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Activity and Behavior of Free-Living *Sylvilagus nuttallii*

Abstract

A paucity of published information on activity and behavior of Nuttall's cottontail (*Sylvilagus nuttallii*) and of free-living leporids in general caused us to study these attributes in central Oregon in 1980-1981. Of 1,192 behavioral acts of free-living cottontails recorded between 1 hr before sunrise to 1 hr after sunset during 327.3 hr of observation from an elevated stand in March-August 1981, 92.9 percent were nonsocial and accounted for 92.6 percent of the time that cottontails were in view. Of time in view, cottontails spent 58.5 percent feeding, 23.0 percent resting, and 6.3 percent moving. Social behavior was observed among adults only during the reproductive season and accounted for only 7.4 percent of their activity budget. A bimodal pattern of daytime activity peaked 1-2 hr after sunrise and 0-1 hr before sunset. Activity of adult females was relatively constant seasonally, but adult males became extremely secretive after the reproductive season. Although no single environmental factor or group of factors was a significant determinant of activity in Nuttall's cottontail, the relatively solitary life-style and near absence of reproductive interactions during daylight hours may be behavioral mechanisms related to equitable division and conservation of available moisture.

Introduction

Knowledge of the biology of Nuttall's cottontail (*Sylvilagus nuttallii*), an endemic to the intermountain West (Hall 1981), is limited to descriptive accounts (Bailey 1936, Hall 1951, Ingles 1965, Janson 1946, Orr 1940) and to recent ecological studies in central Oregon (Hundertmark 1982, McKay and Verts 1978*a*, 1978*b*, Powers and Verts 1971, Skalski and Verts 1981, Verts *et al.* 1984) and British Columbia (Sullivan *et al.* 1989). Accounts of the behavior of this and other leporid species are based largely on scattered field observations or on observations of animals in pens or enclosures. The description and classification of behavioral patterns of the black-tailed jackrabbit (*Lepus californicus*) by Lechleitner (1958) remains the only detailed published account based on observations of free-living leporids. Herein, we categorize behavior, quantify relationships among various activities and environmental variables, and relate specific behavioral acts to ecology of Nuttall's cottontail in central Oregon.

Study Area and Methods

Field research was conducted on a portion of a 115.7-ha site approximately 5 km W Terrebonne, Deschutes County, Oregon (elevation, 835-842 m) used in several previous studies of *S. nuttallii* (Hundertmark 1982, McKay and Verts 1978*a*, 1978*b*, Powers and Verts 1971, Skalski and Verts 1981, Verts *et al.* 1984). The study area lies within 30 km of the western edge of the geographic range of *S. nuttallii* (Hall 1981). Climate is semiarid with hot dry summers and relatively cold winters; mean annual precipitation is 22.9 cm (U.S. Department of Commerce 1981). Vegetation in this section of the Columbia Basin Physiographic Province is most similar to the *Juniperus occidentalis/Artemisia tridentata-Purshia tridentata* association (Franklin and Dyrness 1973).

Field observations were conducted from early June-30 August 1980 and 7 February-30 August 1981 by systematic live trapping, ad libitum cruises, cruises during operation of traplines, and systematic observations by focal-animal sampling (Altmann 1974) from an elevated ($\approx$6 m) stand in a tree. In an effort to reduce bias in activity budgets related to differential ease of sighting individuals engaged in different behavior, the entire area observable from the stand was scanned until a cottontail was sighted, whereupon that individual was observed and its behavior recorded for 5 minutes; then, the area was scanned for additional cottontails for 5 minutes before observing and recording behavior of the previously sighted cottontail for another 5-minute period. The only deviation from this routine was when individuals interacted; interacting cottontails were observed until the interactions were complete or the cottontails were no longer in view.

