AN ABSTRACT OF THE THESIS OF

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Title: FOOD SELECTION AND JUVENILE SURVIVAL IN NUTTALL'S COTTONTAILS IN CENTRAL OREGON

Abstract approved: Signature redacted for privacy.

B. J. Verts

A population of Nuttall's cottontails (*Sylvilagus nuttallii*) in Deschutes County, Oregon, decreased fromm 166 individuals in August 1978 to 76 individuals in August 1979. Survival rates of four annual litter groups in 1978 were 0.74, 0.35, 0.72, and 0.93; survival rates for the same litter groups, respectively, in 1979 were 0.12, 0.28, 0.07, and 0.18. Population density and juvenile survival decreased between the 2 years possibly because of alterations in forage quality and quantity caused by precipitation. Numbers of cottontails on the study area on 30 August were related significantly ($P < 0.01$) to initial breeding density and to precipitation falling during the breeding season (February - July). Survival in juvenile cottontails from birth to 30 August was related significantly to precipitation in the first ($P < 0.05$), third ($P < 0.01$), and fourth ($P < 0.01$) annual litter groups. Vegetative abundance at the end of the growing season (September) decreased by approximately 30% between the 2 years; the decline corresponded with a 45% decrease in crop-year (September - June) precipitation. Succulence of grasses, forbs, and shrubs was greatest in spring, declined in summer, and increased slightly in late summer.

Forbs consistently were the most succulent group, except in September when shrubs were most succulent. Grasses exhibited the greatest variation in succulence in response to precipitation; shrubs exhibited the least. A moisture availability index (MAI) indicated that, despite approximately equal estimates of succulence between the 2 years, moisture was more available to cottontails in 1978 because of greater abundance of vegetation. Cottontails seemingly selected forage groups in relation to their relative succulence, within limits. Shrubs were avoided, and succulent juniper (*Juniperus occidentalis*) foliage was eaten only in dry periods, possibly because of low tolerance in cottontails to plant secondary compounds, particularly terpenoids. Juveniles selected forbs in significantly ($P < 0.05$) greater proportions than adults, possibly to aquire additional moisture for growth; diets of younger (<600 g) and older (>600 g) juveniles did not differ. Breeding females selected forbs in significantly ($P < 0.05$) greater proportions than males, possibly because of moisture demands associated with reproduction and lactation. Other nutrients, especially protein, that are associated with moisture content of plants, possibly were as important as moisture in determining food habits and population fluctuations in Nuttall's cottontails in central Oregon. The relationship between juvenile survival and precipitation possibly was caused by genotypic variation in efficiency in cottontails to utilize moisture and nutrients.

Food Selection and Juvenile Survival in
Nuttall's Cottontails in Central Oregon

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FOOD SELECTION AND JUVENILE SURVIVAL IN NUTTALL'S COTTONTAILS IN CENTRAL OREGON

Nuttall's cottontail, *Sylvilagus nuttallii* (Bachman), inhabits semiarid rangelands throughout the western United States (Hall, 1981); its range in Oregon is restricted to the Upper Sonoran Life Zone and portions of the Transition Life Zone east of the Cascade Mountains (Bailey, 1936). McKay and Verts (1978*a*) suggested that extremes in temperature and precipitation characteristic of such semiarid regions possibly were responsible for annual fluctuations in density of Nuttall's cottontail populations in central Oregon. Annual and seasonal variation in survival among juvenile cottontails seemed to be the proximate factor altering cottontail densities (McKay and Verts, 1978*a*).

Juvenile and reproductive female mammals require more water than other members of the population to meet the demands of growth and lactation (Maynard et al., 1979). Richards (1979) reported higher rates of metabolism of water in juvenile and lactating female European rabbits (*Oryctolagus cuniculus*) than in adults and reproductive males, respectively, in the wild in Australia. Because herbivorous mammals living in semiarid environments depend on vegetation as their primary source of water (Bailey, 1923), the availability of highly-succulent forage seems essential for growth and lactation in these species.

In many instances, herbivores consumed more succulent vegetation during drought than at other times (Vorhies and Taylor, 1933, 1940; Riegel, 1940; Vorhies, 1945; Fitch, 1947; Taylor, 1968; Turkowski, 1975; deCalesta, 1979; Newsome, 1980). Radwan and Crouch (1974) reported that black-tailed deer (*Odocoileus hemionus*) consumed forage species in relation to the moisture contained therein. In instances when age- and sex-specific feeding strategies were examined, juveniles (Clark, 1980) and females (Clark, 1980; Newman, 1980) consumed higher-quality forage than other members of the population. Despite changes in foods eaten, the quality of available forage often was not adequate to maintain populations of herivores feeding thereon (Sinclair, 1974; Nagy et al., 1976; Westoby, 1980). Maternal condition of herbiovres during pregnancy and lactation was related to postpartum survival of juveniles (Myers, 1963; Newsome, 1965; Murphy and Coates, 1966; Short et al., 1969; Weege, 1975; Thorne et al., 1976; Richards, 1979; Wood, 1980). Much of the mortality of juvenile Nuttall's cottontails occurred between the times of parturition and weaning (Skalski, 1977), a pattern observed in other species of mammals (Myers, 1963; Rusch and Reeder, 1978). Also, young cottontails required highly-succulent plants in vigorous growth stages to survive when they became independent (Bailey, 1969; Snyder et al., 1976). Thus the quality of forage available to females during pregnancy and lactation, and the quality of forage available to juveniles during the first few weeks after weaning possibly were factors that variable precipitation altered significantly.

Precipitation was implicated in the regulation of populations of rodents (Vorhies and Taylor, 1933; Gomez, 1960; Lee, 1963; Chew and Butterworth, 1964), ungulates (Taylor, 1968; Anthony, 1976; Sinclair, 1977; Smith and LeCount, 1979), macropods (Newsome, 1965), and leporids (Vorhies and Taylor, 1940; Myers and Parker, 1975) living in semiarid environments. In all these instances, precipitation seemingly acted through the food source by altering the quality and quantity of vegetation. However, only Newsome (1965) and Smith and LeCount (1979) examined relationships between survival of juveniles and precipitation.

Many investigators reported direct relationships between production of forage and precipitation (Sneva and Hyder, 1962; Currie and Peterson, 1966; Beatley, 1969, 1976; Cable 1975; Phillipson, 1975; Smith and LeCount, 1979) and relationships between succulence of forage and precipitation (Nagy et al., 1976; Richards, 1979) on semiarid rangelands. Survival of juvenile cottontails possibly varies with precipitation because of the influence of precipitation has on the availability and succulence of forage for juveniles and their mothers. To offset the effects of drought, Nuttall's cottontails, especially juveniles and lactating females under greater moisture stress than other members of the population, possibly become more selective of forage that retains relatively high amounts of moisture. Thus, food habits of Nuttall's cottontails might be expected to differ by sex, age, reproductive condition, and season, that, in turn, might reflect water demands of cottontails, and availability of succulent forage.

OBJECTIVES

The purpose of this research was to determine if precipitation acted through the food source to regulate survival of juvenile Nuttall's cottontails and if cottontails changed food habits in relation to their need for high-moisture-content forage. Specific objectives were:

1. To determine if survival rates of juvenile Nuttall's cottontails were related to precipitation.
2. To determine if composition of diets differed between age- and sex-classes of Nuttall's cottontails.
3. To determine if food items of Nuttall's cottontails differed seasonally.
4. To determine if food items of Nuttall's cottontails were selected in relation to their potential to contribute to the need for water of the cottontail feeding thereon.

THE STUDY AREA

The study was conducted on an 87-ha tract located approximately 4.8 km W of Terrebonne, Deschutes County, Oregon (44°21' N, 121°14' W), and administered by the U.S. Bureau of Land Management. Elevation of the study area ranged between 835 - 842 m (McKay and Verts, 1978*b*).

The study area was located within the Upper Sonoran Life Zone (Bailey, 1936) and the vegetation (Table A, Appendix) resembled the *Juniperus occidentalis / Artemisia tridentata - Purshia tridentata* association of the *Juniperus occidentalis* Zone of central Oregon (Franklin and Dryness, 1973). McKay and Verts (1978*b*) recognized three habitat types based on topographic, edaphic, and vegetative characteristics. Basically, their habitat type 1 consisted of flat sandy plains characterized by low vegetative diversity, habitat type 3 consisted of numerous flattened lava hummocks with shallow, stoney soils and high vegetative diversity, and habitat type 2 was intermediate between types 1 and 3 in vegetative and topographic attributes.

The climate of the area was semiarid; mean annual precipitation was approximately 22.9 cm, approximately one-third of which fell during the cottontail breeding season (February - July) (U. S. Department of Commerce, 1972 - 1976, 1978, 1979).

METHODS AND MATERIALS

Unbaited cedar box traps measuring 15 x 18.7 x 58 cm were set in a 9- x 13-trap grid with approximately 90 m between traps. The traps were operated for periods of 3 consecutive days weekly from 9 - 25 July and daily from 1 - 30 August 1978. In 1979, traps were operated for 3 consecutive days in alternate weeks from 14 April - 29 June, 3 consecutive days weekly from 1 - 26 July, and daily from 1 - 30 August. Traps were examined from 0730 - 1100h on days of operation.

Livetrapped cottontails were weighed to the nearest 0.1 g and the sex of each cotontail was determined by examination of external genitalia (Petrides, 1951). Juvenile cottontails were assigned to litter groups on the basis of weight at first capture (McKay and Verts, 1978*a*)(Figs. 1 and 2). Cottontails captured more than once in a 7-day period were weighed only at first capture of that period. A numbered aluminum ear tag (National Band and Tag Co., Newport, KY) was placed in each ear of each cottontail captured. All cottontails were released at point of capture.

