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DAILY AND SEASONAL PATTERNS OF ACTIVITY AT PYGMY RABBIT BURROWS IN UTAH

Janet E. Lee^{1,3}, Randy T. Larsen¹, Jerran T. Flinders¹, and Dennis L. Eggett²

ABSTRACT.—The pygmy rabbit (*Brachylagus idahoensis*) is a secretive, obligate sagebrush-steppe resident of the Intermountain West and is one of two rabbits in North America that digs its own burrows. Although the pygmy rabbit has a recorded home range of 0.21–67.9 ha in relatively high sagebrush cover (21%–36%), they spend much of their time within 30–100 m of a burrow system. Due to big sagebrush cover in preferred habitat and the secretive behavior of pygmy rabbits, it is often difficult to study this leporid through direct observation. We used remote cameras to document pygmy rabbit activity at burrow systems in south central Utah from 2006 to 2008. We analyzed photographs from remote cameras for daily and seasonal patterns of activity. Our results suggested that time of day and season were important influences on activity level, while year and site were less so. Pygmy rabbits were active during all time periods of the day, but the greatest activity occurred in the morning, except during winter. Numerous other species were recorded by remote cameras, including other leporids, birds, rodents, reptiles, and terrestrial predators. Remote cameras are a valuable tool in understanding pygmy rabbit behavior, in addition to confirming rabbit presence in areas of interest.

Key words: aboveground activity, big sagebrush obligate, *Brachylagus idahoensis*, diurnal, home range, nocturnal, remote camera.

A resident of the big sagebrush (*Artemisia tridentata*) biotype, the pygmy rabbit (*Brachylagus idahoensis*) is found in the Intermountain regions of the United States (Green and Flinders 1980a, 1980b). The pygmy rabbit is an obligate of big sagebrush-steppe and is one of only two rabbits in North America that digs its own burrows (Green and Flinders 1980a, 1980b, Katzner and Parker 1997). Pygmy rabbits consume a diet of up to 99% big sagebrush during winter and 51% during summer (Green and Flinders 1980a, 1980b, Gahr 1993).

As the smallest leporid in North America, the pygmy rabbit has an estimated home range as small as 0.21 ha in winter (Katzner and Parker 1997) and 67.9 ha during the breeding season (Heady and Laundré 2005) in relatively high (21%–36%) sagebrush cover (Weiss and Verts 1984, Katzner and Parker 1997, Flinders 1999). Home-range estimates of 2.6 ± 0.5 ha (nonbreeding) to 2.8 ± 0.6 ha (breeding) for females and 3.7 ± 0.9 ha (nonbreeding) to 12.0 ± 1.6 ha (breeding) for males may be more common (Sanchez and Rachlow 2008). Despite these estimates, this unique leporid spends much of its time within 30–100 m of a burrow

system (Katzner and Parker 1997, Heady and Laundré 2005, Sanchez and Rachlow 2008). Evidence suggests that the pygmy rabbit is a central-place forager (Rosenberg and McKelvey 1999), which may account for its restricted movement (Heady and Laundré 2005).

Recent research has emphasized describing pygmy rabbit geographic distribution, habitat, home range, and diets (Green and Flinders 1980a, 1980b, Katzner et al. 1997, Katzner and Harlow 1998, Bartels and Hays 2001, Heady et al. 2001, Siegel 2002). Only one study has documented daily or seasonal pygmy rabbit activity levels (Larrucea and Brussard 2008, 2009). Because pygmy rabbits use burrows year-round (Larrucea 2007), it is essential to gain a more thorough knowledge of daily and seasonal use of burrows. Furthermore, knowledge of seasonal activity patterns can inform habitat selection and movement studies, as pygmy rabbits are known to occupy more than one burrow system (Janson 2002, Oliver 2004, Sanchez 2007, Larrucea and Brussard 2009). Information on diurnal space use was recently published (Sanchez and Rachlow 2008), but it is somewhat unclear how active pygmy rabbits

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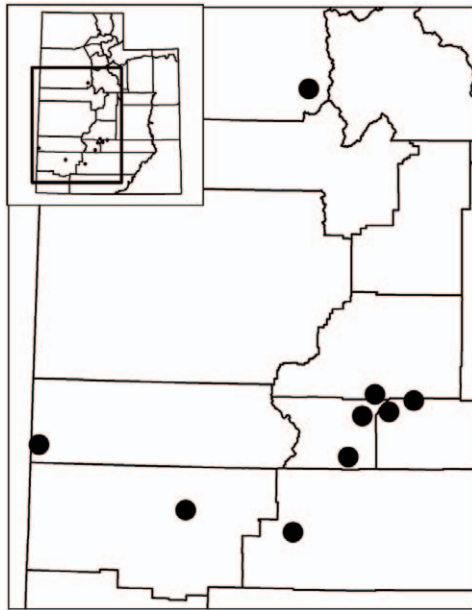


