope × week	3.709[b]	0.606	0.0086	0.0073	0.019	0.011

[a] $P < 0.01$ for estimate based on Wald chi-square (χ^2).
[b] $P < 0.001$ for estimate based on Wald chi-square (χ^2).
[c] $P < 0.05$ for Receiver Operator Curve contrast; significant difference in Area Under the Curve in comparison to model without this interaction term.

Female bighorn sheep exhibited significant use of areas with high slope and ruggedness at 0500 hours and 2000 hours in January and February (Table 2). Slope was a very strong predictor of location in both time periods, whereas ruggedness was a strong predictor at 0500 hours but a weak predictor at 2000 hours. Habitat selection of areas with high slope and ruggedness and distance to recreation trails was significant in March and April for sheep locations sampled at 0500 hours (Table 3). Additionally, the interaction of week and slope indicates that sheep increased their odds of habitat use by a factor of 40 for every 0.1 or 10% unit of increase in slope on weekends compared with weekdays, although this interaction did not have a significant ROC contrast.

The effect of proximity to a trail was significant in March and April at 1200 hours (Table 3) during weekdays, although the odds ratio revealed that the odds of habitat use increased by a factor of only 1.12 for every kilometer increase in distance from a hiking trail. The effect of distance to water was also significant, with the odds of sheep use decreasing by a factor of 0.95 (5%) for every 1-km increase in distance to water. In considering the effect of weekday versus weekend recreational activity on habitat selection, there was a significant interaction of week and distance to recreation trails in sheep locations at 1200 hours in March and April, when recreational use of trails was highest (Table 3). The AUC for the model with interaction was 0.864 and the difference in AUC for the model without the distance to trail × week interaction was significant, indicating that the change in location on weekends was an important aspect of sheep habitat selection at mid-day (ROC contrast χ^2, $P = 0.026$; area 0.864 vs. 0.801). However, that was the only interaction in any of the models for any time period or season that was significant in a ROC contrast (Table 3).

The distance to trail × week interaction at 1200 hours is a relatively robust feature of habitat selection because the delta AICs for all possible models containing the interaction ranged from 0 to 2.6, whereas delta AICs for models without this interaction ranged from 2.9 to 71.2. The model-averaged estimate of distance to trail × week interaction was 0.598 ± 0.144 (calculated using the set of all models that contained the interaction term) whereas the maximum likelihood estimate from the full model was 0.776 ± 0.0003 (Table 3). The odds ratio for the model-averaged interaction was 1.82 and that for the full model was 2.71. Thus, conservatively, the odds of sheep use of habitat increased by a factor of 1.8 on weekends compared with midweek with every 1-km increase in distance from a recreation trail.

At 2000 hours, habitat selection was significant again for slope and ruggedness, but there was no significant effect of distance to recreation trails, distance to water, or any interactions with days of the week. Overall, changes in habitat use at 0500 hours and 1200 hours on weekends result in bighorn sheep being more likely to occur in areas with high slope that are also farther from recreation trails than locations utilized by sheep during the week.

DISCUSSION

Our results suggest that female bighorn sheep in JOTR responded to human recreation by changing their spatial and temporal use of habitat in response to weekend recreation activity. By comparing properties of sheep locations at different times of day and before and during periods of peak recreation activity, we were able to detect bighorn sheep responses to anthropogenic activity indicative of short-term behavioral state changes (Morales and Ellner 2002, Patterson et al. 2008). This method of analysis allowed us to determine the period of day that sheep were most responsive to the influence of recreational activity on their use of habitat across seasons and between mid-week and weekends.

The response of wildlife to disturbance from human recreation can be considered to be equivalent to the response of animals to indirect cues of predator risk (Gill et al. 2001, Frid and Dill 2002). Predators affect prey demographics indirectly through the costs of antipredator behavioral responses (Gill et al. 2001, Creel and Christianson 2008) such as changes in vigilance, foraging and aggregation, movement patterns, sensitivity to environmental conditions (Knight and Cole 1995, Taylor and Knight 2003), and ultimately, temporary avoidance or abandonment of habitat (Gill et al. 2001, Creel and Christianson 2008). Short-term behavioral responses of wildlife to human activities are similar to antipredator behaviors and include increased vigilance, flight, cessation of foraging, and altered reproductive behavior (Knight and Cole 1995, Taylor and Knight 2003). Energetic losses due to flight, loss of foraging time, and an increase in cortisol levels can cause deleterious effects on physiology, behavior and the accumulation of fat reserves, all of which can cause a reduction in survival and reproductive success of individuals (MacArthur et al. 1982, McGowan and Simons 2006). Chronic disturbance by humans can also affect habitat use; responses can vary from temporary avoidance to abandonment of habitat (Creel and Christianson 2008) and ultimately, disruption of metapopulation dynamics (Epps et al. 2005).