Cottontails were collected by shooting at approximately monthly intervals during the periods of livetrapping and in September, during periods of not more than 3 days in habitats similar to, but not within 0.5 km of, the study area. Cottontails were weighed, and their sex and age were determined. Juveniles were distinguished from adults on the basis of reproductive condition and degree of closure of epiphyseal cartilages (Hale, 1949). Stomachs were removed and were stored in a solution of 10% formalin until prepared for analysis.

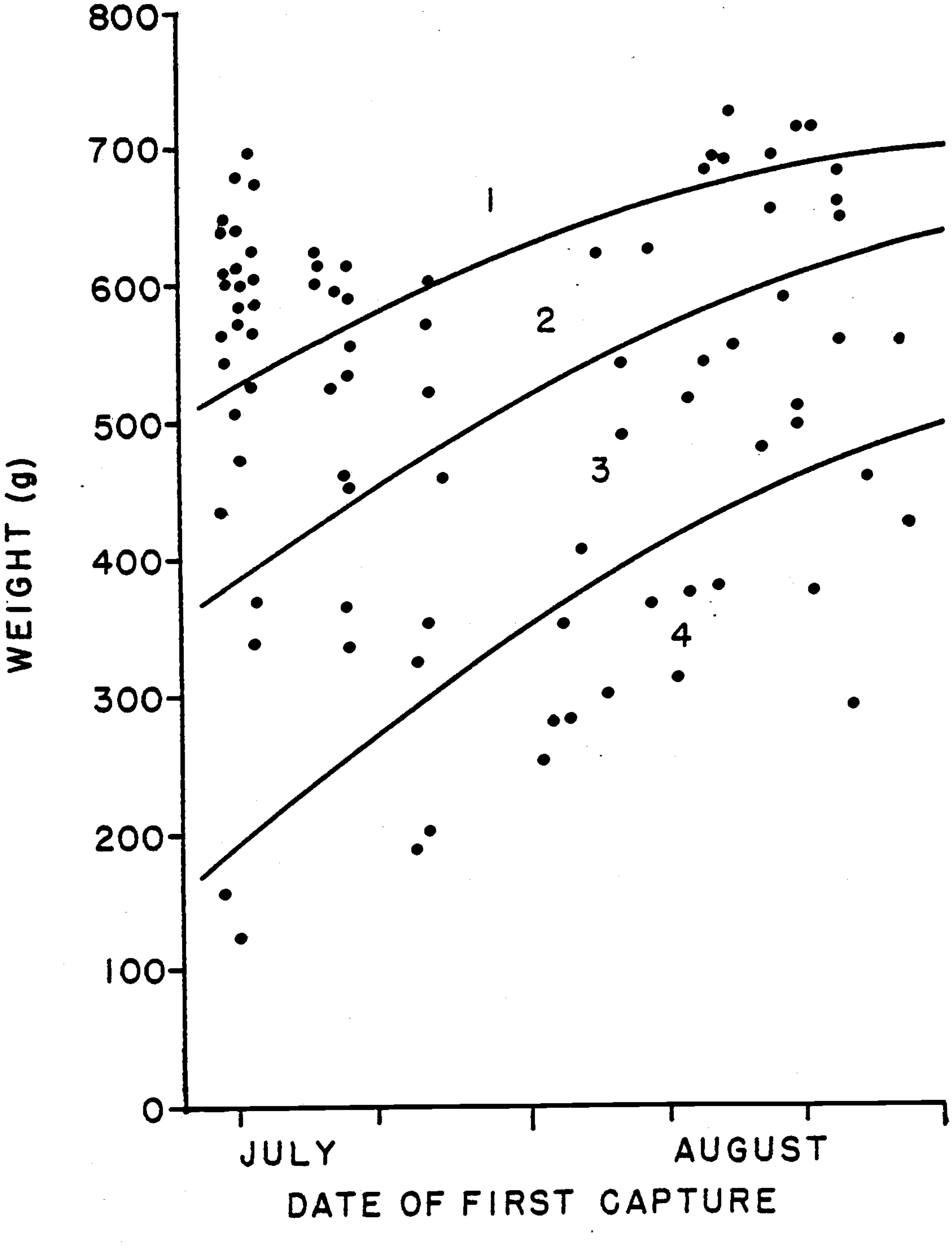

Figure 1. Designation of litter groups based on weight at first capture of juvenile Nuttall's cottontails, Deschutes County, Oregon, 1978.

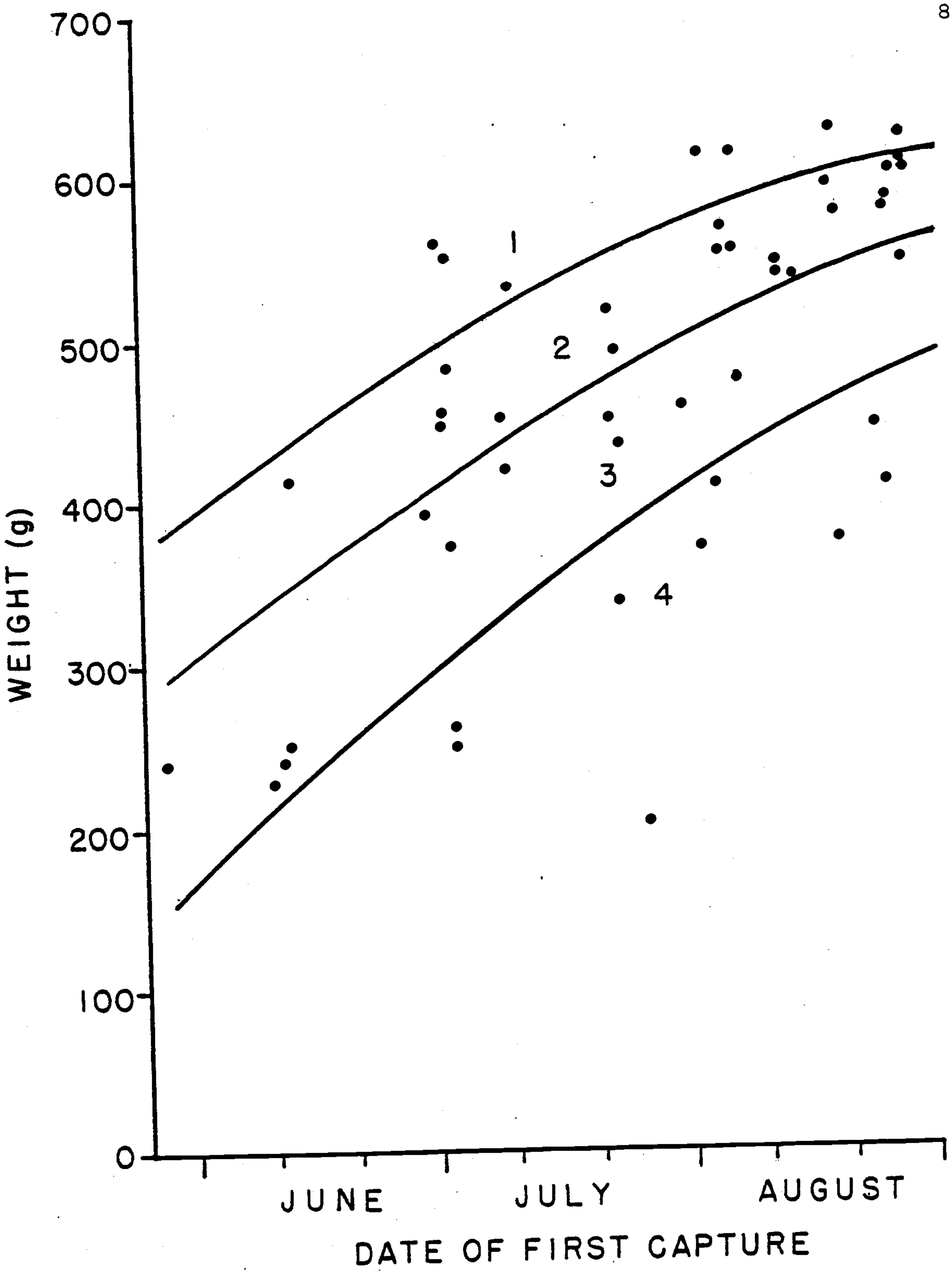

Figure 2. Designation of litter groups based on weight at first capture of juvenile Nuttall's cottontails, Deschutes County, Oregon, 1979.

The numbers of cottontails produced in each of the four annual litter groups were estimated with the equation:

$$N_i = (F_i)\ (L_i)$$

where N_i = estimated number born in litter group i,

F_i = estimated number of breeding females in the population on the estimated date of birth (Powers and Verts, 1971) of litter group i,

L_i = estimated mean litter size of litter group i (Powers and Verts, 1971).

The number of breeding females on the study area was estimated with the equation:

$$F_i = \frac{(P)\ (A)}{R^{X_i}}$$

where P = proportion of adults trapped in August that were female,

A = estimated number of adults on the study area on 30 August,

R = monthly survival rate for adults (0.92, Skalski, 1977),

X_i = number of months between the estimated birth date of litter group i and 30 August.

Skalski's estimate of adult survival was used in lieu of the rate I calculated because I believed insufficient numbers of cottontails were captured during my study to produce reliable estimates of breeding density or survival rates of adults.

The density of cottontails on the study area on 30 August was estimated with a frequency-of-capture estimator (Edwards and Eberhardt,

1967) based on captures during 1 - 30 August. Numbers of adults on the study area on 30 August (A) was estimated by multiplying the estimate of cottontail density by the percentage of cottontails captured in August that were adults. The survival rate from birth to 30 August of litter group i (S_i) was estimated with the equation:

$$S_i = \frac{(J_i)\ (A)}{N_i}$$

where J_i = proportion of cottontails captured in August that were assigned to litter group i.

Arcsine transformations of estimates of survival rates were used in statistical analyses to satisfy the assumption of normality required for application of parametric statistical tests (Zar, 1974).