Unbaited wooden box traps (15 X 19 X 58 cm) set in a 9- X 13-trap grid with approximately 90 m between traps were operated alternate weeks in June, 3 consecutive days each week in July, and daily 1-30 August in 1980. Traps also were operated 3 consecutive days during 3, 3, 2, and 4 weeks in April, May, June, and July, respectively,

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and daily 1-30 August in 1981. From 25 February to 3 March 1981, live traps were set at four sites within the study area chosen as potential areas for systematic behavioral observations. On the basis of the relative abundance of cottontails and of the physiognomy and vegetation that did not interfere greatly with observations of cottontails, one site (≈6 ha) was selected. This report is based largely on the systematic observations conducted from a tree stand from which most of the ≈6-ha area was visible. All cottontails captured were marked with aluminum ear tags; weight, sex, and age (based on size, pelage, and reproductive status) for each cottontail were recorded. Cottontails captured also were marked for individual recognition by clipping guard hairs to form numerals along the flanks and dying the exposed underfur with Nynazol-D (females) or Rhodamine-B (males).

Initially, periods of 0.75-4.00 hr of observations from the stand were scheduled at all hours of the day and night during March-August 1981; however, observations were restricted to the period from 1 hr before sunrise to 1 hr after sunset when artificial light and a Star-tron night scope proved unsuitable for nighttime observations of Nuttall's cottontail. All subsequent observations were with the aid of 7 X 35 wide-angle binoculars. Because Lord (1961) reported that most activity of free-living eastern cottontails (*S. floridanus*) was before 0900 or after 1600, we sampled the interval between these hours less intensively.

During systematic observations from the elevated stand, time, location, identifying marks, and detailed descriptions of behavior were recorded on microcassette tapes and subsequently transcribed to field notes for all cottontails observed. The classification scheme devised for behavior of eastern cottontails and swamp rabbits (*S. aquaticus*) in enclosures (Marsden and Holler 1964) served as a framework for identifying and describing movements, postures, and other behavior exhibited by *S. nuttallii*. Site-and time-specific weather conditions were recorded before and after observation periods and cruises. Additional climatological data were obtained from records of the Redmond FAA AP weather station approximately 11 km S and 6 km E of the study area (U.S. Department of Commerce 1980, 1981). Data related to astronomical phenomena were obtained from the U.S. Naval Observatory (1979, 1980).

Coefficients of multiple correlation were computed for all combinations of activity and environmental variables. Data collected during observation periods were subjected to principal-component analysis; five dependent variables (total number, and number of adult, adult male, adult female, and juvenile cottontails observed/hr) and nine independent variables (date; time of day relative to sunrise or sunset; number of avian predators observed/hr; mean temperature, cloud cover, and windspeed during the period; number of consecutive days without precipitation; length of the previous night; index to lunar illumination during the previous night) were chosen for analysis based on correlation coefficients. Multiple regression was used to determine if principal components were related significantly ($P \leq 0.05$) to activity.

Results and Discussion

The Subjects

A minimum of 19 Nuttall's cottontails (individuals captured or observed) used the ≈6-ha site between 24 February and 30 August 1981. Among this group, 12 were adults: four marked females, six marked males, and at least one unmarked individual of each sex. If all 12 adults resided solely on the ≈6-ha area observable from the stand, population density of adults was ≈2/ha, approximately equal to the maximum density recorded on the Terrebonne Study Area during the preceding 8 years (Skalski and Verts 1981). Likely, several of these individuals included areas in their home range beyond the limits at which observations were recorded.

The Behavioral Repertoire

The 1,192 behavioral acts recorded during 327.3 hr of scheduled observations were classified initially into eight categories of posture and seven categories of movements, and these into 20 nonsocial and seven social behavioral patterns (Gehman 1984). The 27 behavioral patterns were combined into seven categories of nonsocial behavior (feed, rest, locomote, groom, tree-climb, interspecific interactions, and transitional acts) and two categories of social behavior (reproductive and nonreproductive). Nonsocial behavior accounted for 92.8 percent of the total number of acts observed and 92.6 percent of the total time that cottontails were in view (Table 1).

