J. Mamm., 65(1):131–135, 1984

SYLVILAGUS NUTTALLII: A SEMIARBOREAL LAGOMORPH

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Lagomorphs generally are considered to be terrestrial mammals, and the leporids are adapted for cursorial locomotion. Nevertheless, observations incidental to investigations of the population ecology of Nuttall's cottontail (*Sylvilagus nuttallii*) in central Oregon since 1968 (Powers and Verts, 1971; Sullins et al., 1976; McKay and Verts, 1978*a*, 1978*b*; Skalski and Verts, 1981; Hundertmark, 1982) revealed that some individuals climbed in western juniper (*Juniperus occidentalis*) up to 3 m above the ground. We now quantify the arboreal activity, and use aspects of the population and feeding ecology of the species to provide an explanation for the unusual activity.

Our 87-ha study area, 7 km W Terrebonne, Deschutes Co., Oregon (44°22′N, 121°13′W, elev., 945 m), lies within 30 km of the western limit of the geographic range of *S. nuttallii* (Hall, 1981). Precipitation averages 21.6 cm annually (U.S. Department of Commerce, 1978). The area is scabland: a substrate of bare basalt with pockets of eolian pumice soil (State Water Resources Board, 1969). Vegetation is big sagebrush (*Artemisia tridentata*)-dominated shrub-steppe with widely-spaced western junipers and an understory principally of cheatgrass (*Bromus tectorum*), squirreltail (*Sitanion hystrix*), and needlegrass (*Stipa thurberiana*); rabbitbrush (*Chrysothamnus viscidiflorous* and *C. nauseosus*) and bitterbrush (*Purshia tridentata*) are other common shrubs (McKay and Verts, 1978*b*).

From 1972 to 1981, wooden box traps (15 by 18.7 by 58 cm) set in a 9- by 13-trap grid were operated 3 days each week in July and daily in August and, except for 1972, 1974, 1978, and 1980, 3 days during alternate weeks April to June. Each livetrapped cottontail was measured, weighed, and marked, and was assigned to a sex and age cohort (McKay and Verts, 1978*a*). Densities of cottontail populations were estimated at about monthly intervals, and estimates of natality and juvenile survival were made for each litter cohort (McKay and Verts, 1978*a*).

Contents of stomachs from 43 cottontails collected in similar habitats near, but more than 0.8 km from, the study area in 1978 and 1979 were analyzed by histological microtechniques (Flinders and Hansen, 1972). Succulence of available forage, estimated by drying samples of at least 100 g of each plant species collected on the study area at intervals of about 1 month, was expressed as mean percentage wet weight lost through drying for each class of forage (grasses, forbs, and shrubs).

From 1 March to 29 August 1981, 351.8 h of observations in 143 periods ranging from 0.8 to 4.0 h each were conducted from a platform about 7 m above the ground on the study area. Identifying marks, location, and time and duration of each activity (e.g. feeding, grooming, moving, resting, social interaction, and tree climbing) were recorded for each cottontail observed. In addition, we recorded activities of cottontails seen during 450.6 h of observations made while we examined traps, walked to the observation platform, and made routine walks through the area.

Population and feeding ecology.—Except for 1977 when too few individuals were captured to estimate density, prerecruitment densities of cottontails in late March or early April ranged from 19/100 ha in 1974 to 69/100 ha in 1975, and peak densities in August or early September ranged from 66/100 ha in 1973 to 254/100 ha in 1972 (Table 1). Precipitation during the February to July breeding season (Powers and Verts, 1971), combined with prerecruitment density, accounted for 56.4% of the variation in the August density of cottontails (Table 1).

Nuttall's cottontails on our study area produced offspring synchronously, usually in four well-defined litter groups (Powers and Verts, 1971; McKay and Verts, 1978*a*). Curvilinear regression indicated that precipitation falling during pre- and post-natal development accounted for 30 to 64% of the variation in survival of young from the estimated mean date of birth to 30 August (end of our field season) for three of four litter groups.