Fig. 1. Remote camera study sites in south central Utah (Beaver, Garfield, Iron, Piute, Sevier, Tooele, and Wayne counties), evaluated between May 2006 and December 2008.

are during nighttime darkness. Remote photography provides an opportunity to address daily and seasonal activity patterns (Kucera and Barrett 1993, Cutler and Swann 1999, Larrucea and Brussard 2008, 2009).

Many researchers prefer remote photography over more traditional methods for a variety of reasons (Savidge and Seibert 1988, Kleintjes and Dahlsten 1992, Major and Gowing 1994, Larrucea 2007, Larrucea and Brussard 2008). Remote photography may reduce observer bias (Cowardin 1969) and can be less costly and time consuming compared to long-term observation of wildlife (Cutler and Swann 1999). Remote cameras are also ideal for recording data at night and in inclement weather (Enderson et al. 1972, Craig and Craig 1974, Capen 1978, Mace et al. 1994). Remote photography also can be effective in the study of secretive wildlife that are difficult to observe (Mace et al. 1994, Karanth 1995). Larrucea and Brussard (2009) demonstrated the effectiveness of using remote cameras in certain applications for studying pygmy rabbits. Our specific objective was to document daily and seasonal patterns of activity at pygmy rabbit burrows in Utah and to determine the influence of time of day,

season, and site on activity. By doing so, we hope to inform both management and research efforts for this species of concern.

METHODS

Study Area

We conducted this study in parts of Beaver, Garfield, Iron, Piute, Sevier, Tooele, and Wayne counties, south central Utah, between May 2006 and December 2008. We evaluated activity at burrow entrances across a total of 9 sites within the Great Basin (Fig. 1). Precipitation, snowfall, and temperature varied between study sites. Precipitation ranged from 13.5 to 39.8 $\text{cm} \cdot \text{year}^{-1}$. Snowfall ranged from 13.2 to 114.6 cm and temperature from -13.6 to 41.0 $^{\circ}\text{C}$ (WRCC 2007). Elevation was variable, but all study sites were between 1589 m and 2581 m. Despite the wide range of locations across Utah, all sites were within the Great Basin and had similar vegetation types. Upper hillsides of our study areas were dominated by juniper (*Juniperus* spp.), pinyon pine (*Pinus edulis*), and aspen (*Populus tremuloides*). Lower elevations gave way to foothills dominated by big sagebrush and other shrubs and then to wet, grassy valley bottoms (mostly agricultural fields). We focused our study in big sagebrush communities preferred by pygmy rabbits.

Field Methods

Beginning in May 2006, we placed Digital Ranger S600 SB CamTrak cameras (CamTrak South Inc., Georgia) at pygmy rabbit burrows showing varying levels of activity. We set the motion-activated cameras to take photographs at any time during the day or night with a 30-second delay between photos, and all cameras remained on standard time for the entire year (Larrucea 2007). We placed cameras consistently within 3 m of a burrow entrance to minimize problems associated with differential detection (Culter and Swann 1999). In most cases, cameras were placed so that they focused on a single burrow and the immediate surrounding area. We left cameras at burrows for 2–4 weeks, with a few exceptions (i.e., at remote locations, during inclement weather), before moving them to a new location a minimum of 500 m from the previous one.

We placed cameras at least 100 m from each other to reduce the possibility that the same individual would be recorded on multiple



Fig. 2. Images of pygmy rabbits from photographs taken in south central Utah by Digital Ranger S600 SB CamTrak cameras.

cameras. At the resolution settings we used, cameras were capable of storing over 900 images, and we encountered few problems with full memory cards or faulty cameras. Nonetheless, in the event that a memory card became full or a camera quit working before it was collected, we determined the elapsed sampling time from captured images. We placed cameras

indiscriminately at known locations of burrows discovered during prior walking transects.