Bighorn sheep have been found to respond more intensely to hikers than to other types of recreation disturbance (mountain bikes, automobiles) because these activities tend to be more unpredictable (MacArthur et al. 1982, Miller and Smith 1985, Papouchis et al. 2001. Our results suggest that bighorn sheep in the Wonderland of Rocks–Queen Mountain region of JOTR apparently avoid areas of perceived higher risk on weekends by moving to similar habitat nearby, and then return to use locations closer to recreation trails at other times of the week when visitor use in the park is lower. During early morning, sheep also adjusted habitat use temporarily by selecting for steeper terrain on weekends when visitor use was higher than weekdays. These changes in behavioral state (Morales and Ellner 2002, Patterson et al. 2008) could be related to direct exposure on weekends to visual, auditory, or olfactory stimuli that invoke some form of avoidance or escape behavior or by learned avoidance of trail areas on weekends due to past experience of human disturbance and stimuli related to recreation activity.

Habitat selection is the product of trade-offs between costs and benefits associated with each habitat (Sih 1980, Lima and Dill 1990, Ratikainen et al. 2007); thus, decisions made by animals of whether to move in response to disturbance depends on the intensity of the disturbance, availability and quality of other suitable sites, and the relative risk of predation or density of competitors in different sites (Ydenberg and Dill 1986, Gill et al. 2001, Frid and Dill 2002, Mao et al. 2005). Animals with habitat of similar quality nearby can avoid disturbance because they have alternate sites to occupy. This avoidance behavior may vary both temporally and spatially, depending on the prevailing conditions. Those without suitable habitat nearby may be forced to remain despite the disturbance, regardless of whether survival or reproductive success is affected (Gill et al. 2001). Movements of sheep away from trail areas on weekends appeared to be temporary shifts into habitat of similar quality. There was no indication that poor habitat quality caused sheep to avoid areas near trails because sheep used these areas during days before and after weekends. Additional research is necessary to establish the nature and extent of costs associated with responses to this potential risk factor.

MANAGEMENT IMPLICATIONS

Long-term, intense disturbance stimuli may cause habitat shifts that are often not detected until after habitat is lost. Where the continued coexistence of wildlife and recreation is a major management goal, the use of GPS telemetry to provide frequent and accurate relocations of large mammals makes it possible to detect fine-scale behavioral responses to anthropogenic disturbance at a variety of temporal and spatial scales. The detection of early or low-level responses to disturbance is particularly important because it may facilitate implementation of conservation efforts before negative impacts to the population become irreversible. We suggest that comparisons of the behavior of animals exposed to repeated time periods of human disturbance, such as recreational activity on weekends, can provide a method for estimating the effects of disturbance on habitat use and the duration of such effects.

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LITERATURE CITED

Bangs, P. D., P. R. Krausman, K. E. Kunkel, and Z. D. Parsons. 2005. Habitat use by desert bighorn sheep during lambing. European Journal of Wildlife Research 51:178–184.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134.

Bleich, V. C., J. D. Wehausen, R. R. Ramey, II, and J. L. Rechel. 1996. Metapopulation theory and mountain sheep: implications for conservation. Pages 353–374 *in* D. R. McCullough, editor. Metapopulations and wildlife conservation. Island Press, Covelo, California, USA.

Boyce, M. S. 2006. Scale for resource selection functions. Diversity and Distributions 12:269–276.

Boyce, M. S., M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10:421–431.

Bruggeman, J. E., R. A. Garrott, D. D. Bjornlie, P. J. White, F. G. R. Watson, and J. Borkowski. 2006. Temporal variability in winter travel patterns of Yellowstone bison: the effects of road grooming. Ecological Applications 16:1539–1554.

Chilelli, M., and P. R. Krausman. 1981. Group organization and activity patterns of desert bighorn sheep. Desert Bighorn Council Transactions 25:17–24.

Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. Trends in Ecology and Evolution 23:194–201.

Creel, S., J. Winnie, Jr., B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

DeLong, E. R., D. M. DeLong, and D. L. Clarke-Pearson. 1988. Comparing the areas under two or more correlated receiver operating characteristic curves: a nonparameteric approach. Biometrics 44:837–845.

Dussalt, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience 11:321–328.

Epps, W. C., D. R. McCullough, J. D. Wehausen, V. C. Bleich, and J. L. Rechel. 2004. Effects of climate change on population persistence of desert dwelling mountain sheep in California. Conservation Biology 18:102–113.