Because August density, and natality and survival of juveniles, seemed related to amounts and seasonal distribution of precipitation, we postulated that precipitation operated to affect those attributes by altering amounts and succulence of forage available to pregnant and lactating does, and to growing young. Our

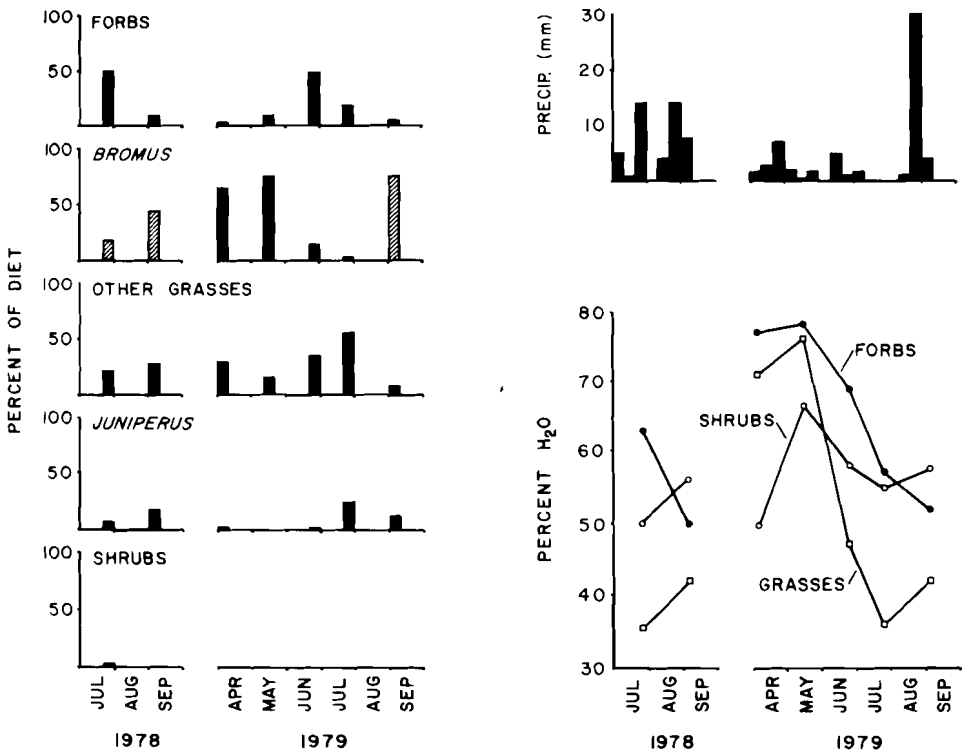

FIG. 1.—Percent frequency of occurrence of each class of forage in the diet of *Sylvilagus nuttallii*, succulence (percent water) for each class of forage available, and precipitation that fell (by ½ month). Deschutes Co., Oregon, spring and summer 1978–1979. New growth of *Bromus* denoted by hatching included some *Agropyron*. Precipitation data from U.S. Department of Commerce (1978, 1979).

hypothesis was consistent with relationships reported for *Oryctolagus cuniculus* in Australia (Richards, 1979). Therefore, we suspected that Nuttall's cottontails altered their diet in response to the succulence of forage available as summer drought progressed.

During spring (and corresponding approximately to the period during which the first three litter groups were born), Nuttall's cottontails fed mostly on grasses, especially *Bromus*. As the *Bromus* matured, cottontails fed more on forbs and later-maturing grasses (Fig. 1). During the peak of summer drought, as much as a fourth of their diet was composed of juniper, but, as *Bromus* and *Agropyron* sprouted after late summer rains, cottontails began to feed heavily on new growth of these species (Fig. 1). Shifts in the diet tended to correspond with succulence and maturity of the primary forage groups; shrubs did not constitute a significant part of the spring and summer diet.

Tree-climbing behavior.—Nuttall's cottontails usually climbed by jumping onto the bole of an acutely-leaning juniper and scampering upward and laterally on large branches. Some jumped onto low-hanging boughs and clambered upward toward the bole or laterally on adjacent and slightly higher boughs. As expected from the lack of morphological adaptations for climbing, Nuttall's cottontails were not particularly skilled or graceful climbers, and those in trees, especially when on small boughs, seemed to maintain a precarious balance.

Initially, we were surprised that a behavior as seemingly aberrant for a leporid as climbing in trees was not recorded by naturalists who reported on the life history of Nuttall's cottontail; reviews of available information (Chapman, 1975; Orr, 1940; Janson, 1946) did not mention arboreal activity in the species. However, seasonal distributions of observations and of the time and frequency that Nuttall's cottontails were observed to climb in trees indicated that the behavior was limited to July and August (Fig. 2). In addition,