Data Analysis

For seasonal analysis, we divided the year into fourths: winter (Dec–Feb), spring (Mar–May), summer (Jun–Aug), and fall (Sep–Nov). Using Mountain Standard Time, we

TABLE 1. The *a priori* models we used to investigate factors influencing pygmy rabbit activity at burrows in Utah.

Model ^a	Factors ^b	K ^c	AIC ^d	AIC ^e	w_i ^f	Deviance
3	Time of Day, Site, Season, Time of Day \times Season	24	-1827.3	0.0	0.41	34.80
7	Time of Day, Site, Season	15	-1827.2	0.1	0.39	35.16
2	Time of Day, Site, Year, Season, Time of Day \times Season	26	-1824.3	3.0	0.09	34.77
4	Time of Day, Site, Year, Season	17	-1824.2	3.1	0.09	35.14
1	Time of Day, Site, Year, Season, Time of Day \times Season, Season \times Year	32	-1820.7	6.6	0.02	34.65
8	Time of Day, Site	12	-1817.0	10.3	0.00	35.49
6	Time of Day, Season, Time of Day \times Season	16	-1799.1	28.2	0.00	35.69
5	Time of Day, Year, Season	9	-1798.5	28.8	0.00	35.99
9	Site, Year, Season	14	-1742.8	84.5	0.00	36.95

^aModel number^bFactors (variables) included in model^cNumber of model parameters^dAkaike's Information Criteria^eAIC relative to the most parsimonious model^fAkaike weight

TABLE 2. Coefficients from best-approximating model of pygmy rabbit photo rate during 2006–2008 in Utah.

Factor	Coefficient	Estimate	SE	t	P
	Intercept	-0.014	0.033	-0.426	0.67
Time of day	Evening	-0.007	0.017	-0.424	0.67
	Morning	0.072	0.017	4.071	<0.001
	Night	-0.007	0.017	-0.423	0.67
Site	CedarCity	-0.028	0.052	-0.529	0.59
	EHillside	0.059	0.033	1.785	0.07
	Hamlin	0.007	0.048	0.147	0.88
	North	0.001	0.034	0.036	0.97
	Ottercreek	0.068	0.033	2.054	0.04
	Panguitch	0.032	0.043	0.771	0.44
	Parker	0.016	0.034	0.477	0.63
	Treatment	0.029	0.032	0.903	0.36
Season	Spring	0.032	0.019	1.674	0.09
	Summer	-0.010	0.016	-0.638	0.52
	Winter	0.051	0.028	1.812	0.07
Time of day \times Season	Evening \times Spring	0.008	0.027	0.327	0.74
	Morning \times Spring	-0.008	0.027	-0.322	0.74
	Night \times Spring	-0.018	0.027	-0.671	0.56
	Evening \times Summer	0.010	0.023	0.468	0.63
	Morning \times Summer	0.013	0.023	0.572	0.56
	Night \times Summer	0.002	0.023	0.120	0.90
	Evening \times Winter	0.051	0.040	1.291	0.19
	Morning \times Winter	-0.094	0.040	-2.351	0.02
	Night \times Winter	-0.047	0.040	-1.169	0.24

also grouped photographs of pygmy rabbits into 4 blocks of time (morning, afternoon, evening, and night), using the sunrise and sunset times of the central date of each season to help account for the change in photoperiod. We defined morning and evening time blocks as 3 hours before and after sunrise or sunset, respectively. Afternoon and night blocks were determined by the remaining time between morning and evening blocks and varied somewhat

throughout the year. Definitions of season and time-period blocks follow Larrucea and Brusard (2009).

We divided the number of photographs in each time block by sampling time to obtain the activity level per hour (Larrucea and Brusard 2009). In addition, we scaled activity to the number of hours in the relevant time block to compensate for differences in block length. We analyzed activity levels of pygmy rabbits

TABLE 3. Wildlife species photographed by remote cameras focused at pygmy rabbit burrow entrances in Utah, 2006–2008. Percent frequency is the number of photographs of a species divided by the total number of photographs with identifiable animals.