Epps, W. C., P. J. Palsbol, J. D. Wehausen, G. K. Roderick, R. R. Ramey, II, and D. R. McCullough. 2005. Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8:1029–1038.

Etchberger, R. C., P. R. Krausman, and R. Mazaika. 1989. Mountain sheep habitat characteristics in the Pusch Ridge Wilderness, Arizona. Journal of Wildlife Management 53:902–907.

Fernández-Juricic, E., and J. L. Tellería. 2000. Effects of human disturbance on blackbird (*Turdus merula*) spatial and temporal feeding patterns in urban parks of Madrid (Spain). Bird Study 47:13–21.

Fretwell, S. D., and H. L. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

Frid, A., and L. M. Dill. 2002. Human-caused disturbance stimuli as a form of predation risk. Conservation Ecology 6:11. < http://www.consecol.org/vol6/iss1/art11/ >. Accessed 7 Jul 2011.

Fryxell, J. M., J. F. Wilmshurst, A. R. E. Sinclair, D. T. Haydon, R. D. Holt, and P. A. Abrams. 2005. Landscape scale, heterogeneity, and the viability of Serengeti grazers. Ecology Letters 8:328–335.

Geist, V. 1971. Mountain sheep: a study in behavior and evolution. University of Chicago Press, Chicago, Illinois, USA.

Gill, J. A., K. Norris, and W. J. Sutherland. 2001. Why behavioral responses may not reflect the population consequences of human disturbance. Biological Conservation 97:265–268.

Graham, H. 1971. Environmental analysis procedures for bighorn in the San Gabriel Mountains. Desert Bighorn Council Transactions 15:38–45.

Hamilton, K. M., S. Holl, and C. L. Douglas. 1982. An evaluation of the effects of recreational activities on bighorn sheep in the San Gabriel Mountains, California. Desert Bighorn Council Transactions 26:50–55.

Hicks, L. L., and J. M. Elder. 1979. Human disturbance of Sierra Nevada bighorn sheep. Journal of Wildlife Management 43:909–915.

Holl, S. A. 1982. Evaluation of bighorn sheep habitat. Desert Bighorn Council Transactions 26:47–49.

Holl, S. A., and V. C. Bleich. 1987. Mineral lick use by mountain sheep in the San Gabriel Mountains, California. Journal of Wildlife Management 51:383–385.

Horesji, B. 1976. Some thoughts and observations on harassment and bighorn sheep. Pages 149–155 *in* T. Thorne, chairman. Proceedings of the Biennial Symposium of North American Bighorn Sheep Council, American Bighorn Sheep Council, 10–12 February 1976, Jackson, Wyoming, USA.

Hutto, R. L. 1985. Habitat selection by nonbreeding migratory land birds. Pages 455–476 *in* M. L. Cody, editor. Habitat selection in birds. Academic Press, Orlando, Florida, USA.

Jaccard, J. 2001. Interaction effects in logistic regression. Sage, Thousand Oaks, California, USA.

Johnson, C. J., S. E. Nielsen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use–availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Johnson, C. J., K. L. Parker, D. C. Heard, and M. P. Gillingham. 2002. Movement parameters of ungulates and scale-specific responses to the environment. Journal of Animal Ecology 71:225–235.

King, M. M., and G. W. Workman. 1986. Response of desert bighorn sheep to human behavioral responses of desert bighorn sheep to human harassment: management implications. Transactions of the 51st North American Wildlife & Natural Resource Conference 51:74–85.

Kittle, A. M., J. M. Fryxell, G. E. Desy, and J. Hamr. 2008. The scale dependent impact of wolf predation risk on resource selection by three sympatric ungulates. Oecologia 157:163–175.

Knight, R. L., and D. N. Cole. 1995. Wildlife responses to recreationists. Pages 51–65 *in* L. Knight and K. J. Gutzwiller, editors. Wildlife and recreationists: coexistence through management and research. Island Press, Washington, D.C., USA.

Krausman, P. R., S. Torres, L. L. Ordway, J. J. Hervert, and M. Brown. 1985. Diel activity of ewes in the Little Harquahala Mountains, Arizona. Desert Bighorn Transactions 29:24–26.

Krausman, P. R., M. C. Wallace, C. L. Hayes, and D. W. DeYoung. 1998. Effects of jet aircraft on mountain sheep. Journal of Wildlife Management 62:1246–1254.

Leary, P. J. 1977. Investigation of the vegetational communities of Joshua Tree National Monument, California. University of Nevada, Cooperative National Park Resources Studies Unit Contribution No. CPSU/UNLV 004/07, Las Vegas, USA.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation. Canadian Journal of Zoology 68:619–640.

