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HOME RANGE AND ACTIVITY PATTERNS OF BLACK-TAILED JACKRABBITS

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ABSTRACT.—Home range use and activity patterns of black-tailed jackrabbits (*Lepus californicus*) in northern Utah were studied using telemetry. Home range sizes ranged from <1 km^2 to 3 km^2 and did not differ between sexes or among seasons. Jackrabbits were inactive during daylight, became active at dusk, and remained active throughout the night. Animals often traversed their home ranges in a few hours. During the breeding season, males were more active than females. Jackrabbits were most active during well-lit nights, and high winds decreased jackrabbit activity.

The black-tailed jackrabbit occupies a wide geographic area and is an important component of the biota throughout its range. In the Great Basin the jackrabbit is the most abundant large herbivore (Wagner 1981) and serves as an important prey item for many predators. Considering the central role of the jackrabbit in many ecosystems, little research on the species has been reported. Detailed quantitative information regarding activity patterns and home range use is lacking. Home range use varies with the patterns of food, cover, and water distribution (Dunn et al. 1982). I examined patterns of jackrabbit activity and home range use throughout a calendar year in shrub-steppe vegetation in northern Utah.

STUDY AREA

The study was conducted in northern Utah near the Wildcat Hills in Curlew Valley, about 10–35 km north of the Great Salt Lake. Topography and vegetation of the area are described in detail by Gross et al. (1974). Four major vegetation types occur in Curlew Valley: (1) open stands of juniper (*Juniperus osteosperma*) at higher elevations, (2) big sagebrush (*Artemisia tridentata*) in the northern portions of the study area, (3) greasewood (*Sarcobatus vermiculatus*) in more saline soils closer to the Great Salt Lake, and (4) expanses of salt-desert vegetation, primarily shadscale (*Atriplex confertifolia*) and saltbush (*Atriplex falcata*), scattered throughout the study area.

Southern portions of the valley are typically more xeric than northern portions, and precipitation is most abundant during winter and spring. Accumulated snowfall in 1983–1984 was 69 cm at Snowville, Utah, 15 km east of the study area, with snowcover persisting from mid-November through mid-March (National Oceanic and Atmospheric Administration 1984).

METHODS

Black-tailed jackrabbit activity and home range use were monitored via telemetry. Incidental direct observations of jackrabbits also aided in describing activity patterns.

Black-tailed jackrabbits were captured by night-lighting and netting (Griffiths and Evans 1970); they were then equipped with radio-transmitters and released. Periodically during each season additional animals were caught and instrumented to replace those that had died. During winter some jackrabbits were captured in live traps and handled similarly to those captured by netting. Sex was determined from external examination of genitalia, and age class was estimated from body size, color, and relative eye size (L. C. Stoddart, unpublished data).

Transmitter collars were designed to minimize chafing of the jackrabbit's neck (Wywialowski and Knowlton 1983). I assume the transmitters had little discernible effect on jackrabbit behavior (Stoddart 1970, Donoho 1972, Brand et al. 1975, Keith et al. 1984).

Telemetry stations on the Wildcat Hills overlooked areas with instrumented jackrabbits. Each station was equipped with two horizontally stacked 5-element yagi antennas, coupled out of phase with a sum-and-difference hybrid junction. A compass rose

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mounted on the antenna mast indicated the directional orientation of the antennas. A transmitter placed at a known azimuth from each station was used as a beacon to orient the compass rose to true north.

Home range use was assessed by repeatedly recording azimuths of animals simultaneously from two tracking stations. Four-hour tracking sessions were distributed throughout the 24-hour day with most occurring between dusk and dawn. Locations were recorded every 20 minutes for a 4-hour period on all animals whose transmitter signals could be detected. For each reading it was noted whether the signal varied in amplitude, suggesting movement of the transmitter antenna, which was interpreted as movement by the animal. The amount of night light was classified into one of three categories (low, medium, or high), depending upon the phase of the moon and cloud cover. Wind intensity during the 4-hour period was classified as low or high by noting the wind conditions at the tracking shelters. Periods of no wind were included in the low category.