Family or species binomial	Common name	Photos taken	Percent frequency
<i>Brachylagus idahoensis</i>	Pygmy rabbit	12,603	66.71%
<i>Sylvilagus spp.</i>	Cottontail species	3265	17.28%
<i>Lepus californicus</i>	Black-tailed jackrabbit	1260	6.67%
<i>Peromyscus maniculatus</i>	Deer mouse	570	3.02%
<i>Tamias minimus</i>	Least chipmunk	235	1.24%
<i>Mustela frenata</i>	Long-tailed weasel	157	0.83%
<i>Sceloporus spp.</i>	Spiny lizard species	137	0.72%
<i>Oreoscoptes montanus</i>	Sage Thrasher	125	0.66%
<i>Taxidea taxus</i>	American badger	97	0.51%
<i>Dipodomys ordii</i>	Ord's kangaroo rat	75	0.40%
Cricetidae/Muridae	Mice/rats	58	0.31%
<i>Ammospermophilus leucurus</i>	White-tailed antelope squirrel	52	0.28%
<i>Bos taurus</i>	Domestic cow	47	0.25%
<i>Salpinctes obsoletus</i>	Rock Wren	39	0.21%
<i>Odocoileus hemionus</i>	Mule deer	28	0.15%
<i>Canis latrans</i>	Coyote	25	0.13%
<i>Felis domesticus</i>	Feral house cat	15	0.08%
<i>Amphispiza belli</i>	Sage Sparrow	14	0.07%
<i>Pipilo chlorurus</i>	Green-tailed Towhee	11	0.06%
<i>Spizella breweri</i>	Brewer's Sparrow	10	0.05%
<i>Spermophilus variegatus</i>	Rock squirrel	8	0.04%
<i>Lynx rufus</i>	Bobcat	8	0.04%
<i>Spilogale gracilis</i>	Western spotted skunk	8	0.04%
<i>Tyrannus verticalis</i>	Western Kingbird	6	0.03%
<i>Zonotrichia leucophrys</i>	White-crowned Sparrow	6	0.03%
<i>Pipilo maculatus</i>	Spotted Towhee	5	0.03%
<i>Spizella passerina</i>	Chipping Sparrow	4	0.02%
<i>Gymnorhinus cyanocephalus</i>	Pinyon Jay	3	0.02%
<i>Ovis aries</i>	Domestic sheep	3	0.02%
<i>Sialia currucoides</i>	Mountain Bluebird	3	0.02%
<i>Junco hyemalis</i>	Dark-eyed Junco	2	0.01%
<i>Pica hudsonia</i>	Black-billed Magpie	2	0.01%
<i>Pooecetes gramineus</i>	Vesper Sparrow	2	0.01%
<i>Procyon lotor</i>	Northern Raccoon	2	0.01%
<i>Buteo jamaicensis</i>	Red-tailed Hawk	1	0.01%
<i>Catharus sp.</i>	Thrush species	1	0.01%
<i>Circus cyaneus</i>	Northern Harrier	1	0.01%
<i>Corvus corax</i>	Common Raven	1	0.01%
<i>Microtus sp.</i>	Vole species	1	0.01%
<i>Spermophilus sp.</i>	Ground squirrel species	1	0.01%
<i>Zenaida macroura</i>	Mourning Dove	1	0.01%

in 2 stages. First, given model uncertainty, we used model selection to identify a best approximating model (lowest AIC value) from an *a priori* candidate list of 9 models containing variables likely to influence activity (Burnham and Anderson 2002). We did this by modeling photographs (scaled to sampling effort) as a function of site, season, time of day, year, and their interactions. These linear models essentially functioned as analyses of variance (ANOVA) because variables were categorical. Once a best approximating model was selected, we evaluated the strength and direction of estimates associated with coefficients

from this model. We considered coefficients with $P < 0.05$ as significant. We used program R (version 2.7) to perform the analyses (R Development Core Team 2007).

RESULTS

A total of 436 burrows were analyzed for aboveground pygmy rabbit activity. Remote cameras took 12,603 photographs of pygmy rabbits (e.g., Fig. 2) at 302 (69%) different burrow complexes. Model 3 (Table 1) was the best-approximating model for pygmy rabbit activity rates. This model included effects for time of day, site, season, and the interaction

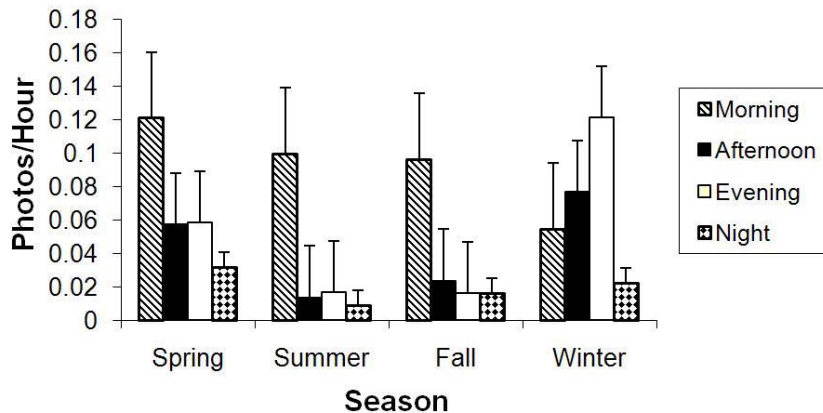


Fig. 3. Daily and seasonal activity patterns for pygmy rabbits in Utah from 2006 to 2008.