The relationship between survival rates of litter groups from this and other studies of Nuttall's cottontails in central Oregon (McKay and Verts, 1978*a*; Skalski and Verts, 1981; R. Deering, in litt.) and amounts of precipitation falling during certain critical periods was analysed by curivilinear regression. I chose as the critical period for each litter group the 40 days before and 60 days after the estimated date of conception for that litter group (Powers and Verts, 1971) (Table 1). I believed the designation of critical periods was broad enough to account for the effects of precipitation on all juveniles produced in each litter despite variation in dates of conception reported for this species (Powers and Verts, 1971; McKay and Verts, 1978*a*). The general regression model,

Table 1. Median dates of conception (Powers and Verts, 1971) and critical periods for the four annual litter groups produced by Nuttall's cottontails, Deschutes County, Oregon.

Litter group	Median date of conception	Critical period
1	5 March	24 January - 4 May
2	1 April	20 February - 31 May
3	28 April	19 March - 27 June
4	25 May	15 April - 24 July

$$Y = 90(1-e^{a+bX}),$$

a curvilinear function asymptotic to the ordinate and to Y = arcsin S = 90 (S = 1.00), was chosen rather than a linear model because I believed the curvilinear model more nearly represented the actual relationship between survival and precipitation and could serve as a predictive tool.

Stomach contents were dried in an oven at 55° C and ground over a 20-mesh screen in a micro-Wiley mill. The contents were soaked in a 0.1 - 0.5 M solution of NaOH for approximately 1 h (Vavra and Holochek, 1980) and rinsed with tap water over a 100 mesh screen. The rinsed material was mixed in a blender at high speed for 2 min with enough water to cover the blender blades. After mixing, the contents were rinsed again and a small portion (approximately 3 cc) was placed on a microscope slide. The sample was fixed over a flame with Hertwig's solution and a cover slip was mounted with Hoyer's solution (Hansen, 1971). Two slides were prepared from the contents in each stomach, oven-dried for 3 days at 55° C, and the better of each pair, in terms of distribution and density of particles (Hansen, 1971), was selected for analysis.

Twenty randomly-located fields were examined at 100x on each slide displaying stomach contents, and plant epidermal fragments located within each field were identified. The frequency of occurence of each identified taxon was converted to relative density (Sparks and Malechek, 1968).

Known plants from the study area were mounted on microscope slides in the same mammer as stomach contents. Epidermal fragments of known plants were photographed at 100x and 430x and the photomicrographs were used for comparison with unknown material in stomach contents. An additional collection of reference slides that contained plants in different phenological stages than those in the original collection was obtained from M. Vavra, Eastern Oregon Agricultural Research Center, Union, OR.

A forage ratio (Hess and Rainwater, 1939), often referred to as a relative preference index (Turkowski, 1975), was computed for each identified taxon and each major forage group (grasses, forbs, shrubs, juniper) in the stomach contents of each cottontail. The forage ratio was computed with the equation:

$$FR_i = \frac{RPD_i}{RPC_i}$$

where FR_i = forage ratio for plant taxon or forage group i exhibited by a cottontail,

RPD_i = relative percent density of plant taxon or forage group i in the stomach contents as estimated with the microtechnique,

RPC_i = relative percent coverage of plant taxon or forage group i on the study area corresponding to the period in which the cottontail was collected.

Mean forage ratios were computed for groups of cottontails classified by age, sex, and season of collection, and means of appropriate groups were tested for differences in dietary selection. A Mann-Whitney U test (Zar, 1974) was used to judge statistical significance; the P = 0.05 level was accepted as signigicant.

Vegetation on the study area was sampled to estimate succulence and availability of forage during periods of cottontail collections; succulence was estimated on days of collection of cottontails and availability was estimated during a 2- or 3-day period following collections. Fifty randomly-located 1-m^2 plots were established in each habitat type in July 1978; 100 plots per habitat type were sampled in September 1978 and subsequently to reduce sampling error. Percentages of plots covered by aerial portions of each plant taxon were estimated visually and converted to cover-class categories (Daubenmire, 1959). Percent ground cover of each plant taxon in each habitat type was calculated by a CDC CYBER 170/720 computer with program COVR2 (R. H. Sauer, in litt.), a modification of program COVER (Sauer and Owzarski, 1979). Percent ground cover of each taxon on the study area was extrapolated by computing the mean coverage for the three habitat types weighted by their respective areas (McKay and Verts, 1978*b*).

Succulence of forage was expressed as the percentage of weight of living aerial portions of a plant attributable to moisture. Only growth of the current season was sampled for shrubs except in March 1979 when shrubs were dormant; buds and tips of twigs were sampled in that month. Succulence was estimated by weighing at least 100 g of freshly-collected material of a species to the nearest 0.01 g with a Mettler P120 analytic balance, drying it, and reweighing it. The difference in weights was assumed to the weight of moisture contained in the tissues of the plant. In 1978, plants were air-dried at ambient temperature but were subject to molding; therefore, in 1979, plants were oven-dried at approximately 60° C for 48 h.

Seasonal trends in availability of moisture to cottontails were represented by a moisture availability index (MAI). Estimated succulence of each major forage group, except juniper, determined by sampling representative species of each class and obtaining a mean, was multiplied by the availability of that class and the products were summed.

Scientific nomenclature of vascular plants followed Hitchcock and Cronquist (1973).

Climatological data were obtained from records of the Redmond 2W weather station, 11.3 km SSW of the study area (U. S. Department of Commerce, 1972 - 1976, 1978, 1979).

RESULTS AND DISCUSSION

The estimated number of cottontails on the study area on 30 August 1978 was 166; an estimated 76 cottontails were present on the same date in 1979. The decrease in numbers of cottontails between the 2 years corresponded with a 52% decrease in precipitation during the breeding season. Multiple regression analysis indicated that frequency-of-capture estimates of density on 30 August 1972 - 1976 (McKay and Verts, 1978*a*; Skalski and Verts, 1981; R. Deering, in litt.) and 1978 - 1979 were related significantly to initial breeding density and to precipitation falling during the breeding season ($R^2 = 0.93$, $P < 0.01$) (Table B, Appendix).

Juvenile Survival

The decrease in cottontail density from August 1978 to August 1979, despite an increase in production of juveniles (Table 2), likely was related to differential survival of juveniles between the 2 years (Table 2). Those litter groups born in 1978 exhibited relatively high survival but those born in 1979 survived poorly. Regression analysis of estimates of survival rates of juveniles demonstrated a relationship between survival and precipitation. Significant amounts of variation in litter-specific survival rates were explained by precipitation during the critical periods for three of the four annual litter groups (Fig. 3). The second litter group exhibited no significant relationship; however, the presence of one extreme observation was responsible for much of the variation in the dependent variable. No errors in estimation of the outlier were evident; thus, no

Table 2. Estimated breeding density, natality, numbers of juveniles alive in August, and survival rates for each annual litter group produced by Nuttall's cottontails, Deschutes County, Oregon, 1978 - 1979.

Year	Litter group	Breeding density	Number young produced	Number young alive in August	Survival rate
1978	1	29.7	59.4	43.9	0.74
1978	2	27.3	69.7	24.4	0.35
1978	3	25.1	57.8	41.6	0.72
1978	4	23.1	39.3	36.7	0.93
1979	1	42.3	84.6	10.0	0.12
1979	2	38.9	99.3	27.8	0.28
1979	3	35.8	82.4	5.9	0.07
1979	4	33.0	56.0	9.8	0.18