Longshore, K. M., C. Lowrey, and D. B. Thompson. 2010. Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. Journal of Arid Environments 73:280–286.

MacArthur, R. A., V. Geist, and R. H. Johnston. 1982. Cardiac and behavioral responses of mountain sheep to human disturbance. Journal of Wildlife Management 46:351–358.

Manly, F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Kluwer Academic, London, United Kingdom.

Mao, J. S., M. S. Boyce, D. W. Smith, F. J. Singer, D. J. Vales, J. M. Vore, and E. H. Merrill. 2005. Habitat selection by elk before and after wolf reintroduction in Yellowstone National Park. Journal of Wildlife Management 69:1691–1707.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Ecoscience 16:238–247.

McCutchen, H. E. 1981. Desert bighorn zoogeography and adaptation in relation to historic land use. Wildlife Society Bulletin 9:171–179.

McCutchen, H. E. 1995. Desert bighorn sheep. Pages 333–336 *in* E. T. LaRoe, G. S. Farris, C. E. Puckett, P. D. Doran, and M. J. Mac, editors. Our living resources, a report to the nation on the distribution, abundance and health of U.S. plants, animals and ecosystems. U.S. Department of Interior, National Biological Service, Washington, D.C., USA.

McGowan, C. P., and T. R. Simons. 2006. Effects of human recreation on the incubation behavior of American oystercatchers. Wilson Journal of Ornithology 118:485–493.

Mech, D. L. 1977. Productivity, mortality, and population trends in northeastern Minnesota. Journal of Mammalogy 58:559–574.

Miller, G., and E. Smith. 1985. Human activity in bighorn sheep habitat: what disturbs sheep? Desert Bighorn Council Transactions 29:4–7.

Morales, J., and S. Ellner. 2002. Scaling up animal movements in heterogeneous landscapes: the importance of behavior. Ecology 83:2240–2247.

Murdock, E. 2004. Understanding recreation flow to protect wilderness resources at Joshua Tree National Park, California. Proceedings of the Second International Conference on Monitoring and Management of Visitor Flows in Recreational and Protected Areas. Working Papers of the Finnish Forest Research Institute 2. < http://www.metla.fi/julkaisut/workingpapers/2004/mwp002.htm >. Accessed 14 May 2011.

Papouchis, C. M., F. J. Singer, and W. B. Sloan. 2001. Responses of desert bighorn sheep to increased human recreation. Journal of Wildlife Management 65:573–582.

Patterson, T. A., L. Thomas, C. Wilcox, O. Ovaskainen, and J. Matthiopoulos. 2008. State-space models of individual animal movement. Trends in Ecology and Evolution 23:87–94.

Ratikainen, I. I., P. Panzacchi, A. Mysterud, J. Odden, J. Linnell, and R. Anderson. 2007. Use of winter habitat by roe deer at a northern latitude where Eurasian lynx are present. Journal of Zoology 273:192–199.

Sappington, J. M., K. M. Longshore, and D. B. Thompson. 2007. Quantifying landscape ruggedness for animal habitat analysis: a case study using bighorn sheep in the Mojave Desert. Journal of Wildlife Management 71:1419–1426.

Schoenecker, K. A., and P. R. Krausman. 2002. Human disturbance in bighorn sheep habitat, Pusch Ridge Wilderness, Arizona. Journal of Arizona-Nevada Academy of Science 34:63–68.

Seip, D. R., C. J. Johnson, and G. S. Watts. 2007. Displacement of mountain caribou from winter habitat by snowmobiles. Journal of Wildlife Management 71:1539–1544.
Shackleton, D. M. 1985. *Ovis canadensis*. Mammalian Species 230:1–9.
Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? Science 210:1041–1042.
Taylor, A. R., and R. L. Knight. 2003. Wildlife responses to recreation and associated visitor perceptions. Ecological Applications 13:951–963.
Thompson, D., K. Longshore, and C. Lowrey. 2007. The impact of human disturbance on desert bighorn sheep (*Ovis canadensis nelsoni*) in the Wonderland of Rocks/Queen Mountain region of Joshua Tree National Park, California Final report to the National Park Service. U.S. Geological Survey, Las Vegas Field Station, Las Vegas, Nevada, USA.
U.S. Fish Wildlife Service. 1999. Draft recovery plan for the bighorn sheep in the Peninsular Ranges. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
Ydenberg, R. C., and L. M. Dill. 1986. The economics of fleeing from predators. Advances in the Study of Animal Behavior 16:229–249.
Zeigenfuss, L. C., F. J. Singer, and M. A. Gudorf. 2000. Test of a modified habitat suitability model for bighorn sheep. Restoration Ecology 8:38–46.

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