Home range use was assessed using program HOME RANGE (Samuel et al. 1985b). This program offers a series of statistical tests to derive the appropriate home range estimator (Samuel and Garton 1985). Within each data set locations outside the home range were identified statistically (Samuel and Garton 1985) and discarded (given a weight of 0) if they appeared to be errors or excursions outside the normal home range area (Burt 1943). "Core areas" were identified (Samuel et al. 1985a). As recommended by Samuel and Garton (1985), only data sets with $\geq$50 locations were analyzed. Comparisons of the sizes of areas used by subsets of the jackrabbit population were made using a two-way analysis of variance (SAS Institute Inc. 1985).

Because of the model-selection criteria of the program, I used the harmonic mean estimator (Dixon and Chapman 1980) for all area-of-use analyses. Dixon et al. (1981) recommended this technique to analyze lagomorph spatial use because it eliminates many problems associated with other analyses.

Choice of a contour isopleth to represent the home range is somewhat arbitrary (Anderson 1982). I chose the 80% contour for jackrabbits because it appears to reflect observed patterns of land use by these animals. To allow comparisons with other published accounts, I also report the 95% contour interval, although it probably overestimates home range size. No statistical rationale exists for the choice of the 95% level, and its use may result from biologists confusing utilization distributions with alpha levels in statistical tests (White and Garrott 1990).

The relationships of time of day, season, sex, amount of moonlight, and wind intensity to jackrabbit activity were assessed using log-linear analyses (Sokal and Rohlf 1981). Terms included in the resulting models reflect significant relationships within the data. Seasons were defined by Curlew Valley weather patterns. Winter ended with the melting of snow in March. Summer began in late June 1984 with the onset of hot temperatures and ended in early September with the arrival of fall rains.

RESULTS

The daily movements of 16 jackrabbits were monitored from February through April 1984, and those of an additional 44 jackrabbits were monitored from June through November 1984. I determined the sizes of areas used by 30 jackrabbits, with 5 animals having 2 areas each, for a total of 35 areas of use (Table 1). The time periods for which areas were measured ranged from eight days to five months. Home range has been defined as the area used by an animal on a day-to-day basis (Burt 1943). How an animal uses its home range affects how long the animal must be monitored before it traverses its entire home range. Typical home range use by black-tailed jackrabbits involved extended use of an area measuring <1 km^2. Animals often traversed the whole area of activity in less than four hours. By dawn a jackrabbit was usually back near the previous day's resting location. Some animals maintained this pattern of space use for up to three months.

Periodically, jackrabbits changed their areas of use. These changes involved extensions of the areas of use into previously unused areas and abandonment of portions of the previously used areas. New areas were then generally used for extended periods. These shifts in areas of use enlarged overall home ranges to 1.5–3 km^2. No differences in the patterns of shifts in areas of use among different sex and age segments of the population

TABLE 1. Black-tailed jackrabbit home range sizes (km^2) (and standard errors) in Curlew Valley, Utah, 1983–1984.

Season	Number of animals	Harmonic contour area					
		95%	SE	80%	SE	core	SE
Adults							
Winter							
Male	2	2.51	0.77	1.66	0.64	0.96	0.33
Female	6	1.25	0.45	0.83	0.28	0.47	0.15
Spring							
Male	5	1.08	0.25	0.73	0.18	0.43	0.13
Female	4	0.85	0.16	0.55	0.13	0.32	0.06
Summer							
Male	5	2.88	0.72	1.83	0.45	1.07	0.31
Female	4	1.63	0.49	1.05	0.29	0.62	0.16
Fall							
Male	1	2.21	—	1.30	—	0.72	—
Female	2	0.87	0.14	0.52	0.10	0.26	0.06
Juveniles							
Summer-fall							
Male	1	1.13	—	0.73	—	0.43	—
Female	5	1.70	0.35	0.92	0.21	0.57	0.15

Two-way analysis of variance using the 80% contour

	df	*SS*	*F*	*P*
Season	3	3.10	2.35	.10
Sex	1	2.14	4.85	.04
Season × sex	3	0.56	0.42	.74
Error	21	15.41		

were apparent. Core-areas, as identified by program HOME RANGE, encompassed areas slightly larger than half the size of home ranges (the 80% contour) (Table 1) and tended to be near the center of the home range areas.