Of nonsocial behaviors, feeding accounted for the greatest proportion of the time during which

TABLE 1. Number and percent of total of each behavior observed, total and percent of total time each act was observed, and mean duration of each act for Nuttall's cottontail, Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Behavior Type and Behavior	Number Acts Observed	Percent of Acts Observed	Time Acts Performed (min)	Percent of Time Observed (min)	Mean Duration of Act (min)
Nonsocial					
Feed	303	25.4	2,202.8	58.5	7.27
Rest	163	13.7	863.9	23.0	5.30
Locomote	459	38.5	238.7	6.3	0.52
Groom	97	8.1	59.2	1.6	0.61
Tree-climb	47	3.9	114.2	3.0	2.43
Interspecific Interactions	15	1.3	7.5	0.2	0.50
Transitional Acts	23	1.9	1.8	0.1	0.08
Social					
Reproductive Interactions	77	6.5	261.0	6.9	3.39
Nonreproductive Interactions	8	0.7	15.0	0.4	1.88

S. nuttallii was observed (Table 1); 72.2 percent of feeding bouts were on grasses (principally *Bromus tectorum, Stipa thurberiana*, and *Sitanion hystrix*), 7.9 percent on juniper (*Juniperus occidentalis;* only in July and August), 1.0 percent on shrubs (flowers of green rabbitbrush, *Chrysothamnus viscidiflorus*, only), and 18.8 percent on unidentified plants. No cottontail was observed to feed on forbs.

Resting accounted for the next greatest proportion of the time during which cottontails were observed (Table 1). Nuttall's cottontails sat motionless in either an alert or hunched posture for 92.1 percent of the time they rested; they were in a lying position 6.9 percent of resting time and sprawled in a loafing posture 1.0 percent of resting time. One female was observed to sprawl in a loafing posture immediately after dusting on four occasions. Contrary to the conclusions of McKay and Verts (1978*b*), *S. nuttallii* used forms much more frequently (78 [12.4 percent] of 630 cottontails observed during February-August 1981) than crevices and fissures in rock outcrops (four [0.6 percent] of 630 cottontails). However, numerous cottontail tracks were observed to lead to and from openings in rock outcrops during cruises conducted when snow covered the ground in winter 1980-1981.

Movements (locomote) from one area to another accounted for the largest proportion of behavioral acts observed but accounted for less time than three other behavioral categories (Table 1). Movements tended to be of relatively short duration ($\bar{X}$ = 31 s). Tree climbing accounted for the next greatest proportion of time cottontails were in view (Table 1), but was observed only during July and August. Grooming, interspecific interactions, and transitional acts accounted for the remainder of time that *S. nuttallii* engaged in nonsocial behavior (Table 1).

Social interactions accounted for only 7.3 percent of the total time that cottontails were in view (Table 1), and reproductive interactions accounted for 94.6 percent of the time spent in social interactions. Following of females by males at distances of $\leq$2 m and passive attendance of stationary females by males accounted for 75.3 percent of reproductive interactions observed and for 87.4 percent of the time that *S. nuttallii* engaged in reproductive interactions. Male-male interactions accounted for 5.2 percent of reproductive interactions and 3.8 percent of time spent in reproductive interactions. However, no physical contact between males was observed. Although no copulations, attempted mounts by males, or presentations by females were observed, on one occasion (2.6 percent of reproductive interactions, 1.5 percent of time spent in reproductive interactions) the entire "face-off," "male-dash," "jump-sequence," and "reproductive-chase" repertoire that usually is a prelude to mating in *S. floridanus* and *S. aquaticus* (Marsden and Holler 1964) was observed. Presumably, most reproductive interactions occur during the hours of darkness.

Nonreproductive interactions (9.4 percent of social interactions, 5.4 percent of time spent in

social interactions) consisted of a juvenile approaching and investigating an adult female that was feeding and three instances of adult females chasing juveniles that approached them. No physical contact was observed.