between time of day and season. A closely competing model (number 7) included the same structure, with the exception of the interaction term. Models with year effects received comparatively little support (Table 1). Coefficients from the best-approximating model indicated that higher pygmy rabbit activity rates ($P < 0.05$) were associated with morning and with the Ottercreek site, whereas lower rates occurred during winter mornings (Table 2). No other significant influences were found.

In addition to pygmy rabbits, we photographed more than 18 birds, 22 mammals, and at least 3 reptile species at burrow entrances (Table 3). Photographs of pygmy rabbits occurred with the highest percent frequency (the number of photographs of a species divided by the number of photographs with identifiable animals) of appearance (66.71%), while other leporids such as cottontails (17.28%) and black-tailed jackrabbits (6.67%) also occurred at high frequencies (Table 3).

DISCUSSION

Pygmy rabbits inhabit large stands of mature big sagebrush with relatively high cover (21%–36%; Weiss and Verts 1984, Katzner and Parker 1997, Flinders 1999). This preference for high cover can make it difficult to detect and observe pygmy rabbits (Weiss and Verts 1984, Dobler and Dixon 1990). We found that remote cameras placed at burrow entrances recorded valuable information on behavior, sociality, and above-ground activity that would otherwise be difficult

to obtain. While there is some indication that the presence of remote photography equipment may affect animal behavior (Pearson 1959, Osterberg 1962, Knudsen 1963), many species appear to accept the presence of remote photography equipment (Royama 1970, Franzreb and Hanula 1995, Larrueca 2007). This appears to be the case with the pygmy rabbits we studied. Pygmy rabbits seemed unaffected by the presence of the camera, as numerous pictures of the same individual were taken at the same burrow entrances.

Daily and Seasonal Differences

Pygmy rabbits in our study areas were active during all times of the day, but mornings had the highest levels of activity across seasons (Fig. 3). High crepuscular activity has been reported elsewhere (Gahr 1993, Janson 2002, Oliver 2004, Larrueca and Brussard 2009). Pygmy rabbits in our study area have many natural predators including badgers (*Taxidea taxus*), Bald Eagles (*Haliaeetus leucocephalus*), Barn Owls (*Tyto alba*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), Ferruginous Hawks (*Buteo regalis*), Golden Eagles (*Aquila chrysaetos*), Great-horned Owls (*Bubo virginianus*), Long-eared Owls (*Asio otus*), long-tailed weasels (*Mustela frenata*), Northern Harriers (*Circus cyaneus*), Prairie Falcons (*Falco mexicanus*), Ravens (*Corvus corax*), red foxes (*Vulpes vulpes*), Red-tailed Hawks (*Buteo jamaicensis*), Rough-legged Hawks (*Buteo lagopus*), Short-eared Owls (*Asio flammeus*), and Swainson's Hawks (*Buteo swainsoni*) (Green and Flinders 1980b, Gahr 1993, Janson 2002, Sanchez 2007).

Interestingly, our remote camera systems recorded 302 images of 5 species of terrestrial, predominately nocturnal predators (Table 1). Bakker et al. (2005) suggested that while the presence of predators may not change actual behaviors such as foraging, it can strongly affect temporal patterns of rabbit activity. Predation risk could explain lower rabbit activity in the evening and night hours, as the rabbits may have adjusted their activity patterns to avoid predators.

Larrucea (2007) noted that while weasels and badgers can enter pygmy rabbit burrows, other terrestrial and avian predators outside of the burrow also pose a great risk. Sanchez (2007) attributed 22% of radio-equipped pygmy rabbit mortalities to mammalian predation and 20% to avian predation. Predation risk is likely reduced by pygmy rabbit morning activity because most avian predators are not fully active at this time and nocturnal predators are less active (Larrucea and Brussard 2009). Many of our study areas had high numbers of diurnal avian predators, and they could be seen hunting in big sagebrush communities from midmorning on. This observation was particularly true during the autumn raptor migration and further supports predation risk as a driving force behind rabbit activity patterns.