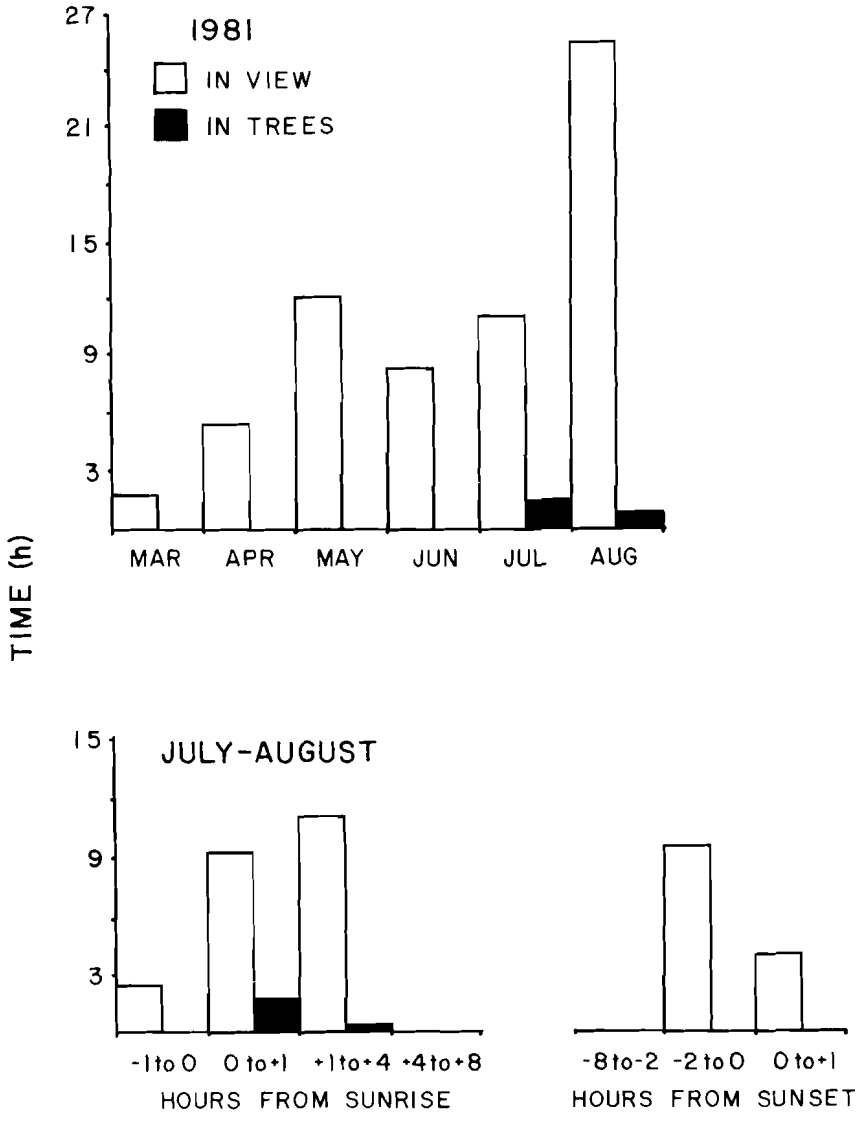

FIG. 2.—Time Nuttall's cottontails were in view and in trees by month, March to August 1981, and in relation to sunrise and sunset, July and August combined, 1981, Deschutes, Co., Oregon. Time spent observing from elevated stand ranged from 47 to 73 h/month and from 4 to 39 h/interval during the day.

observations of Nuttall's cottontails climbing in trees were concentrated during the early morning hours, especially in the hour after sunrise when cottontails under observation spent nearly 20% of their time in trees (Fig. 2). These factors, combined with the absence of trees in much of the range of the species, suggest a plausible explanation for the absence of documentation of such striking behavior.

Of the approximately 2 h that Nuttall's cottontails were observed in trees in July and August, they spent 55.9% of the time feeding on juniper, 41.0% sitting motionless, 3.0% moving, and 0.1% grooming. Between 1 h before and 4 h after sunrise during July and August, Nuttall's cottontails on the ground fed on low boughs of juniper for 8.5% of 22.3 h they were observed; also, 9.3% of those observed during walks through the area at the same hours were feeding on juniper when sighted.

TABLE 1.—*Relationships*[a] *of the estimated density of Nuttall's cottontails in August to the estimated density of breeders in late March–early April and the amount of precipitation falling during the breeding season (February–July), Deschutes Co., Oregon, 1972–1981.*

Year	Cottontails/100 ha		Precipitation[b] (cm) (X_2)
	Late March–early April (X_1)	August (Y)	
1972[c]	61	254	11.54
1973[c]	46	66	5.21
1974[c]	40	174	9.52
1975[c]	52	214	9.91
1976[c]	48	98	7.14
1977	—	—	6.27
1978	35	191	15.95
1979	42	87	7.69
1980	48	124	13.97
1981	59	—	12.12

[a] $Y = 161.84 + 4.08X_1 + 12.18X_2$, $R^2 = 0.564$
[b] Data from U.S. Department of Commerce (1972–1981).
[c] Population estimates from McKay and Verts (1978*b*), Skalski (1977), or R. Deering (in litt.).