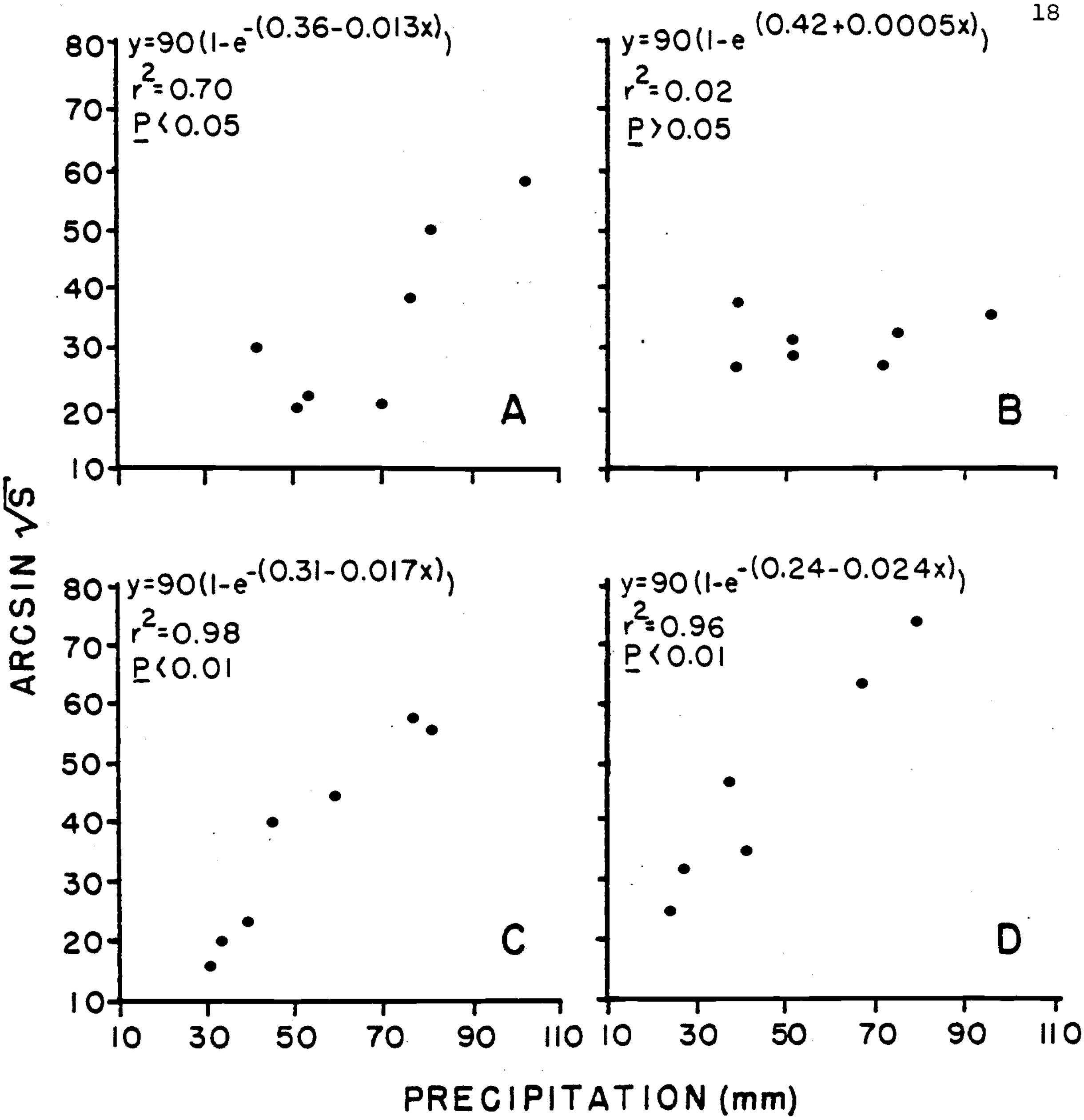

Figure 3. Relationships between survival (S) of juvenile Nuttall's cottontails from birth to 30 August, 1972 - 1976, 1978, 1979, and precipitation during the critical period from 40 days before to 60 days after estimated date of conception for the first (A), second (B), third (C), and fourth (D) annual litters, Deschutes County, Oregon. A fourth litter was not produced in 1973.

statistically valid reason for removing the point from analysis existed (Neter and Wasserman, 1974). However, few data were used in the analysis of each litter group and the presence of one outlier resulted in a disproportionate reduction in the coefficient of determination (r^2). When the outlier was removed from analysis the coefficient of determination approached significance ($r^2 = 0.55$) despite a 20% reduction in degrees of freedom. It was possible that the outlier, or all second litter groups, was influenced disproportionately by one or more additional variables known to influence reproduction and survival in snowshoe hares (*Lepus Americanus*), such as cloud cover and mean maximum temperature (Meslow and Kieth, 1971).

Vegetative Cover and Succulence

Estimated abundance of forage was greater in 1978 than in 1979 (Table 3). At the end of the growing season (September) in 1978 an estimated 28.6% of the study area was vegetated compared with 19.9% in September 1979. The decrease in forage abundance corresponded with a 45.8% decrease in crop-year (September - June) precipitation. These results corresponded well with the results of Sneva and Hyder (1962), who reported a high correlation ($r = 0.98$) between forage production in a vegetative association similar to that found on the study area and crop-year precipitation.

Vegetative abundance in 1979 peaked in May and decreased steadily thereafter (Table 3). Abundance of vegetation decreased in a similar manner from July to September in 1978. Grasses were more abundant in May 1979 than in any other month of the growing season; forbs were

Table 3. Estimates of percent cover of forage species, Deschutes County, Oregon, 1978 - 1979.

	Month of collection						
	Late				Early	Late	
Forage group	Jul 78	Sep 78	Mar 79	May 79	Jul 79	Jul 79	Sep 79
Grasses	9.35	10.55	6.28	10.46	7.35	5.41	5.29
Forbs	3.16	1.16	0.27	0.84	0.11	0.02	0.03
Shrubs	7.80	7.38	5.78	5.13	5.79	5.60	5.96
Juniper	3.44	6.93	5.95	8.65	8.20	5.88	5.07
Moss			3.54[a]				
TOTAL	27.29	28.55	21.81	29.05	26.82	21.66	19.91

a) This was the only sampling period in which moss was not dormant, and live portions of plants were distinguishable from dead portions. This estimate was used in calculating total cover in all months.

most abundant in June 1979. The decrease in abundance of grasses after May 1979 was related mainly to the senescence of cheatgrass (*Bromus tectorum*). The decline corresponded with the beginning of a period in which little precipitation fell (Fig. 4). Julander (1945) found that *Bromus rubens*, a species closely related to cheatgrass, was intolerant to prolonged drought or heat stress. Thus, a major component of the vegetation on the study area (Table C, Appendix) became unavailable to cottontails in search of succulent vegetation at a time of moisture stress. Much of the cheatgrass eaten during dry periods was seeds (45% in July 1979). Cheatgrass, and bluebunch wheatgrass (*Agropyron spicatum*), germinated in September and cottontails utilized the new growth (Fig. 5).

Abundance of forbs decreased between July and September of both years (Table 3). The decrease was a result of maturation and senescence of most herbaceous vegetation. Estimates of abundance of forbs in July and September 1978 were greater than estimates for the same months in 1979.

Estimates of succulence for all forage groups exhibited similar temporal fluctuations throughout the 1979 sampling season (Fig. 4). Estimates of succulence of shrubs varied least throughout the sampling period; succulence of grasses varied the most. Forbs consistently were the most succulent group throughout the summer except in September when shrubs were most succulent. Succulence of grasses was slightly less than that of forbs in spring but declined sharply in summer. Temporal variation in succulence of the three groups corresponded with the seasonal distribution of precipitation (Fig. 4).

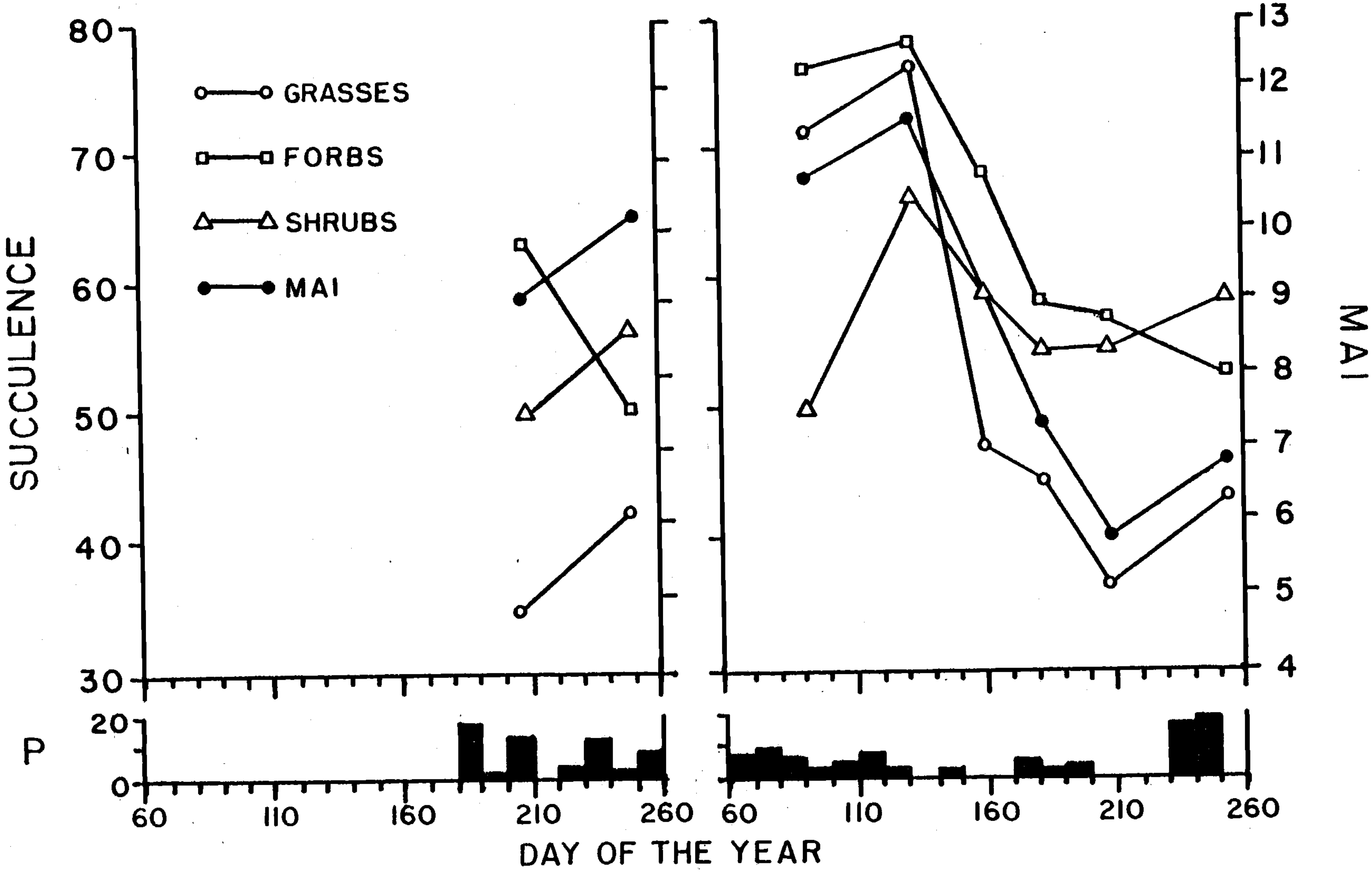

Figure 4. Seasonal trends in succulence of forage groups, excluding juniper, moisture availability index (MAI), and precipitation falling during 10-day intervals, Deschutes County, Oregon.