Jackrabbits changed home range areas seasonally. Where more than one home range was recorded for an animal, each was analyzed independently (Table 1). Areas traversed during seasonal migrations were not considered part of either home range (Burt 1943). In March, just after the winter's snowcover melted, jackrabbits left wintering areas and moved to new home ranges. In the fall many animals abandoned their summer home range areas and moved to wintering areas (Smith 1987).

Wintering areas were located in stands of tall vegetation, primarily greasewood and sagebrush, although a few juniper stands were also used. Wintering areas encompassed only a small portion of the available habitat as jackrabbits concentrated in groups; areas of low vegetation were not used during winter. With spring shifts in home range areas, jackrabbits reoccupied much of the valley (Smith 1987).

Sizes of areas appeared to change seasonally, with areas of use being smaller in spring and fall than in winter and summer. Patterns of home range use also appeared to be similar throughout the year. Males tended to have slightly larger home ranges than females (Table 1). Too few juvenile jackrabbits were instrumented to adequately determine their pattern of home range use. However, sizes of areas used by juveniles and adults did not differ (Table 1). Only juveniles large enough to wear a radio-transmitter (>3 months of age) were instrumented.

Jackrabbit activity changed daily and seasonally (Fig. 1). Significant differences occurred during the day and among the seasons (α = active, β = time, Γ = season; $\ln f_{(ijk)} = \mu + \alpha_i + \beta_j + \Gamma_k + \alpha\beta_{ij} + \alpha\Gamma_{ik} + \beta\Gamma_{jk} + \alpha\beta\Gamma_{ijk}$; $\alpha\beta_{ij}$: $G = 179.5$, 18 df, $P < .001$; $\alpha\Gamma_{ik}$: $G = 594.3$, 20 df, $P < .001$; $\beta\Gamma_{jk}$: $G = 856.3$, 30 df, $P < .001$; $\alpha\beta\Gamma_{ijk}$: $G = 128.8$, 15 df, $P < .001$). Jackrabbits were least active from 0800–1700 hours during the spring, summer, and fall, when they often rested in shallow depressions under shrubs, big sagebrush and greasewood being the most common. In addition, some jackrabbits used badger (*Taxidea taxus*)

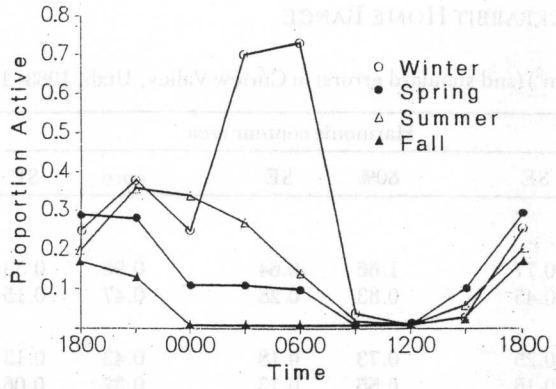

Fig. 1. Frequency of black-tailed jackrabbit activity and relationships with time of day and season of year in Curlew Valley, Utah, 1983–1984.

TABLE 2. Frequency of black-tailed jackrabbit activity and relationships with sex and season of year in Curlew Valley, Utah, 1983–1984. The data are the number of telemetry readings under the categorical conditions. The proportion active is in parentheses.

		Sex (β)	
Season (Γ)	Active (α)	Female	Male
Winter	yes	129 (.24)	100 (.29)
	no	409	240
Spring	yes	108 (.16)	88 (.20)
	no	572	336
Summer	yes	147 (.24)	156 (.22)
	no	456	555
Fall	yes	21 (.17)	4 (.04)
	no	101	87

$\ln f_{(ijk)} = \mu + \alpha_i + \beta_j + \Gamma_k + \alpha\beta_{ij} + \alpha\Gamma_{ik} + \beta\Gamma_{jk} + \alpha\beta\Gamma_{ijk}$
$\alpha\beta_{ij}$: $G = 17.6$, 4 df, $P < .005$
$\alpha\Gamma_{ik}$: $G = 94.3$, 6 df, $P < .001$
$\beta\Gamma_{jk}$: $G = 52.3$, 6 df, $P < .001$
$\alpha\beta\Gamma_{ijk}$: $G = 17.0$, 3 df, $P < .001$

burrows during winter, especially when deep snows reduced mobility.