Daily Activity

Nuttall's cottontails exhibited a bimodal pattern of daytime behavior with peaks in the second hour after sunrise and the hour before sunset (Table 2). As overall activity increased from the hour before sunrise to 2 hr after sunrise cottontails spent a greater proportion of time feeding (Table 2); in the evening the proportion of time spent feeding tended to increase as overall activity declined in the hour after sunset (Table 2). The proportion of time spent moving and grooming increased as overall activity declined in the morning, likely in response to cottontails seeking daytime retreats and settling in for the midday rest period; both activities increased in the 2 hr before sunset (Table 2). Social interactions tended to be greatest during hours that overall activity was greatest (Table 2).

Seasonal Activity

Among adults, activity levels of the two sexes were similar during March-June, but during July and August, adult male cottontails were not observed from the elevated stand, and were trapped or observed during cruises only about one-third as often as adult females (Table 3). The former period corresponds approximately to the last three-fourths of the breeding season (Powers and Verts 1971). Among juveniles, all indices indicated that activity increased from their first appearance in April through July, followed by a decline in August. An increase in density as each litter-group (Powers and Verts 1971) became observable about 1 month after birth likely was responsible for the observed increase rather than an increase in activity by individuals. The decline in observed activity of juveniles in August likely was a result of a decline in density related to mortality that commonly occurs among juveniles during the summer drought (Verts *et al.* 1984).

Environmental Influences

No single environmental factor or group of factors emerged as a significant determinant of activity levels in Nuttall's cottontail. Many activity-environmental relationships analyzed (Table 4) were not significantly correlated ($P > 0.05$); those correlated significantly ($P \leq 0.05$) usually had low coefficients of correlation (r). Furthermore, relationships with moderate r values usually could be

TABLE 2. Proportion of total activity[a] of Nuttall's cottontails observed in relation to sunrise and sunset by behavioral category on the Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Interval[c]	Observation Time[b] (hr)	Observation Time[b] (%)	Proportion Total Activity[a] (%)	Activity Category: Feed	Rest	Locomote	Groom	Tree-climb	Inter-specific Inter-actions	Transi-tional Acts	Social Inter-actions
SR-1hr to SR	17.6	5.0	3.4	65.0	29.1	5.8				0.1	
SR to SR +1hr	53.9	15.3	20.4	56.4	18.1	6.2	1.1	13.5	<0.1	<0.1	4.8
SR+1hr to SR+2hr	51.7	14.7	27.2	61.3	16.4	7.4	1.8	0.5	<0.1	<0.1	12.6
SR+2hr to SR+3hr	23.6	6.7	7.0	57.0	14.3	14.1	5.3		1.0	0.1	8.3
SR+3hr to SR+4hr	8.1	2.3	2.2	9.4	63.5	17.2	4.7		0.2	<0.1	0.2
SR+4hr to SR+8hr	16.5	4.7	0.6	T[d]		T[d]					
SS-8hr to SS-2hr	27.8	7.9	0.2		T[d]	T[d]				T[d]	
SS-2hr to SS-1hr	40.1	11.4	4.9	55.5	34.3	9.4	0.6				0.1
SS-1hr to SS	54.9	15.6	22.7	51.9	34.6	3.1	1.5		0.5	<0.1	8.3
SS to SS+1hr	33.1	9.4	11.4	77.3	16.0	2.3	0.2			0.1	4.1

[a]Activity = number cottontails in view X time cottontails in view.

[b]Excludes observation time at other than intervals listed; thus, the 327.3 hr listed constitutes only 93.0 percent of the total 352 hr of observations.

[c]SR = sunrise; SS = sunset.

[d]Value omitted because total time cottontails in view in interval <1.0 percent of total.

TABLE 3. Number of marked cottontails in each sex and age class sighted per unit effort during cruises and number captured per unit effort each month on the Terrebonne Study Area, Deschutes County, Oregon, March-August, 1981.