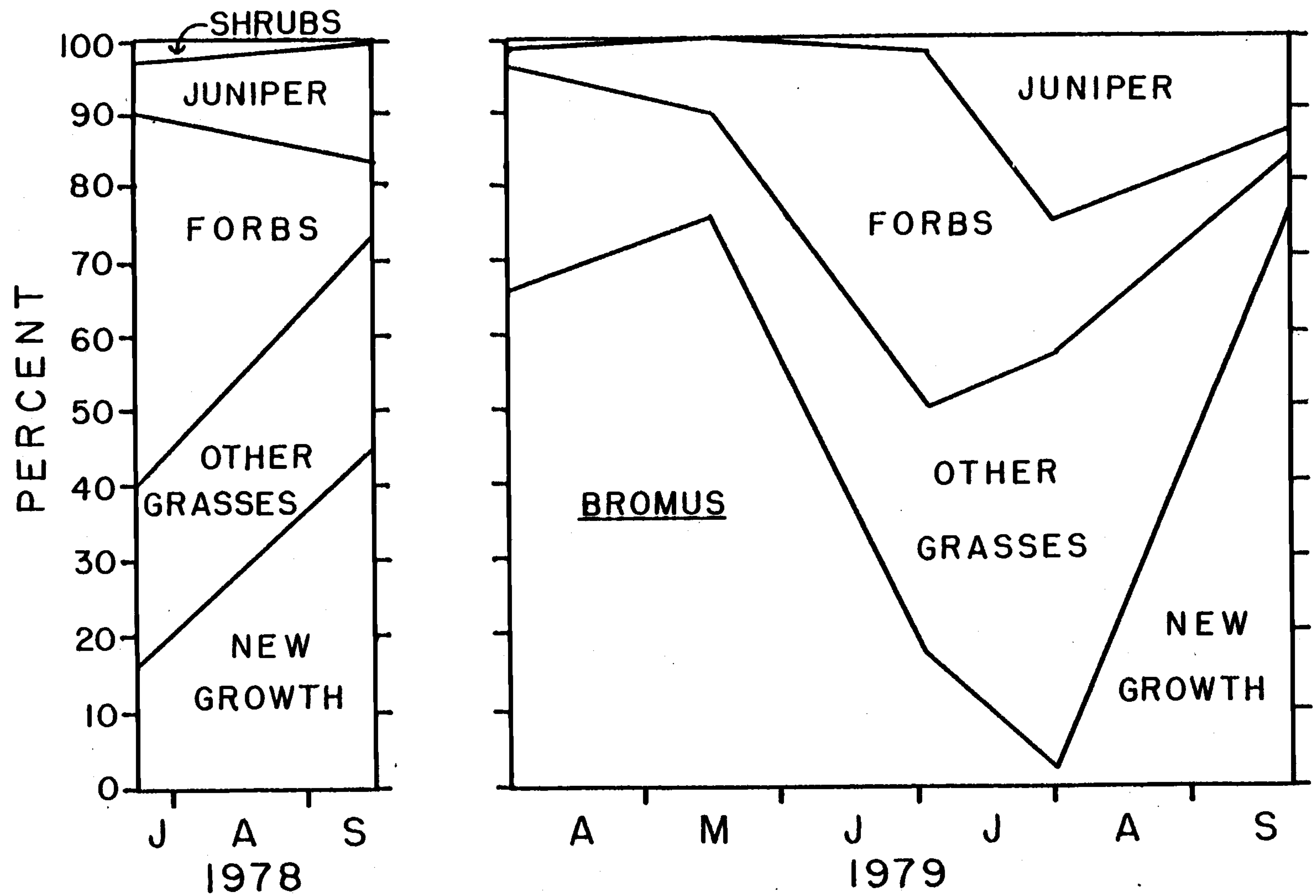

Figure 5. Percent occurence of forage items in diets of Nuttall's cottontails, Deschutes County, Oregon, 1978 and 1979. "New growth" represents seedlings of *Bromus tectorum* and *Agropyron* spp.

Estimates of succulence in 1978 were less than those in 1979 (Fig. 4) because air-drying probably extracted less moisture from plants than oven-drying. However, seasonal trends in succulence between the 2 years were similar (Fig. 4).

The MAI fluctuated in correspondence with seasonal precipitation also (Fig. 4). Depsite the lesser estimates of succulence in 1978, the MAI was considerably greater in that year than in 1979, an indication of the difference in abundance of forage between the 2 years (Table 3). Seemingly, moisture was more available to cottontails in 1978 than in 1979. However, the values of MAI possibly were subject to bias caused by extreme values of succulence and availability. A high value for MAI, caused by an extremely abundant but dry plant, would be misleading if cottontails could not obtain sufficient moisture per meal because of limitations of stomach volume. However, such extreme values of abundance and succulence did not exist in this study.

Food Selection

Twenty-four plant taxa were identified in 43 stomachs of cottontails. The most commonly eaten species was cheatgrass; it occurred in 93% of all stomachs examined. Other frequently found grasses were wheatgrass (*Agropyron* spp.)(72% of all stomachs examined), bottlebrush squirreltail (*Sitanion hystrix*)(63%), and Thurber's needlegrass (*Stipa thurberiana*)(51%). Frequently-eaten forbs were mentzelia (*Mentzelia albicaulis*)(23%), hoary false-yarrow (*Chaenectis douglasii*)(21%), and monkey-flower (*Mimulus nanus*)(16%). Shrubs were uncommon in the diets and occurred in stomachs during 1978 only. The most frequently eaten shrub was rabbitbrush (*Chrysothamnus* spp.)(12%).

Juniper berries and foliage were common items in the diets; these items were found in 53% of all stomachs examined. At least one cottontail had fragments of juniper in its stomach in every month except May 1979. All eight genera of grasses found on the study area were represented in the diets, as were the three genera of shrubs. Of the 17 species of forbs contained in the reference collection, 11 were identified in stomach contents.

Grasses comprised the bulk of individual diets in most months (Fig. 5). In July of both years the quantity of forbs eaten approached or exceeded the quantity of grasses. Juniper was eaten most often in late summer.

In general, grasses and frobs were eaten in greater proportion than a random foraging pattern would have produced, and shrubs and juniper were eaten less often (Table 4). However, the forage ratios for juniper may not have indicated the actual response of cottontails to availability of juniper foliage. Actual availability of juniper was a function of the accessibility and abundance of foliage as determined by behavioral and physical limitations of cottontails (Nudds, 1980). Only those trees with boles easily climbed by cottontails or with foliage within reach of the ground were accessible. Conversely, juniper berries, after they fell to the ground, were available to cottontails despite the growth form of the tree.

One cottontail selected forbs to a much greater degree (forage ratio = 73) than other members of the population (Table D, Appendix); this extreme selection of forbs was not characteristic of the population ($P < 0.001$, Dixon's test for extreme observations, Dixon and

Table 4. Mean forage ratios exhibited by Nuttall's cottontails for plant species, Deschutes County, Oregon, 1978 - 1979.

	Month of collection						
	Late				Early	Late	
Species	Jul 78	Sep 78	Mar 79	May 79	Jul 79	Jul 79	Sep 79
Bromus tectorum	0.7	1.0[a]	2.9	2.5	1.0	0.2	4.6[a]
Agropyron spp.	8.0	–[a]	22.0	1.9	314.2	57.8	–[a]
Festuca idahoensis	0	0	+[b]	1.5	+	7.3	0
Koeleria cristata	+			+	+	+	
Oryzopsis hymenoides	+	34.4	0	+	+		0
Poa spp.	0	0	0	0	0.4	0	0
Sitanion hystrix	1.9	3.7	1.0	2.8	2.0	0.6	0.5
Stipa thurberiana	0.9	0.6		0.9	0.5	0.7	0.1
TOTAL GRASSES	1.2	2.2	3.4	2.5	1.8	2.2	3.1
Achillea millefolium	+				0	0	0
Chaenectis douglasii	+		+	5.3	1.2	0	0
Descurainia pinnata	+				75.5	58.3	
Eriophyllum lanatum	0	+		0	3.5	0	
Eriastrum sparsiflorum	0	0			26.0	0.6	
Gayophytum decipiens	5.4	0		0	0		0
Mentzelia albicaulis	+		+	+	6.8	0	
Mimulus nanus	13.2	0		0	4.3	0	
Penstemon spp.	0			0	+	+	
Phacelia spp.	+				1.7	+	+

Table 4 (cont'd.).

Species	Late Jul 78	Sep 78	Mar 79	May 79	Early Jul 79	Late Jul 79	Sep 79
Tragopogon dubius					+		
TOTAL FORBS	4.0	2.7	2.4	2.8	6.7	3.3	11.9
Artemisia tridentata	0.1	0.1	0	0	0	0	0
Chrysothamnus	0	0.4	0	0	0	0	0
Purshia tridentata	0	0	0	0	0	0	0
TOTAL SHRUBS	0.1	0.3	0	0	0	0	0
Juniperus occidentalis	0.4	0.4	0.1	0	0.5	0.1	0.1

a) Seedlings of *B. tectorum* and *Agropyron* spp. were not distinguishable in stomachs or on the study area, and were combined.

b) A "+" indicates that a plant was eaten but was not recorded as occurring on the study area during that sampling period.

Massey, 1969). Subsequent analyses of diet selection were conducted with and without data from this individual, and outcomes of tests of significance were not affected. However, I believed mean forage ratios computed without these data represented the responses of the population better than those that included the data. Therefore, statistical analyses of diet selection that did not include the extreme observation were reported (Tables 5 and 6).

Cottontails collected in 1978 selected shrubs more often than those collected in the same months in 1979 (Table 5); no other differences in diet selection existed between the 2 years. Cottontails collected in early (March, April, and May) 1979 selected grasses more often than those collected in late (July and September) 1979 and the opposite was true for forbs and juniper (Table 5). Those differences probably represented shifts in the diets from maturing and drying grasses to succulent forbs and juniper. Although these data seemed to indicate a seasonal trend in food selection, the samples of cottontails used in analysis were characterized by different age and sex ratios (Table D, Appendix); therefore, I could not attribute the observed differences solely to seasonal trends.

Forage ratios of older juveniles (those weighing more than 600 g) were not significantly different than those of younger juveniles (weighing less than 600 g)(Table 6), possibly because growth rates of older juveniles had not decreased sufficiently to cause a change in diet. Growth rates of sub-adult European rabbits were 80% of those of juveniles (Wood, 1980), and water turnover rates did not differ between the two age classes (Richards, 1979). Juveniles (of all

Table 5. Mean forage ratios (±SE) exhibited by Nuttall's cottontails for forage groups Deschutes County, Oregon, between late (July and September) 1978 and late 1979, and between early (March, April, and May) 1979 and late 1979.