Jackrabbit activity changed seasonally, with jackrabbits least active during fall and most active in winter and summer (Fig. 1). Daily activity patterns also changed seasonally, with jackrabbits less active during morning hours (after midnight) in the fall.

The sexes showed different patterns of activity (Table 2), with males slightly more active than females during winter and spring. Females were slightly more active than males during summer and much more so during fall. The proportion of observations classified as active was lower during fall (Table 2), consistent with the results of the previous analysis (Fig. 1).

Jackrabbit activity was apparently influenced by the amount of light during night hours (Table 3). The proportion of observations in which jackrabbits were active at night changed seasonally, with jackrabbits most active in summer and least active in fall. The relationship of activity and night light also changed seasonally (Table 3). During fall, winter, and spring, jackrabbits were most active when night light was greatest (a full moon and little cloud cover). During summer the amount of night light did not appear to influence jackrabbit activity.

Jackrabbits were most active when there was little wind; high winds were associated with decreased jackrabbit activity (Table 4). Activity in relation to wind intensity changed seasonally (Table 4), with jackrabbits less likely to be active during the winter when winds were high. Sampling of jackrabbit activity during high winds in the fall was insufficient for basing conclusions.

DISCUSSION

Home Range Shape and Size

The shape of most jackrabbit home ranges tended to be elliptical. The shape is not a result of the locations of the tracking shelters in relation to radio-collared jackrabbits, as very acute or obtuse telemetry bearings were excluded from the analysis. A similar elliptical shape was noted by Rusch (1965), who obtained many locations from snow-tracking.

The sizes of black-tailed jackrabbit home ranges determined in this study (Table 1) are larger than those reported for the species in other studies. Rusch (1965) and Nelson and Wagner (1973), also working in Curlew Valley, reported that jackrabbits used areas <0.2 km^2 (minimum convex polygon) for periods of one to two months in the fall and winter. It is not clear why the home ranges I report are greater in size than those described in these earlier studies. Two factors, however, may have had some influence. My relocation effort was more intensive than those conducted previously, resulting in a greater number of relocations per animal. Moreover, advances in

TABLE 3. Frequency of black-tailed jackrabbit activity and relationships with amount of light at night and season of year in Curlew Valley, Utah, 1983–1984. The data are the number of telemetry readings observed under the categorical conditions. The proportion active is in parentheses.

Season (Γ)	Active (α)	Amount of light (β)		
		Low	Medium	High
Winter	yes	133 (.21)	37 (.60)	23 (.52)
	no	477	25	21
Spring	yes	33 (.19)	81 (.27)	48 (.42)
	no	138	223	66
Summer	yes	234 (.34)	77 (.31)	143 (.34)
	no	449	175	273
Fall	yes	12 (.09)	21 (.17)	6 (.27)
	no	126	104	16

$\ln f_{(ijk)} = \mu + \alpha_i + \beta_j + \Gamma_k + \alpha\beta_{ij} + \alpha\Gamma_{ik} + \beta\Gamma_{jk} + \alpha\beta\Gamma_{ijk}$
$\alpha\beta_{ij}$: $G = 76.0$, 8 df, $P < .001$
$\alpha\Gamma_{ik}$: $G = 103.2$, 9 df, $P < .001$
$\beta\Gamma_{jk}$: $G = 721.5$, 12 df, $P < .001$
$\alpha\beta\Gamma_{ijk}$: $G = 56.1$, 6 df, $P < .001$

TABLE 4. Frequency of black-tailed jackrabbit activity and relationships with wind intensity and season of year in Curlew Valley, Utah, 1983–1984. The data are the number of telemetry readings under the categorical conditions. The proportion active is in parentheses.