Method of Observation, Effort, and Sex and Age Class of Cottontail	Month					
	March	April	May	June	July	August
Cruises in Area of Intensive Study						
Observation Time (hr)	17.1	9.3	13.9	11.4	18.1	15.7
Number Sighted/10 hr						
Adult Males	3.5	13.9	8.6	3.5		
Adult Females	5.2	12.9	18.7	14.9	12.7	9.6
Juveniles		4.4	6.5	8.8	13.8	11.5
Cruises over Entire Study Area						
Observation Time (hr)		48.6	44.7	33.4	59.0	97.0
Number Sighted/10 hr						
Adult Males		2.5	1.8	0.3	0.7	0.8
Adult Females		3.1	3.1	1.8	2.4	2.5
Juveniles			3.6	2.7	4.1	7.1
Live Trapping on Entire Area						
Number Trap-Nights		1,053	1,053	702	1,434	3,510
Number Captured/100 Trap-Nights						
Adult Males		2.1	0.9	0.3	0.2	0.0
Adult Females		0.7	0.8	0.6	0.4	0.1
Juvenile Males		0.2	0.4	0.9	1.0	0.2
Juvenile Females		0.3	0.4	0.9	0.7	

[a] < 0.1

explained in terms of phenomena other than those of the physical environment. For example, significant positive relationships between number of juvenile cottontails observed per hour and day of year, day of 26-day reproductive period, consecutive days without precipitation, and length of the previous night (Table 4) likely were largely a reflection of litter-cohorts being recruited to the population as the season progressed. Also, significant positive correlations between activity of adult cottontails and number of owls (Strigidae) present and time they were present (Table 4) likely is merely a reflection of the correspondence of crepuscular activity of owls and cottontails.

Principal-component analysis performed on nine variables selected because of their moderate r values resulted in the creation of three components that explained 70 percent of the variation in environmental variables. The first of these components was considered representative of seasonal influences (day of year, temperature, consecutive days without precipitation, numbers of avian predators present, length of night, and lunar illumination); the second was considered representative of daily influences (time of day, temperature, and wind speed), and the third representative of astronomical phenomena (length of night and lunar illumination). Multiple regression of the principal components on cottontail activity (number observed/hr) did not explain large proportions of the variation in activity. Although the seasonal component influenced activity of adult males the most, the component explained only 11 percent of the variation in their activity. Similarly, the daily component had the greatest influence on activity of adult females, but only 4 percent of the variation in activity was explained by the component. Juvenile activity was related to the seasonal component ($R^2 = 0.22$) and the astronomical component ($R^2 = 0.35$); again, these latter relationships likely result from the sequential recruitment of litter-groups.

Conclusions

Without doubt, the most spectacular and potentially ecologically significant behavior of Nuttall's cottontail is related to its tree-climbing activities. Occupation of this region by Nuttall's cottontail may be dependent upon at least some individuals climbing trees during the summer drought to acquire water exuded by boughs or concentrated in tips

TABLE 4. Coefficients of multiple correlation for number of Nuttall's cottontails observed per hour and environmental variables, Terrebonne Study Area, Deschutes County, Oregon, March-August 1981.