Season/ Test statisitic	Sample size	Forage group			
		Grass	Forb	Shrub	Juniper
Late 1978	12	1.7±0.2	3.5±0.8	0.2±0.1	0.4±0.2
Late 1979	19	2.2±0.2	5.1±0.8	0.0	0.4±0.1
U		70.0	81.0	210.0[c]	109.0
Early 1979	11	2.9±0.2	1.7±0.6	0.0	0.0
Late 1979	19	2.2±0.2	5.1±0.8	0.0	0.4±0.1
U		145.0[a]	42.0[b]	104.5	22.0[c]

a) $P < 0.05$

b) $P < 0.005$

c) $P < 0.001$

Table 6. Mean forage ratios (±SE) exhibited by Nuttall's cottontails classified by sex and age for forage groups, near Terrebonne, Deschutes County, Oregon, 1978 - 1979.

Classification/ Test Statistic	Sample size	Forage group			
		Grass	Forb	Shrub	Juniper
Juveniles 600 g	8	1.9±0.4	5.5±1.2	0.0	0.4±0.2
Juveniles 600 g	12	2.0±0.3	5.3±1.1	0.0	0.4±0.1
U		44.0	50.5	60.5	59.0
Adults[a]	11	2.2±0.2	2.8±0.7	0.2±0.1	0.3±0.1
Juveniles	20	2.0±0.2	5.4±0.8	0.0	0.4±0.1
U		124.0	61.0[b]	140.5	115.5
Breeding females	11	2.4±0.2	3.1±0.6	0.0	0.2±0.2
Breeding males	7	2.7±0.3	1.7±1.0	0.1±0.1	0.1±0.1
U		51.0	18.5[b]	41.0	34.5

a) Only adults collected in samples containing juveniles were included.

b) $P < 0.05$

weights) selected forbs significantly more often than adults, whereas selection of grasses, shrubs, and juniper did not differ significantly between the two age classes (Table 6). Selection of food by juveniles seemed to be related to the moisture content of the food; forbs, highly-succulent (Fig. 4), were selected.

Breeding (pregnant or lactating) female cottontails selected forbs more often than adult males (Table 6). Again, selection seemed related to succulence of forage. Newsome (1980) attributed greater selection of forbs by female red kangaroos (*Megaleia rufa*) to the increased demands of reproduction.

Although moisture content of forage possibly was an important factor influencing food selection by cottontails, concentrations of other nutrients possibly influenced selection also. Hickman (1975) reported direct relationships between moisture content of forage and concentrations of protein, calcium, and phosphorus; as forage matured and dried in summer, concentrations of these nutrients decreased. Based on data reported by Hickman (1975) and on nutrient requirements of domestic rabbits (National Research Council, 1977), grass could not meet protein or calcium requirements of rabbits after midsummer, and concentrations of phosphorus in grasses and shrubs were not adequate for pregnant or lactating females. Of all these nutrients, nitrogen possibly was primarily responsible for limiting the abundance of cottontails (White, 1978; Mattson, 1980).

To some extent, trends in food selection indicated that cottontails selected the most succulent and nutritious foods of those available. Early phenological stages of grasses were selected in spring and fall, and as grasses matured in summer, forbs, with higher concentrations of protein (Bailey, 1969; Hickman, 1975) and water (Fig. 4) were selected. Forbs were the least abundant of all forage types, and as availability of forbs decreased in summer, cottontails probably were forced to include other items in their diets despite the lower amounts of water and protein accrued by eating those items. Juniper was included in the diets when other forages were dried, presumably because of moisture it retained. Juniper contained high concentrations of terpenoids (Schwartz et al., 1980), which rendered forages unpalatible and undigestible to herbivores (Schwartz et al., 1980; Farentinos et al., 1981). Shrubs contained more protein than juniper on ranges in Colorado (Dietz et al., 1962) but shrubs were avoided by Nuttall's cottontails, possibly because of high concentrations of volatile oils and other secondary compounds therein, reported to be unpalatible to herbivores (Freeland and Janzen, 1974). Possibly, diets in late summer and fall, although not optimal for protein, were optimal for a variety of nutrients (Westoby, 1974, 1978) and water that were essential for growth and maintanence.

Because climatic conditions altered abundance and succulence of Nuttall's cottontail forage, the intake of water and, presumably, nutrients probaly was limited, even if food selection was optimal. The lack of nutritious food resulted in increased mortality, primarily among the young because of inadequte nutrient and moisture balance among juveniles and lactating females. Paucity of nutritious foods altered densities of populations of other herbivores, particularly by altered recruitment (Caughley, 1970; Sinclair, 1974; Weege, 1975;

Thorne et al., 1976; Cole and Batzli, 1979).

Annual variation in nutrient and moisture content of forage, dependent on annual precipitation, might explain the density-independent fluctuations reported for Nuttall's cottontails in central Oregon (Skalski and Verts, 1981). This explanation does not conflict with the observations of Skalski and Verts (1981), who reported a relationship between frequencies of occurrence of transferrin genotypes and survival of juvenile cottontails. Sawin and Curran (1952) suggested that mortality in juvenile domestic rabbits was related to genotypic variation. Ealey (1967) observed different rates of water intake by euros (*Macropus robustus*) in arid regions in Australia and believed the variation possibly was caused by behavioral and physiological traits that were subject to selection. Therefore, it was possible that efficiency of utilization of water and nutrients by Nuttall's cottontails was subject to selection and resulted in the relationship I observed between juvenile survival and precipitation.

LITERATURE CITED

Anthony, R. G. 1976. Influence of drought on diets and numbers of desert deer. J. Wildl. Mgmt., 40:140-144.

Bailey, J. A. 1969. Exploratory study of nutrition of young cottontails. J. Wildl. Mgmt., 33:346-353.

Bailey, V. 1923. Sources of water supply for desert animals. Sci. Monthly, 17:66-86.

______. 1936. The mammals and life zones of Oregon. N. Amer. Fauna, 55:1-416.

Beatley, J.C. 1969. Dependence of desert rodents on winter annuals and precipitation. Ecology, 50:721-724.

______. 1976. Rainfall and fluctuating plant populations in relation to distributions and numbers of desert rodents in southern Nevada. Oecologia (Berl.), 24:21-42.

Cable, D. R. 1975. Influence of precipitation on perrenial grass production in the semidesert Southwest. Ecology, 56:981-986.

Caughley, G. 1970. Eruption of ungulate populations, with emphasis on Himalayan thar in New Zealand. Ecology, 51:53-72.

Chew, R. M., and B. B. Butterworth. 1964. Ecology of rodents in Indian Cave (Mohave Desert), Joshua Tree National Monument, California. J. Mamm., 45:203-225.

Clark, D.A. 1980. Age- and sex-dependent foraging strategies of a small mammalian omnivore. J. Anim. Ecol., 49:549-563.

Cole, F. R., and G. O. Batzli. 1979. Nutrition and population dynamics of the prairie vole, *Microtus ochrogaster*, in central Illinois. J. Anim. Ecol., 48:455-470.

Currie, P. O., and G. Peterson. 1966. Using growing-season precipitation to predict crested wheatgrass yields. J. Range Mgmt., 19:284-288.

Daubenmire, R. 1959. A canopy-coverage method of vegetation analysis. Northwest Sci., 33:43-64.

deCalesta, D. 1979. Spring and summer foods of Audubon's cottontail rabbit (*Sylvilagus audubonii*) in north-central Colorado. Southwestern Nat., 24:549-553.

Dietz, D. R., R. H. Udall, and L. E. Yeager. 1962. Chemical composition and digestibility by mule deer of selected forage species, Cache la Poudre range, Colorado. Colorado Dept. Game and Fish Tech. Publ., 14:1-89.

Dixon, W. J., and F. J. Massey. 1969. Introduction to statistical analysis. McGraw-Hill, New York, 638 pp..

Ealey, E. H. M. 1967. Ecology of the euro, *Macropus robustus* (Gould), in north-western Australia. II. Behavior, movements, and drinking patterns. C. S. I. R. O. Wildl. Res., 12:27-51.

Edwards, W. R., and L. Eberhardt. 1967. Estimating cottontail abundance from livetrapping data. J. Wildl. Mgmt., 31:87-96.

Farentinos, R. C., P. J. Capretta, R. E. Kepner, and V. M. Littlefield. 1981. Selective herbivory in tassel-eared squirrels: role of monoterpenes in Ponderosa pines chosen as feeding trees. Science, 213:1273-1275.

Fitch, H. S. 1947. Ecology of a cottontail rabbit population in central California. California Fish and Game, 33:159-184.

Franklin, J. F., and C. T. Dryness. 1973. Natural vegetation of Oregon and Washington. U. S. Dept. Agric. For. Serv. Gen. Tech. Rept. PNW-8, 417pp.

Freeland, W. J., and D. H. Janzen. 1974. Strategies in herbivory by mammals: the role of plant secondary compounds. Amer. Nat., 108:269-289.

Gomez, J. C. 1960. Correlation of a population of roof rats in Venezuela with seasonal changes in habitat. Amer. Midland Nat., 63:177-193.

Hale, J. B. 1949. Aging cottontail rabbits by bone growth. J. Wildl. Mgmt., 13:216-225.

Hall, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 1:1-600 + 90.

Hansen, R. M. 1971. Drawings of tissues found in herbivore diets and in the litter of grasslands. U. S. I. B. P. Grassland Biome Tech. Rept., 70:1-69.

Hess, A. D., and J. H. Rainwater. 1939. A method for measuring the food preference of trout. Copeia, 3:154-157.

Hickman, O. E. 1975. Seasonal trends in the nutritive content of important forage species near Silver Lake, Oregon. U. S. Dept. Agric. For. Serv. Res. Pap. PNW-187, 32 pp.

Hitchcock, C. L., and A. Cronquist. 1973. Flora of the Pacific Northwest. Univ. Washington Press, Seattle, 730 pp.