It should be noted, however, that winter mornings had very low levels of activity (Fig. 3). This finding supports the idea that thermoregulation plays a role in influencing pygmy rabbit activity levels. Pygmy rabbits are the smallest North American rabbit and measure approximately 26.1–30.8 cm long and weigh between 370 and 524 g (Janson 2002). These dimensions give pygmy rabbits a high surface-to-volume ratio, which may make them more vulnerable to temperature extremes (Larrucea and Brussard 2009). Wilde et al. (1976) reported that pygmy rabbits left in traps over the course of a summer afternoon died due to heat, while those left in traps overnight were found frozen the next morning. Thermoregulation could explain why pygmy rabbits in our study area had lower activity rates on winter mornings when temperatures were cold. Activity rates were also low across most seasons in the afternoon when temperatures may be too high. During winter, evenings had higher pygmy rabbit activity than any other time of day. Afternoons and evenings are often the warmest parts of the day in winter, and pygmy rabbits

may take advantage of the warmer weather to sun themselves next to burrow entrances.

Big sagebrush, the main food source for pygmy rabbits, is available at all times and would likely not drive activity patterns (Larrucea 2007). In our study area, however, many large mechanical treatments have replaced sagebrush with grasses and forbs. Since grasses and forbs compose a portion of pygmy rabbit diet during the spring and summer (grasses 39% and forbs 10%; Green and Flinders 1980a, 1980b), pygmy rabbits may enter these treated areas to feed on vegetation that is absent from stands of big sagebrush. Because these treated areas have very little cover (protective or thermal), pygmy rabbits may feed in the mornings during summer to minimize predation risk and thermal stress. This behavior would provide a possible explanation for our results.

As we found both season and time of day to be important influences on pygmy rabbit activity, our results have implications for research into habitat use, home range, and movement patterns. Pygmy rabbits appear to be more active at burrows in the mornings as well as during the spring and winter. Special focus should be given to ensure that data collection for movement and home-range studies occurs during these times. Given the high frequency of morning activity, location sampling during this time period should be included in order to more accurately reflect habitat and space use. Nocturnal sampling can be difficult (Sanchez and Rachlow 2008) but could be important, as we and others have detected some activity during this time (Janson 2002, Sanchez and Rachlow 2008, Larrucea and Brussard 2009).

There is some evidence that adult pygmy rabbits do not use their burrows as much during the summer and fall months (Kolb 1991, Gahr 1993, Janson 2002, Oliver 2004, Larrucea 2007). Adult pygmy rabbits encountered from late spring to early fall were reluctant to enter burrow systems and instead chose to scamper through the sagebrush (Gahr 1993, Janson 2002, Oliver 2004, Larrucea 2007). Our data are consistent with this idea, as fewer photographs (although not statistically significant) were taken at burrow systems during these seasons (Table 2).

Other Wildlife Species

The presence of other wildlife species at pygmy rabbit burrows was not surprising because a burrow can provide refuge from

predators and weather for other leporids, rodents, birds, lizards, and insects. Thirteen species of birds were recorded by our remote cameras. Little is known about the presence of birds at pygmy rabbit burrows. Whether birds used the actual burrows during the heat of the day or simply used the shade provided by sagebrush is unknown. Birds may also dust-bathe in the soil at the burrow entrances. Further research on this topic is needed to understand avian use of the burrow area and the importance of pygmy rabbits as habitat architects in big sagebrush communities.

Our study is the first to record the presence of the western spotted skunk (*Spilogale gracilis*) and feral house cat (*Felis catus*) at pygmy rabbit burrows. The spotted skunk is a known predator of rodents, leporids, and larger insects. They most likely hunt in pygmy rabbit burrows and use these burrows for thermal and security cover. Feral house cats could be very effective predators on pygmy rabbits in modified landscapes.

Conclusion

Daily and seasonal activity patterns are essential to an understanding of the behavioral ecology of pygmy rabbits. Knowledge of behavior is critical to the conservation of pygmy rabbits because behavior affects things such as predation, habitat use, home-range and movement patterns, and species interactions. Use of remote cameras provides a way to understand these patterns. Moreover, remote cameras can be used to positively identify the presence of pygmy rabbits in areas of interest. Remote photography also provides a way to learn which other species use and may depend upon pygmy rabbit burrows.

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