Environmental Variable	Sex and Age Class					
	Adult Male	Adult Female	All Adults	Juvenile Male	All Juveniles	All Cottontails
Day of Year	−0.34*	0.04	−0.21*	0.67*	0.61*	0.04
Reproductive Period	−0.32*	0.12	−0.13			0.01
Day of 26-day Reproductive Period	−0.28*	−0.05	−0.22*	0.67*	0.61*	0.06
Time of Day	−0.08	−0.16*	0.08	0.08	0.02	−0.09
Time Relative to Sunrise or Sunset	−0.06	−0.16	0.07	0.09	0.01	−0.08
Owls Observed (*n*/hr)	0.29*	0.01	0.21*	−0.03	−0.04	0.11
Time Owls Present (Morning)	0.29*	0.02	0.18*	−0.14	−0.19*	0.05
Time Owls Present (Evening)	−0.05	−0.04	−0.05	−0.15	−0.18*	−0.11
Hawks Observed (*n*/hr)	0.01	−0.04	−0.03	−0.14	0.08	−0.07
Avian Predators Observed (*n*/hr)	0.23*	−0.01	0.14*	−0.07	−0.01	0.05
Minimum Temperature	−0.25*	−0.19*	−0.31*	0.11	0.01	−0.21*
Maximum Temperature	−0.32*	−0.20*	−0.32*	0.24*	0.01	0.19*
Mean Temperature	−0.29*	−0.20*	−0.33*	0.18*	0.07	−0.21*
Minimum Temperature Previous Day	−0.34*	−0.06	−0.30*	0.38*	0.25*	−0.13
Maximum Temperature Previous Day	−0.32*	−0.03	−0.25*	0.43*	0.34*	0.06
Consecutive Days With Precipitation	0.10	−0.03	0.06	0.26*	−0.12	<0.01
Consecutive Days Without Precipitation	−0.23*	−0.05	−0.18*	0.66*	0.57*	0.09
Minimum Cloud Cover	0.05	−0.09	−0.05	−0.23*	−0.26*	−0.16*
Maximum Cloud Cover	0.17*	−0.08	0.03	−0.13	−0.18	−0.08
Mean Cloud Cover	0.12	−0.09	−0.01	−0.18*	−0.22*	−0.12
Minimum Wind Speed	−0.09	−0.21*	−0.17*	−0.09	−0.12	−0.21*
Maximum Wind Speed	−0.06	−0.18*	−0.14*	0.07	0.01	−0.16*
Mean Wind Speed	−0.07	−0.20*	−0.16*	0.04	−0.02	−0.18*
Length of Previous Night	0.21*	−0.15*	0.04	0.69*	0.61*	0.03
Duration of Lunar Illumination	0.16*	−0.06	0.07	0.29*	0.27*	0.06
Fraction of Moon Illuminated	0.01	−0.04	−0.04	0.18*	0.18*	−0.02
Time Lunar Illumination Commenced	0.22*	0.01	0.14*	0.17	0.17	0.14*
Time Lunar Illumination Ended	−0.08	0.01	−0.03	0.14	0.09	<−0.01
Phase of Moon	−0.17*	−0.10	−0.18*	−0.03	−0.01	−0.14*
Duration of Lunar Illumination X Fraction of Moon Illuminated	0.05	−0.08	−0.03	0.24*	0.21*	−0.04

*$P < 0.05$.

of boughs of juniper trees (Verts *et al.* 1984). However, the low rate of social interactions during daylight hours may have a role similar to tree climbing in the same ecological relationship: conservation of water may be as critical as acquisition of water for survival of *S. nuttallii* in the intense rain shadow of the Cascade Mountains at the western periphery of its geographic range.

Among leporids, Nuttall's cottontail is at or near the base of the cline in sociality that extends from the warren-inhabiting European rabbit (*Oryctolagus cuniculus;* Mykytowycz 1968), to the swamp rabbit that displays some of the strong social characteristics of the European rabbit, thence to the solitary eastern cottontail that interacts socially only during the reproductive season (Marsden and Holler 1964). In our study, adult Nuttall's cottontails also interacted socially only during the reproductive season. Orr (1940) claimed that *S. nuttallii* is more solitary than other members of the genus. The solitary life-style may be a factor in the relatively uniform dispersion of *S. nuttallii* (McKay and Verts 1978*b*) which in turn may reduce

intraspecific competition and facilitate optimum-forage (moisture) availability at seasons when available moisture is least (Hundertmark 1982) and moisture requirements of lactating females and growing young are greatest (Richards 1979). Presumably restricting energy-demanding reproductive interactions (Marsden and Holler 1964, Casteel 1966) to nighttime hours (when humidities are highest) may be another behavioral mechanism by which Nuttall's cottontail conserves moisture.

Nevertheless, no single environmental factor exhibited a dominant influence on activity of Nuttall's cottontail, a result similar to that obtained in studies of activity in arid-land rodents (Blaustein and Fugle 1981, O'Farrell 1974). Results of our study suggest that seasonal and daily activity levels of *S. nuttallii* during daylight hours may be determined by complex interrelationships among reproductive condition, temperature and moisture requirements of the animals, and combinations of environmental constraints to which populations are subjected.

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