Julander, O. 1945. Drought resistance in range and pasture grasses. Plant Physiol., 20:573-599.

Lee, A. K. 1963. The adaptations to arid environments in woodrats of the genus *Neotoma*. Univ. California Publ. Zool., 64:57-96.

Mattson, W. J., Jr. 1980. Herbivory in relation to plant nitrogen content. Annual Rev. Ecol. Syst., 11:119-161.

Maynard, L. A., J. K. Loosli, H. R. Hintz, and R. G. Warner. 1979. Animal nutrition. Seventh ed. McGraw-Hill, New York, 602 pp.

McKay, D. O., and B. J. Verts. 1978*a*. Estimates of some attributes of a population of Nuttall's cottontails. J. Wildl. Mgmt., 42:159-168.

______. 1978*b*. Habitat preference and dispersion of Nuttall's cottontails. Northwest Sci., 52:363-368.

Meslow, E. C., and L. B. Keith. 1971. A correlation analysis of weather versus snowshoe hare population parameters. J. Wildl. Mgmt., 35:1-15.

Myers, K. 1963. A study of the biology of the wild rabbit, *Oryctolagus cuniculus* (L.), in confined populations. V. Population dynamics. C. S. I. R. O. Wildl. Res., 8:166-203.

Myers, K., and B. S. Parker. 1975. A study of the biology of the wild rabbit in climatically different regions in stern Australia. VI. Changes in numbers and distribution related to climate and land systems in semi-arid north-western New South Wales. Australian Wildl. Res., 2:11-32.

Murphy, D. A., and J. A. Coates. 1966. Effects of dietary protein on deer. Trans. N. Amer. Wildl. Nat. Res. Conf., 31:124-139.

Nagy, K. A., V. H. Shoemaker, and W. R. Costa. 1976. Water, electrolyte, and nitrogen budgets of jackrabbits (*Lepus californicus*) in the Mohave Desert. Physiol. Zool., 49:351-363.

National Research Council. 1977. Nutrient requirements of rabbits. Second rev. ed. Nutrient requirements of domestic animals, 9:1-30.

Neter, J., and W. Wasserman. 1974. Applied linear statistical models. Irwin, Homewood, Illinois, 842 pp.

Newsome, A. E. 1965. Reproduction in natural populations of the red kangaroo, *Megaleia rufa* (Desmarest), in central Australia. Australian J. Zool., 13:735-759.

______. 1980. Differences in diets of male and female red kangaroos in central Australia. African J. Ecol., 18:27-31.

Nudds, T. D. 1980. Forage "preference": theoretical considerations of diet selection by deer. J. Wildl. Mgmt., 44:735-740.

Petrides, G. A. 1951. The determination of sex and age ratios in the cottontail rabbit. Amer. Midland Nat., 46:312-336.

Phillipson, J. 1975. Rainfall, primary production and 'carrying capacity' of Tsavo National Park (East), Kenya. E. African Wildl. J., 13:171-201.

Powers, R. A., and B. J. Verts. 1971. Reproduction in the mountain cottontail rabbit in Oregon. J. Wildl. Mgmt., 35:605-613.

Richards, G. C. 1979. Variation in water turnover by wild rabbits, *Oryctolagus cuniculus*, in an arid environment, due to season, age group and reproductive condition. Australian Wildl. Res., 6:289-296.

Riegel, A. 1942. Some observations of the food coactions of rabbits in Kansas during periods of stress. Trans. Kansas Acad. Sci., 45:369-375.

Rusch, D. A., and W. G. Reeder. 1978. Population ecology of Alberta red squirrels. Ecology, 59:400-420.

Sauer, R. H., and S. L. Owzarski. 1979. Collection and analysis of vegetative cover data. PNL-3068. Battelle Pacific Northwest Laboratory, Richland, Washington, 21 pp.

Sawin, P. B., and R. H. Curran. 1952. Genetic and physiological background of reproduction in the rabbit. I. The problem and its biological significance. J. Exp. Zool., 120:165-201.

Schwartz, C. C., and W. L. Regelin, and J. G. Nagy. 1980. Deer preference for juniper forage and volatile oil treated foods. J. Wildl. Mgmt., 44:114-120.

Short, H. L., J. D. Newson, G. L. McKoy, and J. F. Fowler. 1969. Effects of nutrition and climate on southern deer. Trans. N. Amer. Wildl. Nat. Res. Conf., 34:137-146.

Sinclair, A. R. E. 1974. The natural regulation of buffalo populations in East Africa. IV. The food supply as a regulating factor, and competition. E. African Wildl. J., 12:291-311.

______. 1977. The African buffalo: a study of resource limitation of populations. Univ. Chicago Press, Chicago, 355 pp.

Skalski, J. R. 1977. Transferrin polymorphism in a mountain cottontail population in central Oregon. Unpubl. M.S. thesis, Oregon State Univ., Corvallis, 57 pp.

Skalski, J. R., and B. J. Verts. 1981. Dynamics of a transferrin polymorphism in a population of *Sylvilagus nuttallii*. Oecologia (Berl.), 49:329-332.

Smith, R. H., and A. LeCount. 1979. Some factors affecting the survival of desert mule deer fawns. J. Wildl. Mgmt., 43:657-665.

Sneva, F. A., and D. N. Hyder. 1962. Estimating herbage production on semiarid ranges in the Intermountain region. J. Range Mgmt., 15:88-93.

Snyder, W. I., M. E. Richmond, and W. G. Pond. 1976. Protein nutrition of juvenile cottontails. J. Wildl. Mgmt., 40:484-490.

Sparks, D. R., and J. C. Malachek. 1968. Estimating percentage dry weight in diets using a microscope technique. J. Range Mgmt., 21:264-265.

Taylor, C. R. 1968. Hygroscopic food: a source of water for desert antelopes? Nature, 219:181-182.

Thorne, E. T., R. E. Dean, and W. G. Hepworth. 1976. Nutrition during gestation in relation to successful reproduction in the elk. J. Wildl. Mgmt., 40:330-335.

Turkowski, F. J. 1975. Dietary adaptability of the desert cottontail. J. Wildl. Mgmt., 39:748-756.

U. S. Department of Commerce. 1972-1976, 1978, 1979. Climatological data: Oregon, 78:5, 26, 45, 66, 85, 105, 127, 264; 79(1):6; 79(2):7; 79(3):6; 79(4):7; 79(5):6; 79(6):6; 79(7):6; 79(13):6; 80(1):7; 80(2):7; 80(3):7; 80(4):7; 80(5):7; 80(6):7; 80(7):7; 80(13):6; 81(1):6; 81(2):6; 81(3):6; 81(4):6; 81(5):6; 81(6):6; 81(7):6; 81(13):6; 82(1):6; 82(2):6; 82(3):6; 82(4):6; 82(5):6; 82(6):6;

82(7):6; 82(13):6; 84(1):6; 84(2):6; 84(3):6; 84(4):6; 84(5):6; 84(6):6; 84(7):6; 84(13):6; 85(1):6; 85(2):6; 85(3):6; 85(4):6; 85(5):6; 85(6):6; 85(7):6; 85(13):6.

Vavra, M., and J. L. Holochek. 1980. Factors influencing microhistological analysis of herbivore diets. J. Range Mgmt., 33:371-374.

Vorhies, C. T. 1945. Water requirements of desert animals in the Southwest. Univ. Arizona Agric. Exp. Sta. Tech. Bull., 107: 487-525.

Vorhies, C. T., and W. P. Taylor. 1933. The life histories and ecology of jack rabbits, *Lepus alleni* and *Lepus californicus* spp., in relation to grazing in Arizona. Univ. Arizona Agric. Exp. Sta. Tech. Bull., 49:471-587.

______. 1940. Life history and ecology of the white-throated woodrat, *Neotoma albigula albigula* Hartley, in relation to grazing in Arizona. Univ. Arizona Agric. Exp. Sta. Tech. Bull., 86:455-529.

Weege, P. 1975. Reproduction and early calf mortality in Norwegian red deer. J. Wildl. Mgmt., 39:92-100.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. Amer. Nat., 108:290-304.

______. 1978. What are the biological bases of varied diets? Amer. Nat., 112:627-631.

______. 1980. Black-tailed jack rabbit diets in Curlew Valley, northern Utah. J. Wildl. Mgmt., 44:942-948.

White, T. C. R. 1978. The importance of a relative shortage of food in animal ecology. Oecologia (Berl.), 33:71-86.

Wood, D. H. 1980. The demography of a rabbit population in an arid region of New South Wales, Australia. J. Anim. Ecol., 49:55-79.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Englewood Cliffs, New Jersy, 620 pp.

APPENDIX

Table A. Plant species known to occur on the study area, Deschutes County, Oregon, in the summer of 1978, and spring and summer of 1979.

Grasses	
Agropyron dasystachum (Hook.) Scribn.	downy wheatgrass
A. spicatum (Pursh) Scribn. & Smith	bluebunch wheatgrass
Bromus tectorum L.	cheat grass
Festuca idahoensis Elmer	Idaho fescue
Koeleria cristata Pers.	prairie Junegrass
Oryzopsis hymenoides (R. & S.) Ricker	Indian ricegrass
Poa cusickii Vasey	Cusick's bluegrass
P. sandbergii Vasey	Sandberg's bluegrass
Sitanion hystrix (Nutt.) Smith	bottlebrush squirreltail
Stipa thurberiana Pers.	Thurber's needlegrass
Forbs	
Achillea millefolium L.	common yarrow
Astragulua filipes Torr.	threadstalk milk-vetch
A. purshii Dougl.	wooly-pod milk-vetch
Calochortus macrocarpus Dougl.	sagebrush mariposa
Chaenectis douglasii (Hook.) Nutt.	hoary false-yarrow
Cryptantha ambigua (Gray) Greene	obscure cryptantha
C. circumscissa (H. & A.) Johnst.	matted cryptantha
Descurainia pinnata (Walt.) Britt.	western tansymustard
Eriastrum sparsiflorum (Eastw.) Mason	few-flowered eriastrum
Erigeron filifolius Nutt.	threadleaf fleabane
Erigonum strictum Benth.	strict buckwheat
E. vimineum Dougl.	broom buckwheat

Table A (cont'd.).