Cottontail-juniper-water relationships.—The availability of water may be critical for Nuttall's cottontails during summer in our region. The breeding season is abbreviated when precipitation is reduced (McKay and Verts, 1978*a*); juvenile survival is correlated with precipitation during pre- and post-natal development; and population density in late summer is correlated with precipitation during the previous breeding season (Table 1). In addition, water requirements for some lagomorphs are greatest among lactating females and growing young (Richards, 1979), cohorts that appear in populations of Nuttall's cottontails near the onset of annual droughts (McKay and Verts, 1978*a*). Cooke (1982) suggested that *Oryctolagus cuniculus* in Australia required forage with at least 55% moisture content to survive without supplementary water, a moisture content not supplied by forbs or grasses on our study area in late summer even in the relatively wet year of 1978 (Fig. 1).

We believe that the association of Nuttall's cottontails with juniper trees may be fundamental to their survival during summer droughts on our study area. Nutritional requirements may not be the primary stimuli for use of juniper as forage; the nutritive value of juniper is usually highest during the summer months, but it is relatively low in comparison with that of several range plants common to our study area (Dietz et al., 1962; Smith, 1952, 1957; Vaughan, 1982). Although junipers provide adequate nutrition for some mammals (Vaughan, 1982), levels of crude protein in juniper in summer (Dietz et al., 1962) are less than those recommended even for a maintenance diet for domestic rabbits (Cheeke, 1977). In addition, junipers contain relatively large amounts of terpenoid compounds that reduce their palatability and interfere with cellulolytic activity of microflora in wild ruminants (Schwartz et al., 1980*a*, 1980*b*). Concentrations of terpenoids differ among species of *Juniperus* (Tatro et al., 1973), within species in relation to site (Schwartz et al., 1980*a*), and within individual trees with season (Adams, 1970; Powell and Adams, 1973) and time of day (Tatro et al., 1973). Usually, concentrations of terpenoids are highest in the morning hours and increase during summer to attain a maximum in late autumn. Terpenoids deter browsing by some lagomorphs (Bryant, 1981), but at least one species of rabbit (*S. idahoensis*) is able to forage extensively on plants with high concentrations by volatilizing much of the terpenoid content during mastication (White et al., 1982). Neither terpenoid content nor relatively low nutritive value completely deterred foraging on juniper by Nuttall's cottontails, but these factors combined with the seasonal occurrence of foraging on juniper tended to indicate that juniper was not ingested solely to satisfy nutritional requirements.

We noticed on numerous occasions in July and August that tips of boughs of some juniper trees were covered with droplets of water during early morning hours. We covered boughs with small plastic bags and found that several milliliters of water collected in each bag overnight; hence, the water exuded from the trees. We believe that the climbing activity of Nuttall's cottontails in juniper trees is related largely to the acquisition of water, either by licking droplets from tips of boughs or by ingesting "waterlogged" foliage (E. L. Klepper, pers. comm.). Although root pressure leading to guttation is not known to occur in conifers (Buttery and Boatman, 1964; O'Leary, 1965), we presume that most salts are removed from water exuded by junipers as they are in guttating plants (Klepper and Kaufmann, 1966). Hence, cottontails likely ingested droplets or "waterlogged" foliage for their water content, not for minerals or nutrients contained therein.

We are unsure whether tree-climbing activities of *S. nuttallii* were not recorded heretofore because they were not observed or because cottontails in parts of their range do not climb. If the latter, climbing may

be a behavioral adaptation that permits S. *nuttallii* to occupy the peripheral portions of its range in central Oregon.

We thank B. E. Coblentz and A. R. Blaustein for providing critiques of an earlier draft of the manuscript. R. M. Deering collected data during 1976 and 1977, R. Sauer and L. N. Carraway assisted with data analysis, and J. W. Kamp suggested the source of water droplets on junipers might be intrinsic. Field work conducted by KJH in 1979 was supported, in part, by an award from The Mazamas. This is Technical Paper 6737, Oregon Agricultural Experiment Station.

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Submitted 3 March 1983. Accepted 3 June 1983.