Season (Γ)	Active (α)	Wind intensity (β)	
		Low	High
Winter	yes	214 (.32)	14 (.09)
	no	459	134
Spring	yes	112 (.18)	52 (.28)
	no	512	211
Summer	yes	392 (.26)	107 (.21)
	no	1125	396
Fall	yes	33 (.09)	6 (.27)
	no	318	16

$\ln f_{(ijk)} = \mu + \alpha_i + \beta_j + \Gamma_k + \alpha\beta_{ij} + \alpha\Gamma_{ik} + \beta\Gamma_{jk} + \alpha\beta\Gamma_{ijk}$
$\alpha\beta_{ij}$: $G = 252.3$, 4 df, $P < .001$
$\alpha\Gamma_{ik}$: $G = 704.1$, 6 df, $P < .001$
$\beta\Gamma_{jk}$: $G = 759.7$, 6 df, $P < .001$
$\alpha\beta\Gamma_{ijk}$: $G = 198.8$, 3 df, $P < .001$

radiotelemetric and analytical procedures since the early 1970s may have played an important role.

Lechleitner (1958a) in California, French et al. (1965) in Idaho, and Tiemeier (1965) in Kansas also reported seasonal ranges of <0.2 km^2. Areas of use were determined in these three studies from visual observations of marked animals. Differences in sizes of home ranges may also reflect differences in habitats among study areas. Habitat in Lechleitner's and Tiemeier's studies consisted of pastures and cultivated land. Plant cover on French et al.'s (1965) study area was similar to the native Great Basin shrub-steppe vegetation of Curlew Valley.

Two limitations of the home range analysis may have influenced the results. These are the precision of the tracking system and serial correlation of the location data. I believe that the precision of the tracking system averaged 200 m (Smith 1987, Mills and Knowlton 1989). Sequential locations had to be at least 200 m apart before I could be certain that movement had occurred. Locations closer to the tracking shelters had greater precision, probably to a minimum of 100 m, while locations more distant from the shelters had less precision, probably less than 300 m. The most precise locations were located along the arc created using the baseline between the two towers as the diameter of a circle. The reduced precision in locating distant jackrabbits may have produced overestimates of home range sizes.

Home range estimation methods assume that locations are serially independent (Swihart and Slade 1984). When serially correlated data are

analyzed, these methods underestimate home range size. All the location data sets showed some degree of serial correlation. I used all locations obtained for each animal and did not subsample to decrease serial correlation because, for many of the animals, too few locations were obtained to allow me to discard data points and still have a minimum sample size of 50 locations per analysis (Table 1). Because home range size is a statistic, the greatest value of which lies in comparisons among subsets of a population (White and Garrott 1990), I opted for the procedure that gave me larger samples.

Home Range Use

Resting in forms during daylight hours is a behavior observed in virtually all black-tailed jackrabbit populations (Vorhies and Taylor 1933, Lechleitner 1958b, Rusch 1965, Haug 1969, Costa et al. 1976, and Flinders and Elliot 1979). Forms are shallow depressions in or under bushes (Vorhies and Taylor 1933). Form use by Curlew Valley jackrabbits appears typical for the species. The use of burrows during the winter in Curlew Valley, however, appears unusual (Lechleitner 1958b). Jackrabbits use burrows to evade predators (Vorhies and Taylor 1933, personal observation) and construct shallow burrows to escape summer heat in the Mohave Desert (Costa et al. 1976), but daily use of deep burrows has not been reported previously. I believe jackrabbits use burrows during winter in Curlew Valley to reduce the risk of predation (Smith 1987).

Jackrabbits have been reported to use systems of trails to travel about their home ranges (Vorhies and Taylor 1933, French et al. 1965, Rusch 1965). Although trails used by jackrabbits in Curlew Valley were obvious in the snow and vegetation, I was unable to study trail use because the tracking system could not locate jackrabbits with sufficient accuracy.

Home ranges of individual instrumented jackrabbits overlapped extensively. I have no data that suggest individual jackrabbits influenced the home range use by other jackrabbits from spring through fall, although such intraspecific interactions may have occurred. My study suggests that during winter jackrabbits were social and gathered in groups (Smith 1987). Similar winter behavior was reported earlier from Curlew Valley (Rusch 1965) and has also been observed in southern Idaho (personal observation).