Eriophyllum lanatum (Pursh.) Forbes	wooly sunflower
Gayophytum decipiens Lewis and Szeyk.	deceptive groundsmoke
Mentzelia albicaulis Dougl.	white-stemmed mentzelia
Mimulus nanus H. & A.	dwarf purple monkey-flower
Penstemon richardsonii Dougl.	Richardson's penstemon
Phacelia glandulifera Piper	sticky phacelia
P. linearis (Pursh) Holz.	threadleaf phacelia
Senecio canus Hook.	wooly groundsel
Sisymbrium altissimum L.	Jim Hill mustard
Tragopogon dubius Scop.	yellow salsify
Zigadenus venenosus Wats.	meadow death-camus
Shrubs	
Artemisia tridentata Nutt.	big sagebrush
Chrysothamnus nauseosus (Pall.) Britt.	gray rabbit-brush
C. viscidiflorus (Hook.) Nutt.	green rabbit-brush
Leptodactylon pungens (Torr.) Nutt.	prickly phlox
Purshia tridentata (Pursh) DC.	bitter-brush
Trees	
Juniperus occidentalis Hook.	western juniper
Pinus ponderosa Dougl.	ponderosa pine
Moss	
Tortula ruralis (Hedw.) Gaertn., Meyer & Scherb.	

Table B. Estimated numbers of Nuttall's cottontails on the study area on 30 August and at the initiation of breeding, and amounts of precipitation recorded at the Redmond 2W weather station, 11.3 km SSW of the study area, during the breeding season (February - July) 1972 - 1979.

	Numbers of cottontails		
Year	30 August (Y)[a]	Breeding (X_1)[a]	Precipitation (mm) (X_2)[a]
1972[b]	222	52	11.54
1973[b]	57	43	5.21
1974[c]	151	40	9.89
1975[c]	186	47	9.91
1976[d]	85	46	6.40
1977[d,e]	-	-	-
1978	166	30	15.95
1979	76	42	7.69

a) $Y = -318.33 + 6.37X_1 + 18.91X_2$, $R^2 = 0.93$ ($P < 0.01$)
b) Population data from McKay and Verts (1978*a*)
c) Population data from Skalski (1977)
d) Population data from R. Deering (in litt.)
e) Too few cottontails were captured in 1977 to permit estimates of density

Table C. Estimates of percent cover of plant species, Deschutes County, Oregon, 1978 - 1979.

Species	Month of Collection						
	Late Jul 78	Sep 78	Mar 79	May 79	Early Jul 79	Late Jul 79	Sep 79
Bromus tectorum	6.99	7.00	4.96	8.97	4.78	3.06	3.21
Agropyron spp.	0.27	0.33	0.12	0.24	0.01	0.08	0.17
Koeleria cristata	0.05	0.17	0.00	0.14	0	0.02	0.01
Oryzopsis hymenoides	0	0	0	0.13	0	0	0
Poa spp.	0.26	0.25	0.07	0.08	0.22	0.50	0.89
Sitanion hystrix	0.50	0.85	0.34	0.37	0.70	0.66	0.54
Stipa thurberiana	1.28	0.93	0	0.53	1.59	1.11	0.48
unidentified grasses	0	0	0	0	0.05	0	0
new growth	0	0	0.78	0	0	0	0
TOTAL GRASSES	9.35	10.55	6.28	10.46	7.35	5.41	5.29
Achillea millefolium	0	0.02	0	0	0.09	0.03	0
Chaenectis douglasii	0	0	0	0.28	0.23	0.03	0
Descuraiania pinnata	0	0	0	0	0.03	0.01	0
Eriophyllum lanatum	0	0	0	0.02	0.07	0.21	0
Eriastrum sparsiflorum	1.34	0.36	0.13	0	0.03	0.26	0
Gayophytum decipiens	0.75	0.28	0	0.02	0.60	0	0.01
Mentzelia albicaulis	0	0	0	0	0.36	0.29	0
Mimulus nanus	0.21	0.05	0	0.11	0.31	0.40	0
Penstemon spp.	0	0	0	0.02	0	0	0

Table C. (cont'd).

Species	Month of Collection						
	Late Jul 78	Sep 78	Mar 79	May 79	Early Jul 79	Late Jul 79	Sep 79
Phacelia spp.	0	0.32	0	0	0.16	0	0
unidentified forbs	0.86	0.13	0.26	0.84	0.11	0.02	0.03
TOTAL FORBS	3.16	1.16	0.27	1.28	1.95	1.24	0.06
Artemisia tridentata	1.93	3.20	2.59	1.78	2.07	2.08	2.11
Chrysothamnus spp.	5.37	3.18	2.23	2.87	3.11	2.74	2.87
Purshia tridentata	0.50	1.01	0.96	0.47	0.61	0.78	0.97
TOTAL SHRUBS	7.80	7.38	5.78	5.13	5.79	5.60	5.96
Juniperus occidentalis	3.44	6.93	5.95	8.65	8.20	5.88	5.07
Tortula ruralis			3.54[a]				
TOTAL	27.29	28.55	21.81	29.05	26.82	21.66	19.91

a) This was the only sampling period in which *T. ruralis* was not dormant, and live portions of plants were distinguishable from dead portions. This estimate was used in calculating total cover in all months.

Table D. Summarization of data used in analysis of food selection by Nuttall's cottontails, Deschutes County, Oregon, summer of 1978, spring and summer of 1979.

Age	Sex	Weight (g)	Period of Collection	Forage ratio Grass	Forb	Shrub	Juniper
Adult[a]	Male	743.1	Late July 1978	2.08	0.97	0.62	0.00
Juvenile	Female	638.3	Late July 1978	0.20	7.25	0.08	0.56
Adult[a]	Female	830.4	Late July 1978	1.20	2.81	0.08	1.90
Juvenile	Male	690.9	Late July 1978	1.08	5.02	0.00	0.00
Juvenile	Female	713.5	Late July 1978	0.41	6.18	0.20	0.22
Juvenile	Male	378.8	Late July 1978	2.33	1.54	0.00	0.00
Juvenile	Female	824.2	September 1978	1.97	4.45	0.07	0.66
Adult	Female	825.1	September 1978	2.71	1.13	0.05	0.17
Adult	Female	702.3	September 1978	2.31	0.85	0.76	0.00
Adult	Male	797.2	September 1978	2.53	1.19	0.25	0.18
Juvenile	Female	640.2	September 1978	1.98	8.60	0.00	0.11
Juvenile	Female	364.3	September 1978	1.43	1.64	0.43	1.37
Adult[a]	Male	593.0	March 1979	3.36	0.95	0.00	0.00
Adult[a]	Male	659.3	March 1979	3.48	0.00	0.00	0.00
Adult[a]	Male	681.3	March 1979	3.48	0.00	0.00	0.00
Adult[a]	Female	881.4	March 1979	3.18	1.94	0.00	0.00
Adult[a]	Female	813.2	March 1979	3.25	1.36	0.00	0.00
Adult[a]	Female	938.4	March 1979	3.38	2.15	0.00	0.00
Adult[a]	Female	897.0	May 1979	2.57	1.71	0.00	0.00
Adult[a]	Female	771.2	May 1979	2.31	3.31	0.00	0.00
Adult[a]	Female	866.1	May 1979	1.92	7.00	0.00	0.00

Table D (cont'd).

Age	Sex	Weight (g)	Period of Collection	Grass	Forb	Shrub	Juniper
Adult[a]	Female	831.3	May 1979	2.47	2.50	0.00	0.00
Adult[a]	Male	692.8	May 1979	2.78	0.00	0.00	0.00
Adult[a]	Male	761.9	Early July 1979	1.00	7.60	0.00	0.51
Adult[a]	Female	782.2	Early July 1979	1.60	5.78	0.00	0.23
Adult[a]	Female	742.9	Early July 1979	2.68	2.88	0.00	0.18
Adult[a]	Male	629.9	Early July 1979	2.74	2.03	0.00	0.13
Adult[a]	Female	641.9	Early July 1979	2.15	4.75	0.00	0.15
Juvenile	Female	552.8	Early July 1979	2.67	3.32	0.00	0.08
Juvenile	Male	456.7	Early July 1979	2.63	3.85	0.00	0.00
Juvenile	Female	453.5	Early July 1979	1.68	6.82	0.00	0.00
Juvenile	Female	261.6	Early July 1979	1.47	8.19	0.00	0.00
Juvenile	Female	375.1	Early July 1979	1.03	7.57	0.00	0.44
Juvenile	Female	256.1	Early July 1979	0.58	11.12	0.00	0.00
Juvenile	Male	201.6	Late July 1979	2.93	1.55	0.00	0.66
Juvenile	Male	466.7	Late July 1979	0.84	7.44	0.00	1.12
Adult	Male	743.2	Late July 1979	2.15	4.75	0.00	0.15
Juvenile	Female	472.6	September 1979	2.90	10.00	0.00	0.79
Juvenile	Female	535.0	September 1979	3.63	0.00	0.00	0.09
Juvenile	Female	665.0	September 1979	2.38	0.00	0.00	1.38
Juvenile	Male	672.6	September 1979	3.29	10.28	0.00	0.32
Juvenile	Male	661.3	September 1979	3.60	2.31	0.00	0.32

Table D (cont'd).

Age	Sex	Weight (g)	Period of Collection	Forage ratio			
				Grass	Forb	Shrub	Juniper
Juvenile[b]	Female	835.6	September 1979	2.97	73.03	0.00	0.28

a) In breeding condition or lactating.
b) This individual was excluded from analysis because of the large forage ratio for forbs.