Jackrabbits appeared to traverse the entire home range in short periods of time. Similar home range use was reported by Lechleitner (1958a), who observed both female and male jackrabbits covering their ranges in about an hour. French et al. (1965) also reported that jackrabbits traversed home ranges in a matter of hours.

Factors Governing Home Range Shape and Size

SEASONAL VARIATION AND WEATHER EFFECTS. —The greater activity of males compared with females (Table 2) during winter and spring is probably related to reproductive activity. The reproductive season for jackrabbits in Curlew Valley usually begins in January and lasts through May or June (Gross et al. 1974). Black-tailed jackrabbits have a complex mating behavior in which males seek out females (Dunn et al. 1982). Males would thus be expected to be more active than females during the breeding season. Lechleitner (1958a) and Haug (1969) also report greater activity by males during the breeding season.

Other researchers have reported seasonal changes in the daily patterns of jackrabbit activity. Donoho (1972) and Costa et al. (1976) reported that jackrabbits were generally less active during winter. The timing of daily activity observed in this study changed seasonally and was probably related to changes in day length and times of sunset and sunrise. Similar results were reported by Donoho (1972). The evening activity peak I observed is similar to that reported by Lechleitner (1958b) and Haug (1969) (Fig. 1). However, Haug (1969) also described a period of heightened activity just before sunrise.

Blackburn (1968) and Knowlton et al. (1968) reported that jackrabbit activity was influenced by ambient air temperature. I was unable to record air temperatures at jackrabbit locations, but my finding that jackrabbits were less active during high winds tends to support the idea that temperature influences jackrabbit activity. Lechleitner (1958a) and Tiemeier (1965) also reported decreased activity during high winds and inclement weather. Lechleitner (1958a) also noted that jackrabbits were more active during bright

moonlit nights, a finding consistent with my results.

The sizes of home ranges measured by this study appeared to change with the seasons, with spring and fall ranges being slightly smaller. Males used larger areas than females. Tiemeier (1965) and Donoho (1972) found no significant differences in home range size between sexes. Other researchers, however, reported that female jackrabbits used larger areas than males in summer, fall (Lechleitner 1958a), and winter (Nelson and Wagner 1973). Differences in procedures, especially analytical, make comparisons among studies difficult. Many jackrabbits changed home range areas on a seasonal basis, with animals moving to wintering areas in the fall and early winter, and leaving in the spring. Rusch (1965), working in Curlew Valley, and Tiemeier (1965), in Kansas, also reported seasonal shifts in home range areas, with animals moving to areas with larger shrubs.

AGE.—As juvenile jackrabbits mature, one would expect their home ranges to increase in size. It appears that juvenile jackrabbits increase the size of their areas of use to roughly that of adults within the first six months postpartum. Young jackrabbits are precocial, are usually weaned by six weeks of age, before the arrival of the next litter, and are independent of their dams at a very young age (Drake 1969).

POPULATION DENSITY.—Jackrabbit populations in Curlew Valley undergo changes in density on a 10-year cycle (L. C. Stoddart and F. F. Knowlton, Mathematical model of coyote-jackrabbit demographic interactions, northern Utah. Poster presented at 4th International Theriological Congress, Edmonton, Alberta, Canada, 1985). My study was conducted during a population low, i.e., < 30 jackrabbits/km^2 (Smith 1987). I do not know whether patterns of jackrabbit home range use change with population density. However, I noted changes in the pattern of use of wintering areas (with fewer wintering areas used during low densities) and habitat types (Smith 1987), suggesting the possibility of other changes in home range use with changing density. Differences between my findings and others reported in the literature may be a function of differing jackrabbit densities.

HABITAT.—Jackrabbit home ranges in this study were contiguous, and separate resting and feeding areas were not used. This reflects the availability of resources within home ranges of Curlew Valley jackrabbits. Where feeding and resting resources are available in the same area, jackrabbits do not need to travel far from daytime forms to nocturnal feeding sites (Vorhies and Taylor 1933, Nelson and Wagner 1973). In areas where feeding resources are separated from cover, jackrabbits have been reported to travel distances >1 km nightly (Vorhies and Taylor 1933, Haug 1969). Jackrabbits have also been reported to shift feeding sites to feed in agricultural fields (Bronson and Tiemeier 1959).

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